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Using state-space time series analysis on wetland bird species to formulate effective bioindicators in the Barberspan wetland

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Abstract

The Coordinated Waterbird Count dataset (CWAC) is a dataset containing waterbird counts from wetlands across South Africa, going as far back as 1970. These data contain valuable information on population sizes and their trends over time. This information could be used more widely if it was more easily accessible to users. The aim of this dissertation is to bridge the gap between the CWAC dataset and the end users (for both experts and non-experts). In so doing the report also provides valuable insight into the state of wetlands in South Africa using various biodiversity indices, starting with Barberspan wetland as the pilot study site. A state-space time series model was applied to the waterbird counts in the CWAC dataset to determine waterbird population trends over the years. State-space models are able to separate observation error from true population process error, thus providing a more accurate estimation of true population size. This qualifies state-space models as an ideal tool for population dynamics. The state-space model produced estimates of true population size for each waterbird per year. Three different indices were applied to the estimates, namely, exponentiated Shannon's index, Simpson's index and a modified Living Planet Index. These indices aggregate the count data to a measure of effective number of waterbirds in an ecosystem, a measure of evenness of an ecosystem, and an abundance index respectively. Using these three indices, in conjunction with each other, and individual waterbird species as bioindicators for various wetland traits, the end user is presented with a broad overview of the state of the Barberspan wetland. The implication of this research is beneficial to various wetland conservation organisations globally (AEWA, Aichi, RAMSAR) and locally (Working for Wetlands), as it provides valuable insight into the state of wetlands of South Africa. Furthermore, it helps managers at a local level in their decision making to enable more evidence-based approaches to protect South African wetlands and its waterbirds.

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1 Introduction

1.1 Problem Description

Wetlands are the most threatened and least protected ecosystems globally and in South Africa (Skowno 2019). Wetlands are areas where the land is covered with water such as marshes, sedges, river deltas, edges of lakes or oceans, etc. Wetlands benefit society in many ways. These include flood control, storm buffering and water quality improvement (Clarkson, Ausseil, and Gerbeaux 2013). Wetlands are invaluable to society and their surrounding communities.

The threat to wetlands has only recently been realised locally. Wetland conservation programs for South Africa have been created as late as 2002 despite the severe wetland degradation experienced since the 1970s (Working for Wetlands 2019). As a result of the relative late response, 35-60% of South Africa's wetlands have been severely damaged or destroyed due to bad agricultural practices (Working for Wetlands 2019). As a result, there have been recent programs for wetland rehabilitation. Most notably, the Working for Wetlands, initiated in 2002. Working for Wetlands was initiated by the Water Research Commission, in partnership with the Department of Environmental Affairs, and aims to rehabilitate and protect wetlands in South Africa.

Destruction or degradation of an ecosystem leads to a decrease in species populations and/or a decrease in biodiversity. According to the WWF's 2018 living planet report, it is stated that there has been a 60% decrease in global population biodiversity of mammals, fish, birds, reptiles and amphibians (Grooten and Almond 2018). These views are supported by the Living Planet Index (LPI) (McRae, Deinet, and Freeman 2017; Loh et al. 2005). As a result, there has been a notable increase in effort to preserve and recover global biodiversity. The most notable being The Aichi Biodiversity targets. The Aichi Convention on Biological Diversity presented a strategic plan in 2011 to improve global biodiversity (Convention on Biological Diversity 2020). This plan is made up of 5 goals and 20 targets. The strategic plan needed appropriate metrics to measure its success, and as a result the Living Planet Index (LPI) was created. The LPI measures the progress of Aichi strategic goal C. Aichi strategic goal C states: "To improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity" (Convention on Biological Diversity 2020).

Biodiversity is invaluable to our ecosystems and society at large. With loss of biodiversity comes reduced ecosystem resilience (Ritchie and Roser 2021). It has thus been imperative to keep track of an ecosystem's biodiversity and species population dynamics to understand the state of an ecosystem. One of the best tools to track biodiversity and species population dynamics are birds

(Amat and Green 2010; Mekonen 2017). Consequently, a citizen scientist initiative, called the Coordinated Waterbird Counts (CWAC), was initiated in 1992 by the Animal Demographic Unit (ADU), to keep track of bird counts in wetlands around South Africa. The CWAC dataset has bird counts of over 200 different bird species from approximately 400 different wetland locations in South Africa. Some of these counts go back as far as the 1970s.

Wetlands and waterbirds are the subject of many conservation projects locally and worldwide. Organisations involved include Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), Convention on Wetlands of International Importance Especially as Waterfowl Habitat (RAMSAR) and the Working for Wetlands initiative. Regarding the waterbirds in South Africa, there is currently a robust citizen-science based bird monitoring programme in the form of the CWAC dataset. Unfortunately, this dataset is not very accessible to the broader community. The aim of this project is to use the CWAC dataset and produce concise and effective data products, using various statistical techniques, that can be used by experts and non-experts to understand the state of the wetland and waterbird species of South Africa.

1.2 Background to Research

My project forms part of a larger project, The South Africa BiodIveRsity Data pIpelinE for wetlands and waterbirds (BIRDIE) https://www.sanbi.org/biodiversity/building-knowledge/biodiversity-monitoring-assessment/freshwater-programme-birdie-project. BIRDIE is a project that aims to collate all types of wetland data, perform statistical analysis, and make the output available to the public.

The output will be relevant at national, regional and local levels. At the national level, the data output provides insights of the state of South African wetlands and waterbirds that can be used by international conservation projects like AEWA and RAMSAR. At the regional level, the data output supports provincial conservation agencies who need to make a range of decisions about the conservation of sites and species. For example, some species are hunted and quotas need to be set. At the local level, the data output aids wetland site managers' decision making regarding the preservation of the wetland and its bird species. Furthermore, the output is also beneficial to bird watchers in helping identify which bird species are present at which wetlands.

The BIRDIE project is being conducted by the South African National Biodiversity Institute (SANBI), in association with FitzPatrick Institute for African Ornithology (FIAO, UCT), the Centre for Statistics in Ecology, Environment and Conservation (SEEC at the University of Cape Town),

Seascape Belgium and the Royal Belgium Institute of Natural Sciences (RBINS). The end goal is to provide automated statistical computing processes on various wetland data and produce effective visualisations and other data specific output hosted on a web app.

One of the key datasets in the BIRDIE project is the CWAC dataset. The CWAC dataset is well managed and maintains standard protocols for the counters to ensure reliable counts. The census data captured are also presented to international biodiversity contributors such as AEWA and the RAMSAR convention.

CWAC counts usually take place twice a year. Once in summer, traditionally during January and February, and once in winter, traditionally during July. The counting protocol is standardised to increase reliability of the counts and the ability to compare counts across different wetland sites. Counters are encouraged to adhere to these methods as closely as possible. Variables such as number of counters, routes followed, time of day, tide, viewing technique, viewing aids, personnel and counting technique are all kept constant for each wetland. Due to varying terrains and environments, each wetland may require slightly different counting techniques, but these techniques remain constant once established. Further information on the CWAC counting procedure can be found on the CWAC website (http://www.adu.org.za/docs/cwac-info4.pdf).

The CWAC dataset is essential in identifying patterns in species abundance, biodiversity and population dynamics over time, which is an important step in identifying wetland health, and to measure if wetland rehabilitation programs have been working.

1.3   State space time series model (SSM)

State-space models (SSMs) have become a popular tool used by ecologists to analyse ecological time series. There is enough evidence to argue that SSMs should be the default tool in analysing time series for ecologists (Auger-Méthé et al. 2021). SSMs have been used in various ecological studies such as fisheries stock assessment (Aeberhard et al. 2021), movement ecology (Patterson et al. 2008) and, most commonly, modelling population dynamics (Newman et al. 2014). These are only a few examples of where SSMs are used. Their application in ecology is vast.

SSMs are able to model temporal autocorrelation in a way that separates observation error from process error (Auger-Méthé et al. 2021). Herein lies the value of SSMs. SSMs are hierarchical models that essentially model two different time series. One being the state process (latent process or hidden process) which is the unobserved time series that represents the true underlying population dynamics. The other being the observation process that represents the observed counts of that state

process. Count data is often prone to observation error, especially when counting large groups of birds. Therefore, separating the observation process from the state process provides a more accurate estimation of the true population. The beauty of this methodology is that variation attributed to population size, population growth rate, environmental stochasticity and any other forms of stochasticity can be estimated from the model (Kéry and Schaub 2011). This allows the ecologist to program the state space time series model such that it accounts for known biological factors that affect the population dynamics. This includes birth rates, death rates, fecundity, immigration, emigration, etc. Figure 1 shows a simple visual illustration of this separation between state and observation processes.
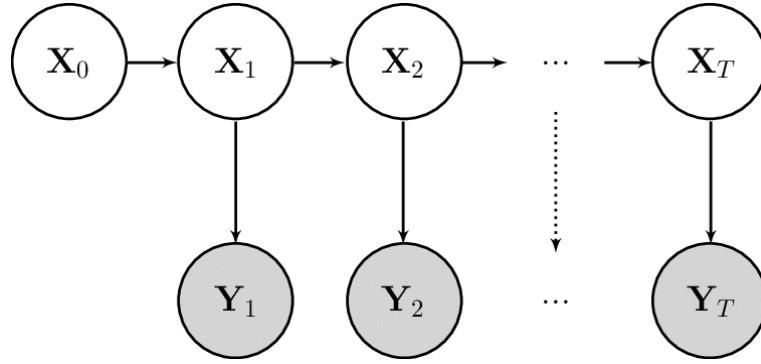
Figure 1: A visual representation of a state space model where X_t represents the unobserved population level changes. SSMs use the observed population counts, Y_t, to estimate the population level changes.

When applying SSMs to count data there are two important conditions that must be met for the SSM to produce unbiased estimates of population size. Firstly, false negative (false detections) and false positive (double counting) observations should cancel out on average. Secondly, there should be no temporal patterns in detection probability or false positive rates over time (Kéry and Schaub 2011).

1.4 Bioindicators

Fitting SSMs to population data helps us understand how the population of individual species have fluctuated over time, but these models don't tell the user much about the biodiversity of the ecosystem. This is where bioindicators and indices come in. In this dissertation, bioindicators refer to biological aspects of an ecosystem that reflect changes in the ecosystem. For example, birds are good organisms to use as bioindicators as they reflect various environmental changes directly (Mekonen 2017). Indices, in this dissertation, refer to summarised population count information. The Living Planet Index (LPI) is an example of such an index.

Environmental assessments play an important role in environmental decision-making. This has lead to a stark increase in assessment reports that are based on bioindicators (Niemeijer and Groot 2008). According to Niemeijer and Groot (2008), the bioindicators used in these reports often follow a common causal chain. This means that the bioindicator in use directly reflects specific changes in an ecosystem. For example, a decrease in wetland water level would be reflected in the declining population of waterbird species of that wetland (Burgess 1969). Niemeijer and Groot (2008) argue that the bioindicators commonly used are too specific. One should instead use bioindicators that reflect multiple changes in an ecosystem. Bird species are ideal bioindicators to use as they reflect many aspects of an ecosystem (Mekonen 2017).

According to Gregory et al. (2003), effective bioindicators are quantitative, easy to collect, simple to interpret, reflect causes of change in an ecosystem and indicate general patterns of taxa in the ecosystem. Bird count data fits this well. As bird counts are relatively easy to collect (and readily available), quantitative, simple to interpret and their population fluctuations are sensitive to various changes in an ecosystem.

Birds have been used to indicate the eutrophication levels in wetlands in the Mar Menor lagoon of south-eastern Spain (Amat and Green 2010). Eutrophication refers to an excess of nutrients (such as Phosphorus, Nitrogen and other plant nutrients) present in a body of water which negatively impacts drinking water and aquatic life. It was discovered that the Great Crested Grebe abundance increased as the eutrophication levels in the lagoon increased. The increase in eutrophication was a result of nutrient run-off from nearby agricultural practices. Another example from Southern Spain shows the use of Red-Knobbed Coots to indicate the siltation rate in the water and soil in wetlands (Amat and Green 2010). The Red-Knobbed Coot experienced a stark decline in abundance in the 20th century in Southern Spain. This decrease in abundance is attributed to the increased siltation rates in the water and soil in the wetlands in Southern Spain, caused by invasive agricultural practices. The

increased rates of siltation negatively affected the quality of food for the Coots in their wetlands, and thus lead to their demise. Thus, the Red-Knobbed Coots population over time could be indicative of siltation rates in the wetlands in which they are based. These are only two examples of how effective waterbirds are as bioindicators. Other examples show how waterbirds can be indicators for changes in water level in a wetland (Burgess 1969) and species abundance at lower trophic levels (Mekonen 2017).

An important aspect of ecosystem health is biodiversity. Rich biodiversity is indicative of a healthy ecosystem. Each species has their part to play in the ecosystem with varying degrees of importance. Tracking biodiversity in an ecosystem can also indicate the presence of invasive species (Hooper et al. 2005). Biodiversity indicators are therefore essential in tracking the overall health of a wetland ecosystem.

Biodiversity can be defined by two basic components. That is, how many different species are present in an ecosystem (Magurran 2003) and how many individuals per species are present in an ecosystem (evenness) (Buckland et al. 2005). Based on these components of biodiversity, a community with more species tends to have higher biodiversity than a community with fewer species and a community that displays high levels of evenness is regarded more diverse than a community with the same number of species but that displays high levels of unevenness. Regarding the concept of evenness, if two communities have the same number of species, the one where each species is equally abundant (high degree of evenness) is more diverse than one where there are a few common species and the rest are rare (high degree of unevenness).

Two of the more common biodiversity indices are the Shannon's entropy and the Simpson's index. The exponentiated Shannon's entropy reflects the effective number of species in an ecosystem based on the species counts (Jost 2006). The Simpson's index presents a measure of evenness in a community with one being perfect evenness and zero being very poor evenness. Evenness refers to how similar the species are in their relative frequencies. If a community has equal counts for each species the Simpson's index would be one and the community of waterbird species would be perfectly even. If there are one or two species that have significantly higher counts than the rest, then the Simpson's index would be closer to zero indicating that the community is uneven, and some species are dominant in the ecosystem.

There are currently various indices used, worldwide, that aggregate and measure species trends. These are used to provide an overview of the species health in an ecosystem. The main index in use, globally, is the Living Planet Index (LPI) (Collen et al. 2009). There are other similar indices such as

the Australian Threatened Species Index (TSX) (Bayraktarov et al. 2020) and the Wild Bird Index (WBI) (Gregory and Strien 2010). Both the TSX and the WBI are based on the calculations used by the LPI. The LPI and the indices based on the LPI, aggregates species population trends to form an overall population trend. This differs from biodiversity indices in that the focus is on population trend instead of individual aspects of biodiversity. As a result the LPI and like indices are better referred to as abundance indices.

The LPI aggregates population trends across species in different systems (Terrestrial, Freshwater, Marine) and realms (Palearctic, Afrotropical, etc) to form a global index. This index is essentially calculating the aggregated population change from a reference year (1970) to every year after that. The index value is initiated to one in year 1970. For example, if the index is 1 in 1970 and 1.2 in 1990 then this would reflect a 20% increase from 1970 to 1990.

Choosing the best index to use is a difficult task as decision science has rarely been applied to these global indices to evaluate their effectiveness and their design (Watermeyer et al. 2021). However, a study by Watermeyer et al. (2021) was conducted that applied decision science techniques to 9 different, commonly used, global environmental indices, one being the LPI. Based on the study, the LPI performed well in 4 of the 5 criteria used. The criteria being: How well the index meets its objectives, design, behaviour, methods to test uncertainty, and feasibility. The LPI performed well in all aspects except for feasibility.

The LPI was initiated in 1997 by the WWF and the World Conservation Monitoring Centre. It is the most used index that monitors average vertebrate trends around the world. These trend estimates are based on data from as far back as 1970. It uses time-series data from around the world and aims to measure the state of the world's population trends of vertebrate species. The Index covers the terrestrial, freshwater and marine habitats. The time series data are further broken up into its specific biomes and geographic realms or oceans.

1.5   Aim and Objectives

The aim of this study is to extract relevant information from the CWAC dataset such as trends and biodiversity indices to track bird species population dynamics and biodiversity. State-space time series models (SSMs) are used to model the population dynamics. SSMs are also good for forecasting future values or estimating missing values which is suitable for the CWAC dataset as it contains missing counts for some years. In this dissertation missing values are treated as unknown values that the SSM predicts.

When applying SSMs in a Bayesian framework, we are able to produce credible intervals for each of the unknown parameters by making use of the posterior distribution. The posterior distribution is the range of predicted values output by the SSM for each unknown parameter. The SSM is key to the following aims as the posterior sample (obtained from the posterior distribution) is used for further calculations to develop bioindicators.

When formulating biodiversity indices from data, it is important to first understand what needs to be monitored (Yoccoz, Nichols, and Boulinier 2001). Given the context of wetland and waterbird conservation, multiple types of indices and indicators were necessary to produce a holistic view of the state of the wetland and waterbirds present. The metrics used, in this dissertation, to measure biodiversity were the exponentiated Shannon's entropy and the Simpson's index (as biodiversity indices) and a modified Living Planet Index (LPI) (as a population trend index).

Wetland and waterbird conservationists will be able to utilise these indices and output from the time series models to understand the state of the wetland in terms of its bird species. Furthermore, it can be used as a tool by AEWA, Ramsar and bird watchers, to monitor the waterbird species in South Africa. The Barberspan wetland is used as pilot study, but if successful, this analysis can be used on all wetland sites represented in the CWAC dataset.

The following are the objectives that, if followed, will lead to successful completion of the aim:

1. Research and develop relevant state-space time series models for bird population dynamics in Barberspan. These models can be used for understanding the change of bird counts over time and forecasting future values.
2. Identify species attributes that may affect the population dynamics.
3. Formulate relevant biodiversity and abundance indices using the output of the state-space model.
4. Formulate both the state-space model and biodiversity indices such that they display a good overview of wetland state that can be used by both non-experts and experts.

2 Methods

2.1 Study Area

The Barberspan wetland is a protected wetland site known as the Barberspan Bird Sanctuary. It is located in the North West province of South Africa. The 3200ha reserve is centred on a shallow lake that covers about 257 to 2000ha of the reserve, depending on rainfall (Remisiewicz and Avni 2011). The Barberspan wetland is placed on an inland African flyway. As a result, it is a popular stopover location for intra-African and Eurasian migrant waders and waterbirds.

According to RAMSAR reports, the wetland regularly supports approximately 20000 waterbirds with 365 different bird species recorded at the Barberspan wetland (Rothman 2015). Barberspan is an important location for the migratory waterbirds that it supports. For this reason, it is one of the first RAMSAR sites in South Africa and the only RAMSAR site in the North West province. It also provides ideal conditions for bird watching and is thus a popular location for bird watchers.

Barberspan supports thousands of Little Stints and Curlew Sandpipers. It's also a popular location for intra-African nomadic waders such as the Kittlitz's Plover and Crowned Lapwing. The more common species of the wetland include the Red-Knobbed Coot, Egyptian Goose, Yellow Billed Duck, Southern Pochard and the South African Shelduck (Remisiewicz and Avni 2011). Appendix A contains further information regarding the waterbirds in Barberspan that were used in the analysis.

Barberspan is a well-protected wetland, home to many different waterbird species and rich in bird count data. As a result, it has been adopted by the BIRDIE project as its pilot site for the construction of its data pipeline and is the focus of this study.

2.2 Exploratory Data Analysis

The data used in this dissertation comes from the Coordinated Waterbird Counts (CWAC) initiative. Counts are conducted twice a year, once every six months. One count in January/February (austral summer) and the other in June/July (austral winter). The counting procedure is standardised for each site with a rigorous set of instructions to follow. The counting procedure, however, could not be standardised across wetlands due to differing wetland sizes and terrains. Protocol ensures that each counting session should take place at, more or less, the same time of day, when the sun is either behind or beside the counter, for ideal visibility. The CWAC datasets can be obtained from the CWAC API (http://api.adu.org.za/cwac/).

The CWAC dataset contains counts from the year 1993 to 2018 for the Barberspan wetland. The original dataset omitted the years without counts. These years were inserted into the dataset as missing values. This was done for the sake of completeness and for the benefit of the state-space models. A time series of combined waterbird counts in the Barberspan wetland can be seen in figure 2.

Only waterbirds with 13 or more non-zero counts were used in the analysis. It was found that the variance parameters for the SSM didn't converge when applied to waterbird counts with fewer than 13 non-zero counts.
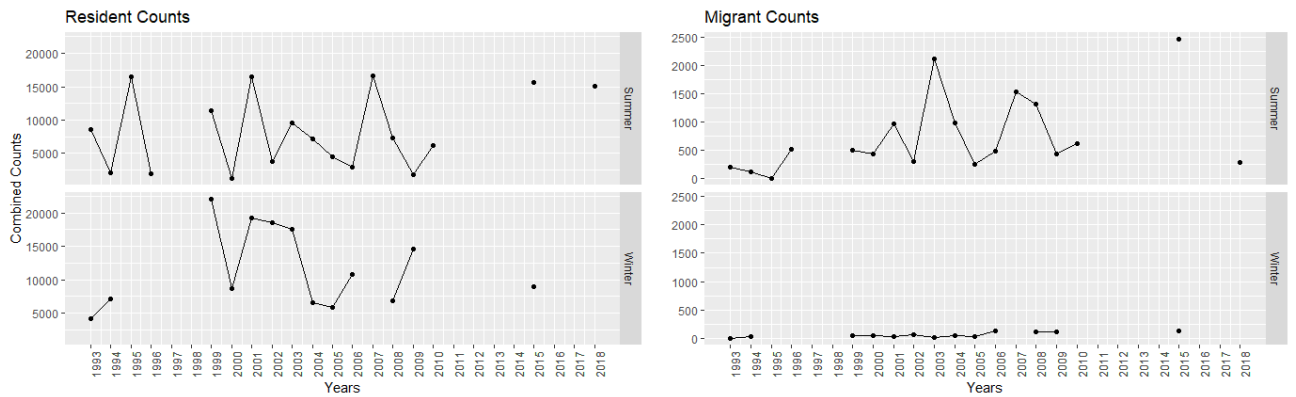
Figure 2: Combined counts of waterbirds per year at Barberspan wetland separated by migratory status with summer counts displayed on the top plot and winter counts displayed on the bottom plot.

Figure 2 shows a large difference between the number of residents and migrants in Barberspan. For this reason the resident and migrant species were modelled and analysed separately. Modelling and analysing migrants and residents together would lead to the model fitting the resident species more accurately than the migrant species.

The residents and migrants have also been analysed separately to account for their differences in seasonal abundance patterns. These patterns present themselves in the data and are evident in figure 2. There are clearly more migrant species present in Barberspan during summer than winter. This is due to their migratory pattern as these waterbirds often migrate to the south for the southern summer. The resident counts do not display this pattern. The resident counts tend to fluctuate randomly throughout the year with no clear reason for these fluctuations.

The CWAC dataset, unfortunately, does not have recorded counts for every year since its inception. The following time periods contained no counts: The winter of 1995, the winter of 1996 to the winter of 1998, the winter of 2007, the winter of 2010 to the winter of 2014, the summer of 2016 to the winter of 2017 and the winter of 2018.

2.3 State Space Model

State-space time series models (SSMs) have been used for modelling population dynamics in this study. SSMs are flexible models that allow one to modify population models to account for known biological processes that affect population variation. This works well when modelling migratory avian species (Barshep et al. 2017; Camp et al. 2016; Wilson et al. 2011). State-space models are also able to separate the observation and latent error. By removing the observation error from the latent error, the model is able to predict population trends more accurately (Kéry and Schaub 2011). Bird count data are often affected by observation error as counters are prone to missing or double counting individuals. This makes SSMs ideal in the current situation.

There have been two studies which applied SSMs to waterbird counts in Southern Africa (Barshep et al. 2017; Simmons et al. 2015). Barshep et al. (2017) used two different SSMs. A univariate model for resident species, "sedentary residents with limited or no seasonal movement between sites" and a bivariate model (with summer and winter as the two variables) for the migrant species, "Palaearctic migrants and intra-African migrants". Both studies utilised the same model for the migrant species. Both models are fitted to the logarithm of the counts.

Model 1 is a univariate model that treats summer/winter as a covariate. The observation process is modelled as follows:

$$ln(y_t) = \mu_t + \gamma_t + \alpha_t, \quad \alpha_t \sim N(0, \sigma_\alpha^2) \tag{1}$$

where $ln(y_t)$ is the natural logarithm of the summer and winter counts, μ_t is the true population

level, α_t is the observation error with variance σ_α^2 and γ_t is the summer/winter variable represented as follows:

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

where a positive γ_t represents the summer effect. To parameterize seasonal effects we use deviations from a mean, so that the level refers to an average population level over the year and seasonal differences are measured as deviations from this overall mean. The seasonal effects add to zero, as is commonly done for effect parameters.

The state process was modelled as a linear trend model as the resident species tend to remain in the same place all year round. The state process is represented as follows:

$$ln(relative\ population\ size\ at\ time\ t) : \mu_t = \mu_{t-1} + \beta_{t-1} + w_t, \quad w_t \sim N(0, \sigma_w^2) \tag{3}$$

where β_t is the rate of change of the population over time and is modelled as follows:

$$ln(population\ change) : \beta_t = \beta_{t-1} + \epsilon_t, \quad \epsilon_t \sim N(0, \sigma_\epsilon^2) \tag{4}$$

the variables α_t, w_t, ϵ_t and ζ_t are all serially independent with variances σ_α^2, σ_w^2, σ_ϵ^2 and σ_ζ^2 respectively. This concludes model one that is applied to resident species. See Figure 3 for a visual illustration of model 1.

Model 2 is applied to the migrants and considers their migratory movement. The migrant species in South African wetlands tend to breed in the northern hemisphere (during the southern winter) then migrate south for the southern summer. The young birds tend to remain in the south during the subsequent southern winter period. Model 2 was thus formulated as a bivariate time series model treating summer counts and winter counts as separate variables with the summer population as the main focus. The proportion of birds that stay over for the subsequent southern winter was modelled as the second variable. Figure 3 shows a visual description of this model. The mathematical representation of model 2 is as follows:

observation process

$$ln(summer\ count) : s_t = \mu_{t-1} + \alpha_t, \quad \alpha_t \sim N(0, \sigma_\alpha^2) \tag{5}$$

$$ln(winter\ count) : w_t = \mu_t + \lambda_t + e_t, \quad e_t \sim N(0, \sigma_e^2) \tag{6}$$

state process

$$ln(summer\ population\ level) : \mu_t = \mu_{t-1} + \beta_{t-1} + w_t, \quad w_t \sim N(0, \sigma_w^2) \tag{7}$$

$$ln(population\ change) : \beta_t = \beta_{t-1} + \zeta_t, \quad \zeta_t \sim N(0, \sigma_\zeta^2) \tag{8}$$

$$ln(summer\ to\ winter\ ratio) : \lambda_t = \lambda_{t-1} + \epsilon_t, \quad \epsilon_t \sim N(0, \sigma_\epsilon^2) \tag{9}$$

where, s_t is the summer count at time t and w_t is the winter count at time t. μ_t is the latent summer population, β_t is the rate of change at time t and λ is the winter to summer ratio. The winter to summer ratio refers to the difference in the bird population from summer to winter. The palearctic migrants usually migrate north for winter, and leave their young behind, thus leaving a smaller proportion of birds in the South African wetlands in winter compared to summer. α_t, e_t, w_t, ζ_t and ϵ_t are all normally distributed, serially independent and independent of each other with variance σ_α^2, σ_e^2, σ_w^2, σ_ζ^2 and σ_ϵ^2 respectively.

Model 2 has been used in this study and applied to both migrant and resident species. The two species differ in migratory patterns but there is reason to believe that observation error may be dependent on the season. Separating the winter and summer counts allows the model to account for season specific observation error. Therefore, the same state-space model was applied to both the residents and the migrants.

(a) Model 1

(b) Model 2
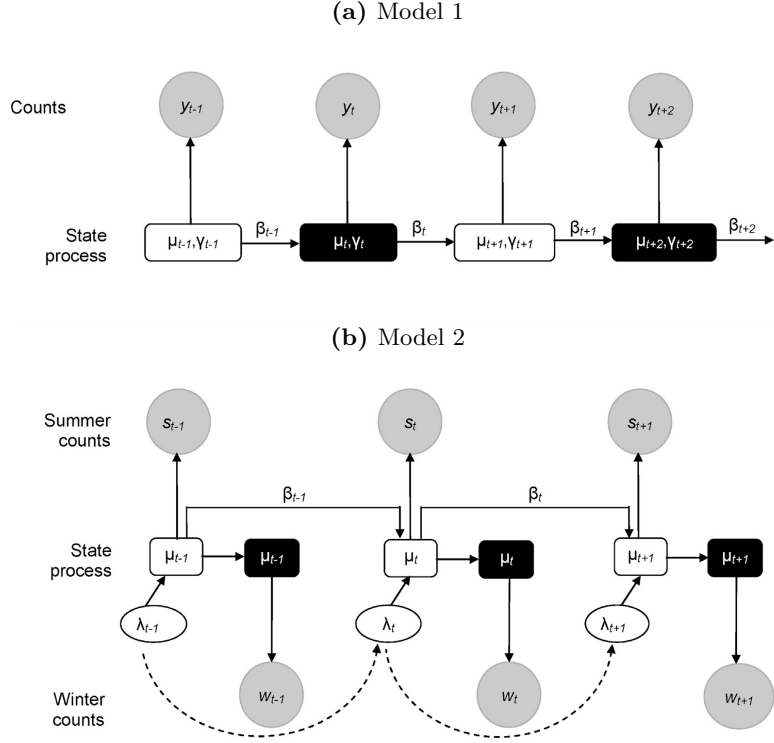
Figure 3: Visual illustrations of State Space Model 1 and 2 to model resident waterbirds and migrant waterbirds respectively (Barshep et al. 2017). The symbol representation is as follows:

$y_t =$ summer and winter count observations for the univariate model at time t
$s_t =$ summer count at time t
$w_t =$ winter count at time t
$\gamma_t =$ seasonal effect at time t
$\mu_t =$ population level at time t
$\beta_t =$ slope at time t
$\lambda_t =$ winter to summer ratio at time t

2.3.1   Inferential approaches to SSMs

There are two fundamentally different ways to fit SSMs. That is a frequentist approach or a Bayesian approach (Auger-Méthé et al. 2021).

Frequentist approach

The frequentist, or classical, approach is common in most statistical analyses. When fitting SSMs according to the frequentist framework, we essentially perform maximum likelihood estimation on the joint likelihood of the parameters, θ, and the states, z. The mathematical structure can be illustrated as follows:

$$L(\theta, z_{1:T}|y_{1:T}) = \prod_{t=1}^{T} g(y_t|z_t, \theta_0)f(z_t|z_{t-1}, \theta_p) \tag{10}$$

where θ_0 and θ_p represent the observation process parameters and the state process parameters respectively, and T representing the length of the time series. The initial state, z_0 at time t_0, is usually defined by setting a vague initial state distribution for z_0 or fixing z_0 equal to the first observation (Auger-Méthé et al. 2021). To simplify the maximum likelihood process, one would first maximise the marginal likelihood and integrate out the hidden states (z) (Auger-Méthé et al. 2021), thus, only having to maximise the marginal likelihood with respect to the parameters (θ). The parameter estimates produced from maximising the marginal likelihood have the necessary statistical properties (consistency and asymptotic normality) to estimate the hidden states (Valpine 2012; Douc et al. 2011). One would use the predicted parameters and calculate the conditional distribution of the hidden states given the observations (y) and the estimated parameters ($\hat{\theta}$). Calculating the maximum marginal likelihood with respect to the parameters is a computationally expensive problem. This is the common limitation for SSMs in general, for both the frequentist and Bayesian approach (Auger-Méthé et al. 2021).

There are two common methods one can use to evaluate the maximum marginal likelihood. Namely the Kalman Filter and the Laplace approximation method (which approximates the maximum marginal likelihood as opposed to evaluating it).

Bayesian approach

The Bayesian approach takes into account previous information that is summarised into a quantitative model known as the prior distribution (Ellison 2004). Bayesian modelling provides a platform to incorporate external evidence or expert knowledge with evidence presented by the study (Goodman 2005).

Bayesian statistics revolves around Bayes' rule. Bayes' rule is a way to calculate unknown conditional probability. That is, to calculate the probability of the parameters of a model given the data (Clyde et al. 2021). The mathematical expression of the Bayes Rule is as follows:

$$p(\theta|y) = \frac{p(y|\theta)p(\theta)}{p(y)} \tag{11}$$

Where y represents the observed data and θ represents the model parameters. $p(y|\theta)$ represents the probability of observing the data given a set of parameters (the likelihood) and $p(\theta)$ represents the prior probability of experiencing those parameters (Clyde et al. 2021).

The need to specify priors is considered to be an advantage by some and criticised by others (Dennis 1996). However, if the expert knowledge is sound, it would greatly benefit the model and will lead to

more biologically sound outcomes.

Given the criticism of subjective priors (Lele and Dennis 2009), the least controversial way for choosing priors is, therefore, to use non-informative priors as far as possible. In this dissertation uniform priors were used for all parameter estimates. It was further discovered that the results were not affected when using different non-informative priors. Uniform and normal priors were tested and both yielded very similar results.

Besides the use of priors being a contentious topic, the Bayesian approach still holds a vast array of benefits. Hierarchical models are conceptually easier to understand when cast within a Bayesian framework (Kéry and Schaub 2011). Count data are observations that are based on the true population of monitored species. The observations and true population relate to each other in a hierarchical manner and are subject to both observation and process error. Given this hierarchical structure, the Bayesian approach is a more intuitive method to use.

When applying SSMs in a Bayesian context, the main goal is to determine the posterior distribution for the states and the parameters based on data and the prior distributions. The mathematical representation of this approach is as follows:

$$p(\theta, z_{1:T}|y_{1:T}, \kappa) = \frac{L_J(\theta, z_{1:T}|y_{1:T})\pi(\theta|\kappa)}{\int\int L_J(\theta, z_{1:T}|y_{1:T})\pi(\theta|\kappa)dz_{1:T}d\theta} \tag{12}$$

where $L_J(\theta, z_{1:T}|y_{1:T})$ is the joint likelihood and $\pi(\theta|\kappa)$ is the prior distribution(s). The denominator of equation 12 represents the probability of the data for all possible values of the states and parameters. Equation 12 forms the basic structure of Bayes' theorem as seen in equation 11.

The posterior distribution is the focus in the Bayesian approach. This is most commonly done by obtaining samples from the posterior distribution through a Markov Chain Monte Carlo (MCMC) approach. This is a computationally expensive task that is nearly impossible to do by hand. There are various MCMC algorithms that approximate the posterior distribution. Namely, Metropolis Hastings samplers, Hamiltonian Monte Carlo and the Gibbs sampler, amongst many (Auger-Méthé et al. 2021).

Another important aspect in the Bayesian approach is to apply convergence tests on the MCMC outcome, regardless of the sampler used. Testing convergence ensures that the sampler used, after approximating the probabilistic distribution many times, has converged to the stationary distribution. This can often be viewed on a trace plot of MCMC outcomes (Auger-Méthé et al. 2021). A more formal approach would be the Gelman-Rubin statistic (Gelman and Rubin 1992),

which is a popular metric to measure convergence in an MCMC context. The Gelman-Ruben statistic compares variation between chains to variation within chains, with values close to one indicating that convergence has been achieved.

A Bayesian approach was used to fit the SSM to the data in this study. The model was fit using the Just Another Gibbs Sampler (JAGS) package and applied in R (Plummer 2003; R Core Team 2020; Kellner 2019). A Gibbs sampler is an MCMC method that samples variables sequentially from a multivariate distribution while keeping all other variables constant (Coro 2017). The JAGS package uses an internally specified variation of a Gibbs sampler to estimate the model states and parameters. In the immediate case, the probability distribution will take on the form of equation 12 which will be based on equations five to nine. Uniform priors were used for all variance parameters (α, e, w, ζ and ϵ) with a range of [0,10] and MCMC trace plots and the Gelman-Rubin metric were used to test convergence of the estimated states and parameters. Appendix C displays the convergence of the variance parameters along with its Gelman-Ruben statistic (or Rhat value). The convergence output for all the waterbirds used were fairly similar, because of this only one waterbird (Egyptian Goose) was used to display convergence output in Appendix C.

2.3.2 Model selection

A major drawback of the SSM is the issue of model selection. Model selection for SSMs are still an area of active research (Jonsen et al. 2013). SSM model selection becomes difficult as the computation power needed to run an SSM is so large (Auger-Méthé et al. 2021). As a result, ecologists end up using only one SSM model in the study because of limited computational power.

Model comparison methods differ depending on whether the SSM is conducted in a Frequentist framework or a Bayesian framework. The most used model selection method for a frequentist SSM is the Akaike Information Criterion (AIC). The AIC is a popular model selection method in many statistical models. The AIC is a relative measure of how well the model fits the data and penalizes models with a higher number of parameters. AIC, however, does not work well for SSMs, even in a frequentist framework, for various reasons (Auger-Méthé et al. 2021).

For SSMs in a Bayesian context, AIC is not well defined (Hooten and Hobbs 2015). There are 3 notable model selection methods used for Bayesian SSMs. These are the Watanabe-Akaike Information Criterion (WAIC), Deviance Information Criterion (DIC) and Bayesian Information Criterion (BIC). Many sources of literature have shown that DIC and BIC do not work well for Bayesian model selection (Auger-Méthé et al. 2021; Gelman, Hwang, and Vehtari 2014; Hooten and

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Hobbs 2015). Sources have found WAIC to be more effective than DIC and BIC, even though it still fails in many cases (Gelman, Hwang, and Vehtari 2014). The method most of the literature agreed upon was a cross-validation method. In this cross-validation method, the SSM would be fit with a training set of the data, while an unused subset of the data (the test set) is used to determine the effectiveness of the SSM's forecasting ability. The SSM that forecasts values closest to the corresponding test set values is then considered the "best" model. This method works well but has its limitations when data is sparse. In the case of sparsity, splitting the data into a training and test set becomes difficult as the training set may not be sufficient to estimate all parameters of the model. Furthermore, splitting time series data into training and test set becomes difficult because of the serial dependence between the data points.

Yoccoz (1991) and Cox et al. (1977), state that, at times, ecologists tend to overemphasize the use of statistical measures for model selection and fail to prioritise biological or ecological factors. Model selection becomes even more dubious when in a Bayesian context (Hooten and Hobbs 2015), and even more so with SSMs (Auger-Méthé et al. 2021). Both Hooten and Hobbs (2015) and Auger-Méthé et al. (2021) agree that cross-validation is the best tool to use for bayesian model selection. However, the sparce and dependent nature of the CWAC data inhibited the ability to create training and test sets for cross-validation.

Given the contentious issues regarding model selection for SSMs, and the inability to use cross-validation, it is beneficial to choose the SSM that is based on sound ecological fundamentals rather than contentious model selection statistics. More time and effort should be focused on the modelling process and ensuring the correct ecological processes are modelled into the SSM.

The model selection process in this study was based on ecological background and knowledge rather than traditional model selection metrics for SSMs such as DIC, AIC or WAIC, thus following the philosophy of Cox et al. (1977) and Yoccoz (1991).

2.4   Biodiversity Indices

There are multiple different ways one can formulate biodiversity indices. The first, and main task, however, is to identify what must be monitored and how (Yoccoz, Nichols, and Boulinier 2001). In the South African wetland's context, one would want to monitor species that directly reflect changes in the ecosystem. This would be species that follow a pressure–state–response network chain (Niemeijer and Groot 2008). As discussed in the introduction, species like the Great Crested Grebe (eutrophication level indicator) and Red-Knobbed Coots (siltation rate indicator) provide known

causal links to environmental changes.

Biodiversity is an important aspect of any ecosystem (Duffy 2009) and subject to large scale conservation efforts such as the Aichi convention. Biodiversity has many definitions. According to Magurran (2003), biodiversity is the "variety and abundance of species in a defined unit of study". Buckland et al. (2005) defines biodiversity as how the abundance is distributed across species, otherwise known as evenness. Evenness refers to the level of homogeneity of the ecosystem, regarding its species. For example, if an ecosystem contains 5 different bird species, with each bird species containing an equal number of individuals, then that ecosystem's bird population would be displaying perfect evenness. Whereas, if the ecosystem contains one or two dominant bird species then it would be displaying an uneven bird population. The research thus exhibits two different types of indicators that reflect the state of a wetland, one to monitor the variety of waterbirds in a wetland and one to monitor the evenness of waterbirds in a wetland.

The two most common indices used to measure the number of species in an ecosystem and evenness are the exponentiated Shannon's entropy and the Simpson's index, respectively. The Shannon's entropy obtains a value that describes the entropy of a community. According to Jost (2006), this entropy measure should ideally be transformed to obtain a more useful and intuitive index value. This can be done by transforming the Shannon's entropy to a measure representing the effective number of species in a community (Jost 2006). This is achieved by exponentiating the Shannon's index. The Simpson's index does not need to be transformed in any way as its output is already an intuitive index value. The Simpson's index presents a value between zero and one with one representing perfect evenness and values closer to zero representing a more uneven population.

Abundance Index

A popular population abundance index is the Living Planet Index (LPI) that is designed to track changes in population sizes over time. The LPI is used as an aggregated abundance index. It calculates the percentage change from a reference year (1970) to all subsequent years. This is done by averaging the rate of change (from reference year to current year) across all species of a species group (McRae, Deinet, and Freeman 2017).

A criticism of the LPI is that it tends to over represent birds and mammals in temperate realms as they are more intensely monitored (Collen et al. 2009). In response, the LPI was modified to include a proportionally weighted index (McRae, Deinet, and Freeman 2017). The weighted LPI tackles the problem of taxonomic and geographical bias. The weighted LPI is applied to the problem of bias that presents itself mostly on a global level.

The LPI is calculated as follows:

$$\overline{d_t} = \frac{1}{n_t} \sum_{i=1}^{n_t} d_{it} \tag{13}$$

where $\overline{d_t}$ is the average annual trend if there were multiple population time series of the same species. n_t refers to the number of populations. d_t is the annual rate of change for a population at time t, and is represented as follows:

$$d_t = log_{10} \left(\frac{N_t}{N_{t-1}} \right) \tag{14}$$

where N_t refers to the population size during year t.

The LPI is conducted using two different methods. One being the LPI-U (unweighted LPI) and the LPI-D (proportionally weighted LPI). In the LPI-U, the data is divided into 6 subsets. Based on region (tropical or temperate) and three realms (terrestrial, freshwater and marine). The index for each system is calculated by averaging the species trends within each system. The systems being (tropical terrestrial, tropical freshwater, temperate terrestrial, etc.). The index for each region (tropical or temperate) is then calculated by averaging the trends for each system. The tropical and temperate trends are then averaged to form a global trend which is converted into an index as follows:

$$I_t = I_{t-1} * 10^{\overline{d_t}}, \quad I_0 = 1 \tag{15}$$

where $\overline{d_t}$, in this case, is the average trend within a region, realm, system or globally.

The LPI-D approach is similar. The only difference is that it applies proportional weights to species when averaging the trends. For example, if birds represent 43.3% of terrestrial vertebrate species in the Palearctic realm, then this value is used in weighting the bird species when calculating the weighted average of the Palearctic realm trend for terrestrial species. The mathematical representation is as follows:

$$\overline{d_{t,realm.region}} = \frac{1}{N_t} \sum_{j=1}^{N_t} d_{jt} w_j \tag{16}$$

where d_t is the average trend of a given realm and region. N_T is the number of taxonomic groups within a realm, d_{jt} is the average trend of taxonomic group j at time t and w_j is the proportional weighting of that taxonomic group (0.43 according to the previous example).

Understanding waterbirds population change over time in South African wetlands is invaluable to our understanding of the wetland they occupy. As discussed previously, some species populations may indicate certain wetland characteristics such as eutrophication levels and siltation rates. Monitoring the combined number of waterbird species can indicate when there are sharp declines or increases in species abundance. These sharp turning points could indicate that the wetland is changing in some way and thus alert wetland managements to further assess the wetland and take necessary action.

A modified LPI approach was used to form an abundance index in this study. The modified LPI used calculates percentage change from each year to the next for a trait specific group of waterbirds.

The modified LPI calculations were applied to the mean summer population posterior value, per year, estimated by the state-space model. The SSM was first applied to each species in a trait specific group separately. The percentage change for each year was calculated for each species, then the average percentage change across all species in the group was calculated, per year. The calculations used are as follows:

$$d_t = \frac{\mu_t - \mu_{t-1}}{\mu_{t-1}} \tag{17}$$

where d_t is the population percentage change at year t for a single waterbird species and μ_t is the mean value of the true summer population at time t, obtained from the state-space output (see equation 5). The average percentage change per year, for a trait specific group, was calculated by taking the average d_t across all waterbirds in the trait specific group per year. The mathematical representation is as follows:

$$\overline{d_{tg}} = \frac{1}{N} \sum_{i=1}^{N} d_{ti} \tag{18}$$

where $\overline{d_{tg}}$ is the average population percentage change for trait group g at year t. N is the total number of waterbirds in group g. d_{ti} is the percentage change of species i at year t.

Unlike the LPI, it does not convert the percentage change to an index value. Converting percentage change from a reference year to an index value resulted in high levels of uncertainty in the index value. Using percentage change only was still subject to high levels of uncertainty but less than if it were converted to an index value after.

The modified LPI can be applied to any groupings of waterbird species. One could group the waterbirds based on different traits and calculate the percentage change per year on that specific

group. The waterbirds could be grouped together based on traits such as habitat, body size, brood size, food type, etc. For this dissertation migrant status, nest site and the number of different foraging sites used by a waterbird were used as examples of how the modified LPI can be used for trait specific groups (Figure 4 and 5).
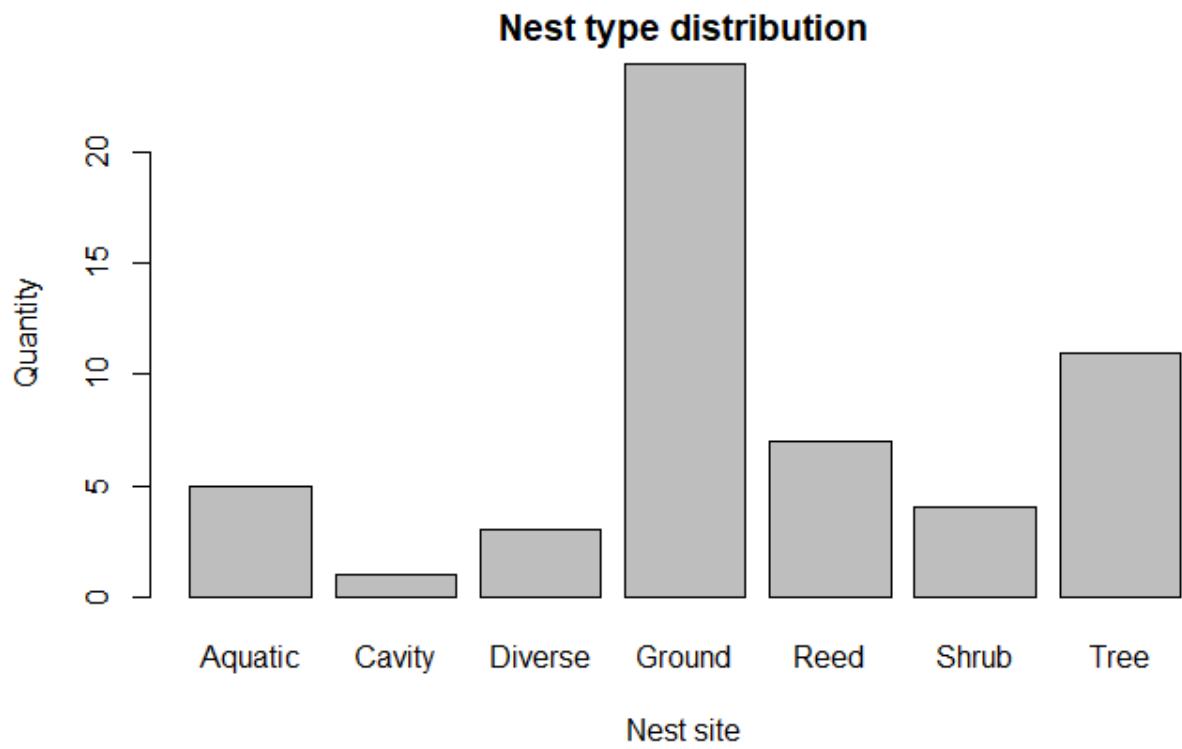
Figure 4: Number of species that use each nest site type

Number of foraging type distribution
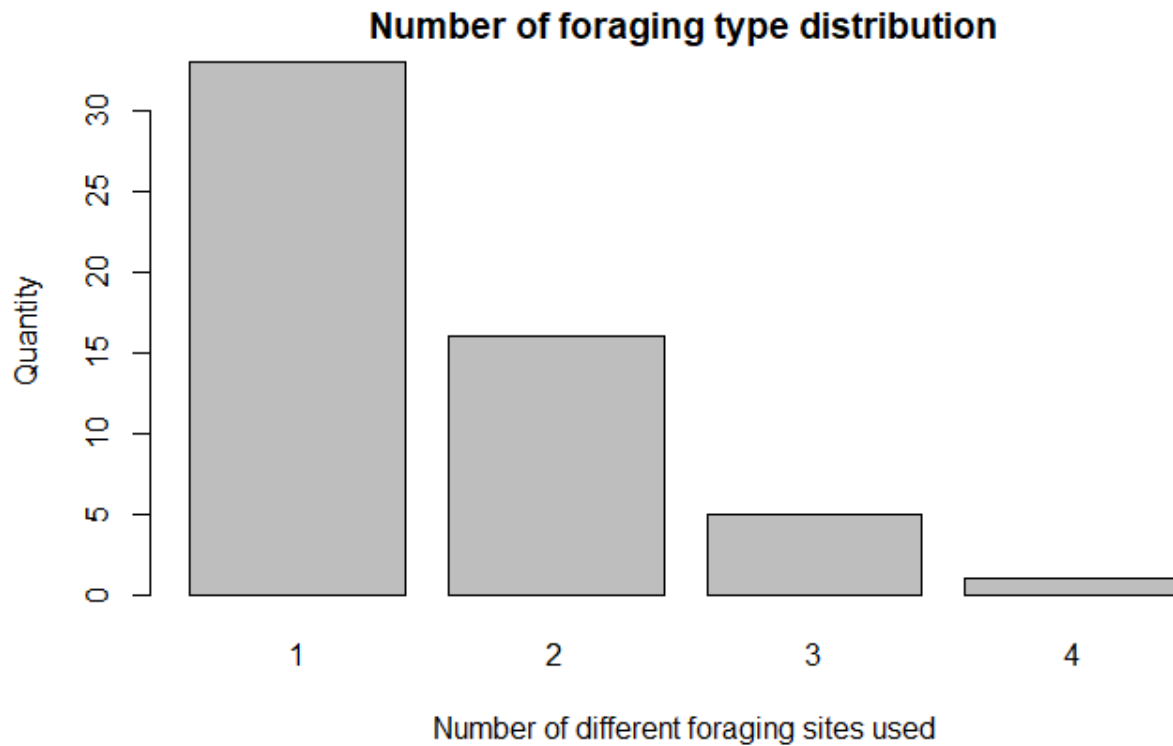
Figure 5: Quantity of species that make use of one, two, three or four different types of foraging sites

The majority of species in Barberspan nest on the ground. These nests are commonly built by creating a depression in the ground lined with grass or feathers. 24 different waterbird species predominantly build their nest on the ground. 7 different species build their nest in the reeds and 11 species use trees to nest. The cavity, aquatic and shrub nest type are attributed to the fewest species (10 different species in total).

There are five different foraging sites represented in the above plot. These sites are: aquatic, ground, off-ground, aerial and mud. Most species in Barberspan only make use of one of these sites (33 different species). 16 different species utilise at least two different foraging sites and only 6 species utilise 3 or more foraging sites.

The modified LPI used in this dissertation was applied to each of the groups represented by the above plots. For each group the SSM was applied to the combined counts of that group. The SSM was then applied to each individual species of the group and the median percentage population change, per year, was calculated across all species in the group to determine the annual percentage population change for the group.

Diversity indices

The diversity of species in an ecosystem is a very important aspect of a healthy ecosystem (Duffy 2009). Richer species diversity, or higher levels of evenness, is indicative of a healthy ecosystem (Hooper et al. 2005). Quantifying diversity has been a contentious measure in ecology (Peet 1974). The literature emphasizes that diversity is dependent on the research questions and the task at hand and there is no universally agreed upon definition of what diversity is (Hurlbert 1971).

In the context of this dissertation, which focuses on South African wetlands and waterbirds, the aim is to monitor the biodiversity of the waterbird species in a wetland over time. The popular indices used to measure species biodiversity are the Shannon Entropy and the Simpson Index. There have been studies aimed at finding the best index for species diversity. These studies agree that one can't identify one all-encompassing index, but using a few together gives one a better overview of the ecosystem (Morris et al. 2014).

The closest framework there is to an all-encompassing diversity index is the Hill Numbers model (Hill 1973). The Hill Numbers framework provides a range of measures of the effective number of species in a system. Each one differing in their propensity to add more, or less emphasis on the rarer species. The Hill Numbers general formula is as follows:

$$N_\alpha = (p_1^\alpha + p_2^\alpha + \ldots + p_n^\alpha)^{\frac{1}{1-\alpha}} \tag{19}$$

where N_α is the diversity number of order α. These diversity numbers reflect an estimate of the effective number of species present in a sample. The p's refer to the proportions of species in the sample and n represents the number of species in the sample. The most commonly used values for α are zero, one and two. N_0 refers to the number of species in a sample. N_1 results in an exponent $\frac{1}{1-1}$ but, according to Hill, the N_1 diversity number approximates to the exponential of the Shannon's Entropy (proof is supplied by Hill). The more general formula for the Shannon Entropy is as follows:

$$x = -\sum_{i=1}^{S} p_i ln(p_i) \tag{20}$$

where x is the index, p_i is the proportion of species i in the sample and S is the number of species in the sample.

N_2 is the inverse Simpson's Index. The more common general formula for the Simpson's Index is as follows:

$$x = \sum_{i=1}^{S} p_i^2 \qquad (21)$$

Different indices measure different aspects of diversity (Hill 1973). The Simpson's Index is more sensitive to the abundance of common species in an ecosystem. For this reason, it is also referred to as the measure of dominance concentration. Whereas the Shannon entropy index measures the entropy of an ecosystem (Jost 2006).

According to Jost (2006), the problem with some diversity indices is the way in which researchers use them. For example, the Shannon's entropy index is not a diversity measure but rather a measure of entropy in the ecosystem (Jost 2006). Thus, it becomes more intuitive and easy to work with when converted to a true diversity (effective number of species in an ecosystem) before any comments can be made regarding diversity in the ecosystem. Jost, uses the example of other fields such as physics, economics and information theory. It is common practice in all these fields to convert entropy values to the effective number of elements in a system instead of reporting on the entropy index value. One simply needs to exponentiate the Shannon Entropy value to determine the effective number of species in the ecosystem.

The Simpson's index can be used without any conversion as it already is an index value and is immediately intuitive and easy to use without any conversions. As a result no transformations were made on the Simpson's index in this dissertation. The Simpson's index is a measure of dominance with values ranging from zero (lowest level of evenness) to one (highest level of evenness) and can be used directly to determine dominance in an ecosystem without any conversion.

Further problems are addressed regarding diversity indices in ecology. Measuring diversity in a system has many differing semantic and technical aspects. Given the different aspects of diversity, and the plethora of possible indices to measure them, some have argued that diversity measures are a "nonconcept" (Hurlbert 1971). However, given the variety of measures one can use, the issue is perhaps not the indices but how to choose which ones to use.

The best way to use diversity indices is to use various indices simultaneously (Whittaker 1965), as each index can tell the user different aspects of the diversity in the system. In terms of the Shannon's entropy and Simpson's index, the Shannon's entropy, when exponentiated, gives a value of the effective number of species in an ecosystem while the Simpson's index tells the user about the dominance concentration of the ecosystem.

Biodiversity has many definitions and applications. The use of more than one biodiversity index is

important to cover as many aspects of biodiversity as possible. This gives the user a more complete understanding of the wetland and waterbird state. This is the reason three different biodiversity indicators were used in the dissertation. When a user analyses these indices in conjunction with one another they are able to see a clearer picture of waterbird and wetland state.

3 Results

The first and foremost objective was to develop and fit a relevant state-space model to the waterbird counts in the Barberspan wetland. The model discussed in the methods section was developed and fitted using the JAGS framework in R. This model was able to account for seasonal fluctuations in the count data. This applies specifically to the palearctic and intra-African migrants. The same model was applied to the resident species to fit potential seasonal patterns caused by the observation process.

When running the SSM on all of the waterbird counts in Barberspan, it was found that the variance parameters didn't converge for waterbirds with fewer than 13 non-zero counts. As a result, these birds were left out of the study. The SSM was then applied to the remaining waterbirds (41 resident and 14 migrant waterbirds). The model was applied to each individual resident and migrant species and then to the summed resident counts and summed migrant counts. Applying the SSM to the combined counts gives an overview of the population dynamics of the Barberspan wetland. When applied to individual species, it provides a more in depth analysis of the population dynamics on the species level. This is done with the user in mind. It is important to display as much information as possible for the user. Displaying only aggregated metrics often hides finer details that may be of importance.

3.1 State-Space Model Output

The SSM was applied to the combined counts of resident species and then applied to the combined migrant species. The SSM models two time series, one for summer and one for winter. Figure 6 and 7 display the output of the SSM on the combined waterbird counts at the Barberspan wetland.
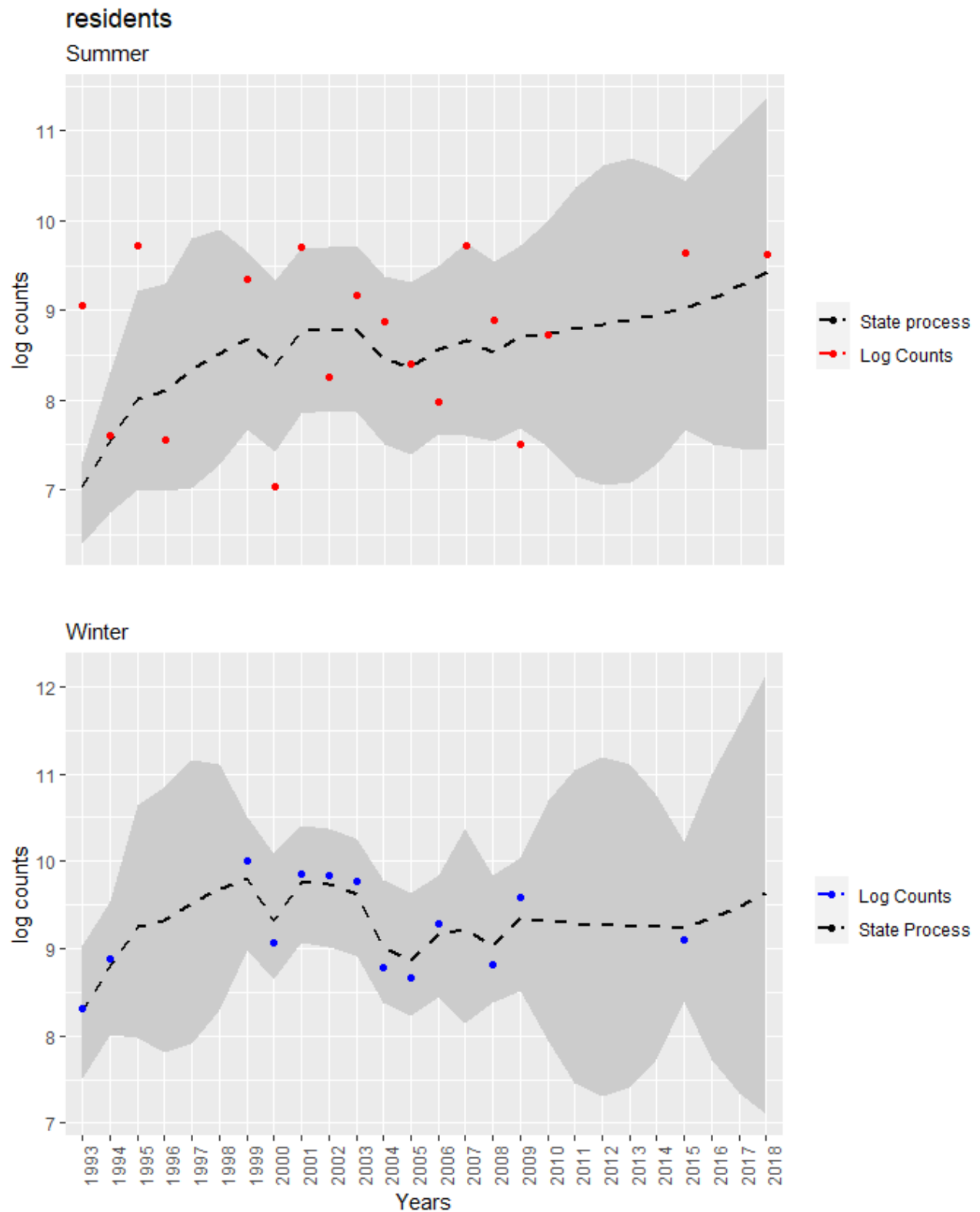
Figure 6: SSM output applied to the combined resident counts at Barberspan wetland, separated by season. The grey area surrounding the black dotted line is the 95% credible interval around the population level produced by the MCMC output.
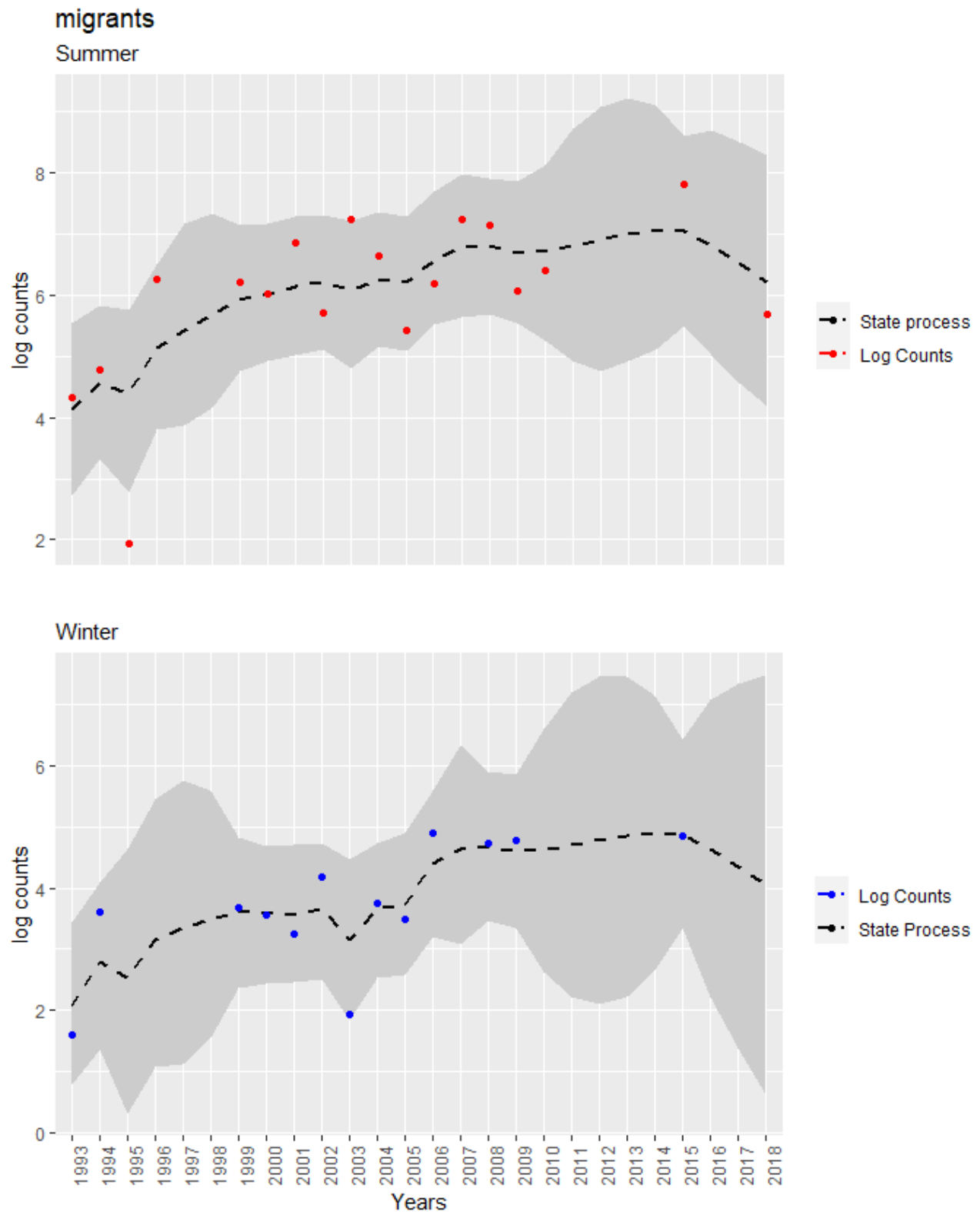
Figure 7: SSM output applied to the combined migrant counts at Barberspan wetland, separated by season. The grey area surrounding the black dotted line is the 95% credible interval around the population level produced by the MCMC output.

Neither model shows significant change over time. The migrant population seems to increase gradually from 1993 till around 2014, after which it experiences a drop in counts. This change in trend is however based only on one count. The resident summer population, on average, displays a positive rate of change over time. The interval estimate of the average rate of change across all the years for the migrant population is [-1.23, 1.28]. The model only focuses on rate of change in the summer counts and models the winter counts as the proportion of species that remain from summer. The interval estimate of the average rate of change across all years for the resident population is [-1.19, 1.32]. These interval values are obtained from the posterior distribution by taking the 2.5th and the 97.5th percentile.

Appendix B shows the state-space model's output when applied to each individual waterbird species. When considering average trends from 1993 to 2018, 35 out of the 41 resident species analysed in Barberspan show positive trends. The other six exhibit no trend or a negative trend. However, none of these trends are statistically significant.

The migratory species display the same number of negative trends and positive trends. seven out of the 14 analysed migratory species exhibit decreasing trends and seven exhibit increasing trends.

It is interesting to note that when the model is applied to the combined migrant counts, a positive average rate of change is seen. This shows how aggregating species count data can hide important aspects at the individual species level. This is one of the criticisms of indices that are based on species aggregation such as the Living Planet Index (LPI) (Ritchie and Roser 2021). The LPI tends to be very sensitive to sharp population increases or decreases. For example, if two out of five waterbirds increase drastically while the other three decrease gradually; the LPI will aggregate the trends in such a way that it will indicate a sharp increase for all five species which is misleading (Ritchie and Roser 2021). To create an effective data dashboard (as the BIRDIE project aims to do) it is essential to have information on individual species and information on an aggregated level.

3.2 Abundance Indices

Despite the criticism of abundance indices such as the LPI, it is still the most popular abundance index. The LPI was developed to track global species population change over time (Collen et al. 2009). This was in response to the Convention on Biological Diversity targets set out in 2010, which aims to reduce the loss of biodiversity on the planet. Due to the popularity of the LPI, a modified LPI was used in this report to track aggregated population change over time for the waterbirds.

The modified LPI was applied to various groups of waterbirds. These groups were based on nest site,

number of different foraging locations and migratory status. For each group the SSM would be applied to each individual waterbird. The posterior output from the MCMC for each waterbird was then summed together across the group, and the modified LPI was then applied to the summed posteriors. The median, 2.5th and 97.5th percentile was then calculated and displayed in figure 8 to figure 20.
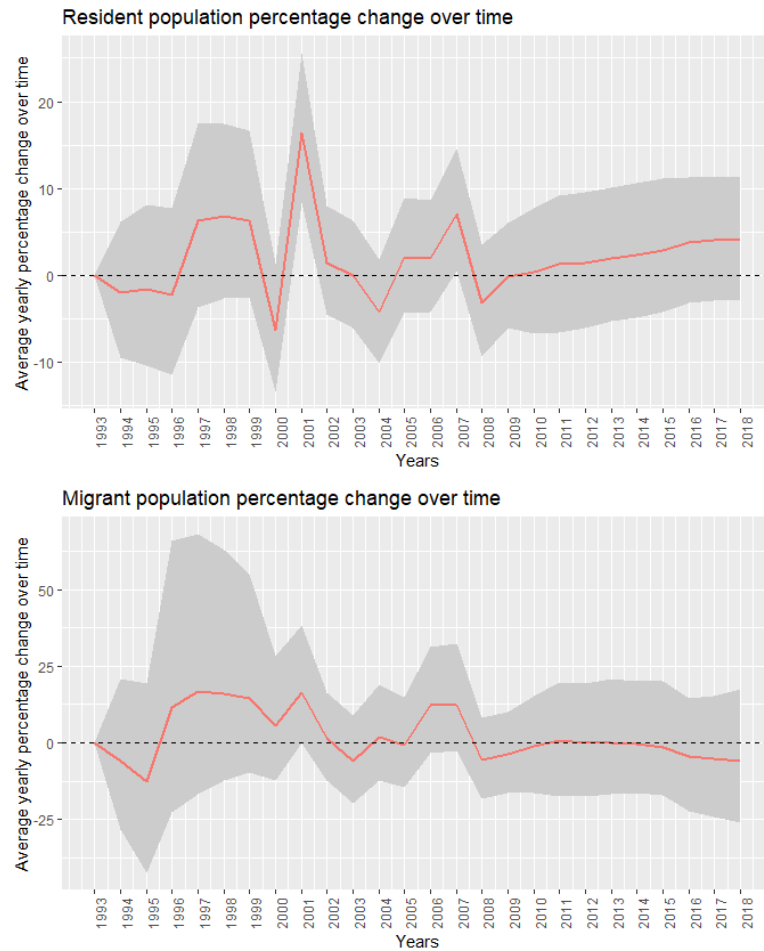

Figure 8: The modified LPI displaying the average yearly percentage change averaged across all resident waterbirds (top) and all migrant waterbirds (bottom) at Barberspan wetland based on trend estimates produced by a state-space time series model. The grey area around the trend line represents the 2.5th and 97.5th percentile.

The resident waterbirds displayed an average yearly percentage increase of 11.71% while the migratory waterbirds displayed an average yearly percentage increase of 5.81%. This agrees with the SSM plots in Figure 7, as both residents and migrants seemed to display slightly increasing trends.

3.2.1 Nest Site Trait

Seven different types of nest sites were considered. Namely, aquatic, cavity, ground, reed, shrub, tree and diverse. The plots showing the abundance indices for each of the nest site traits and the SSM output applied to the combined counts of each group are displayed in Figure 9-15.
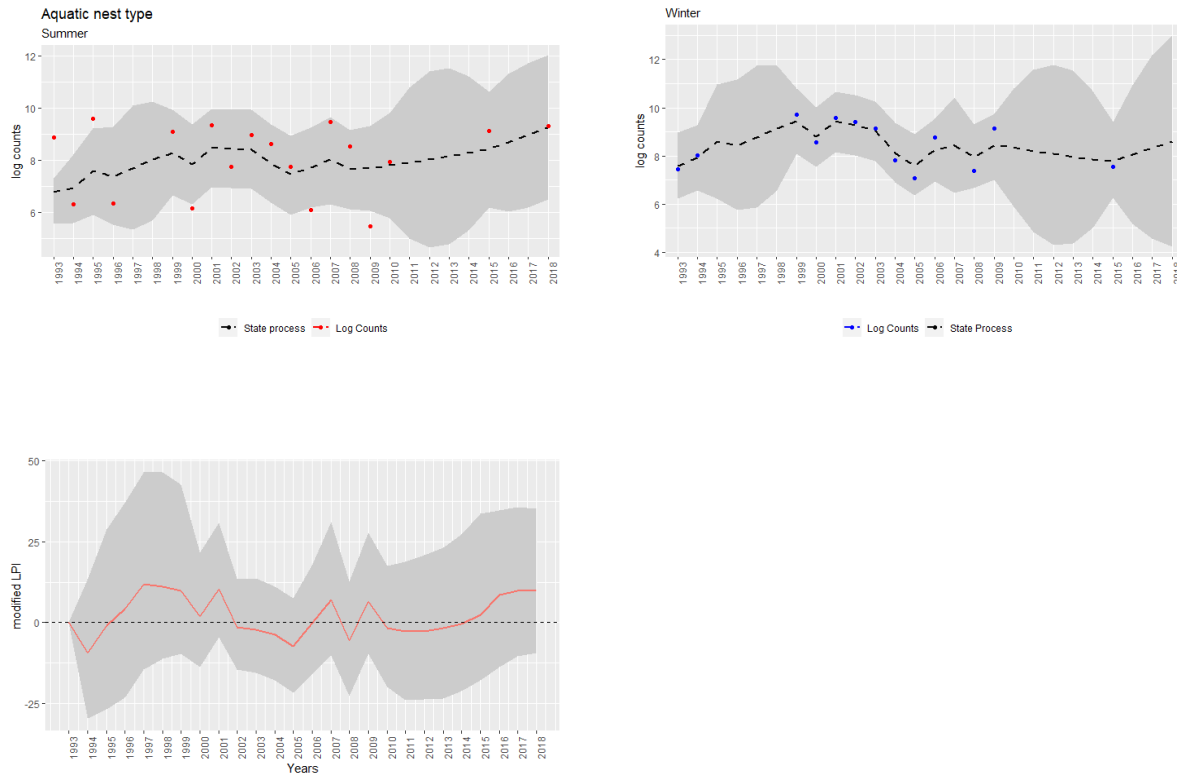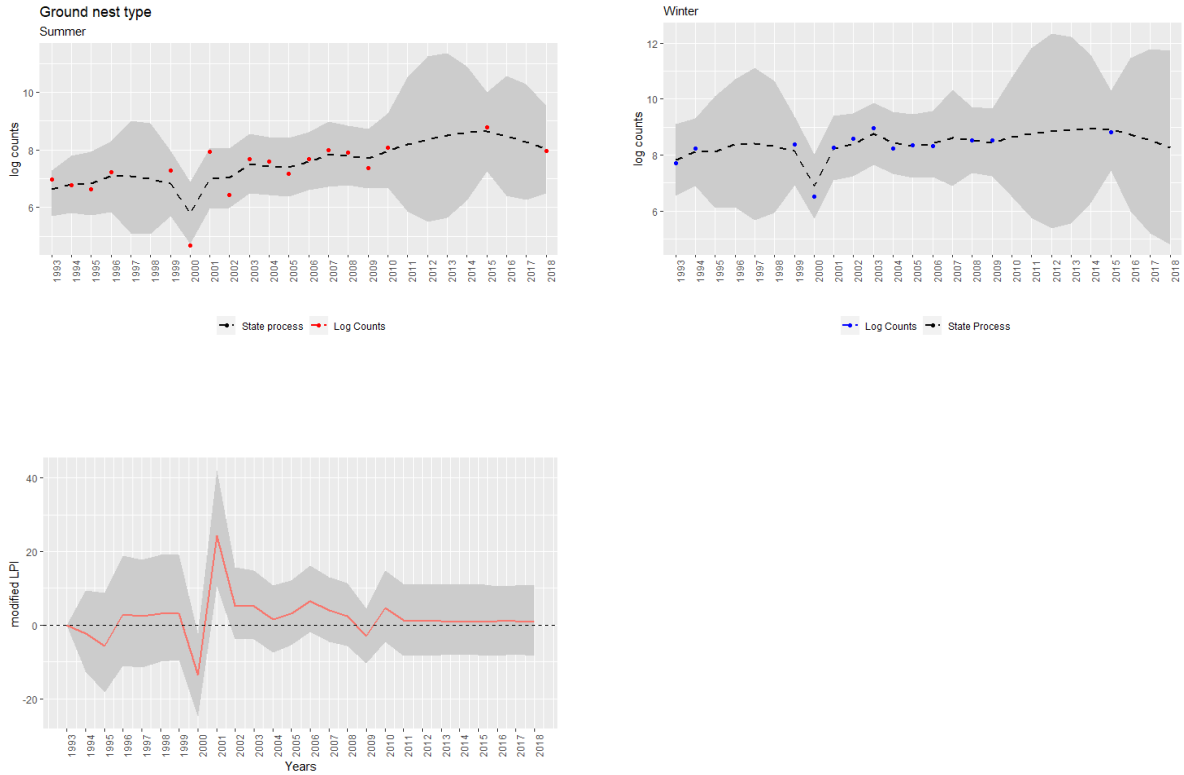

Figure 9: The first two plots are from the SSM output applied to the combined counts of the waterbirds that nest in an aquatic environment, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.
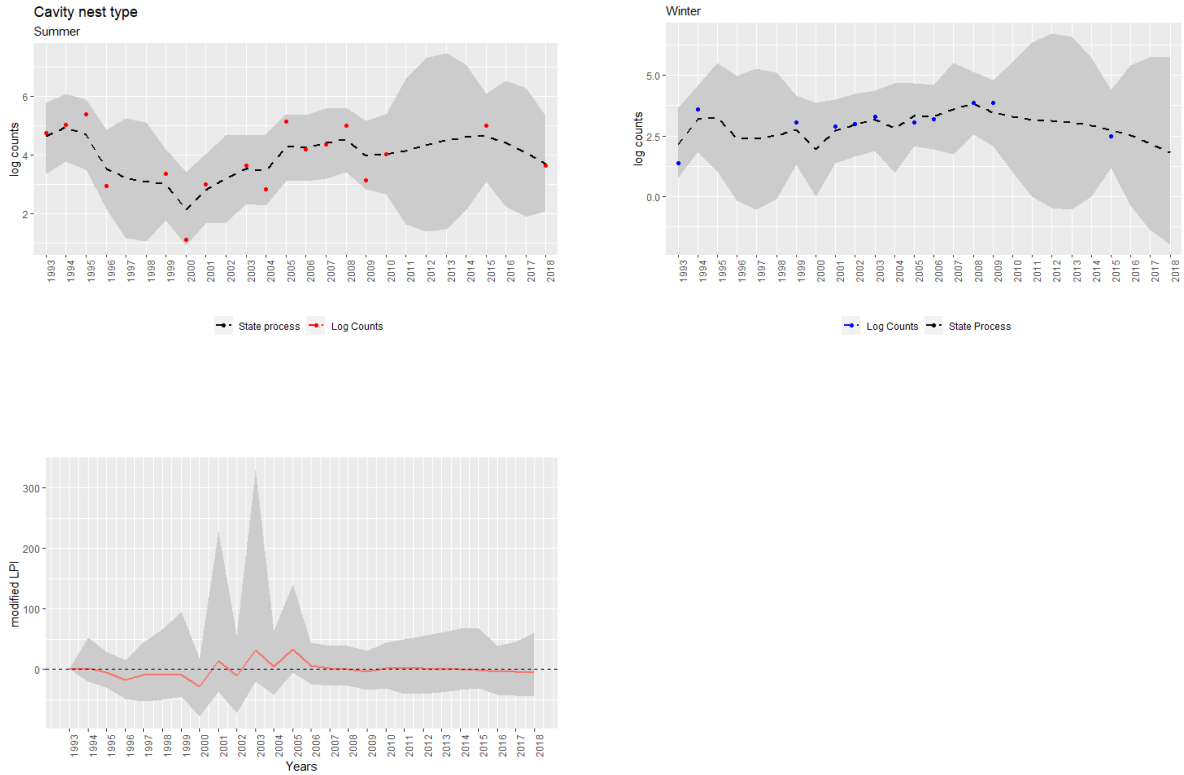
Figure 10: The first two plots are from the SSM output applied to the combined counts of the waterbirds that nest in cavities, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.
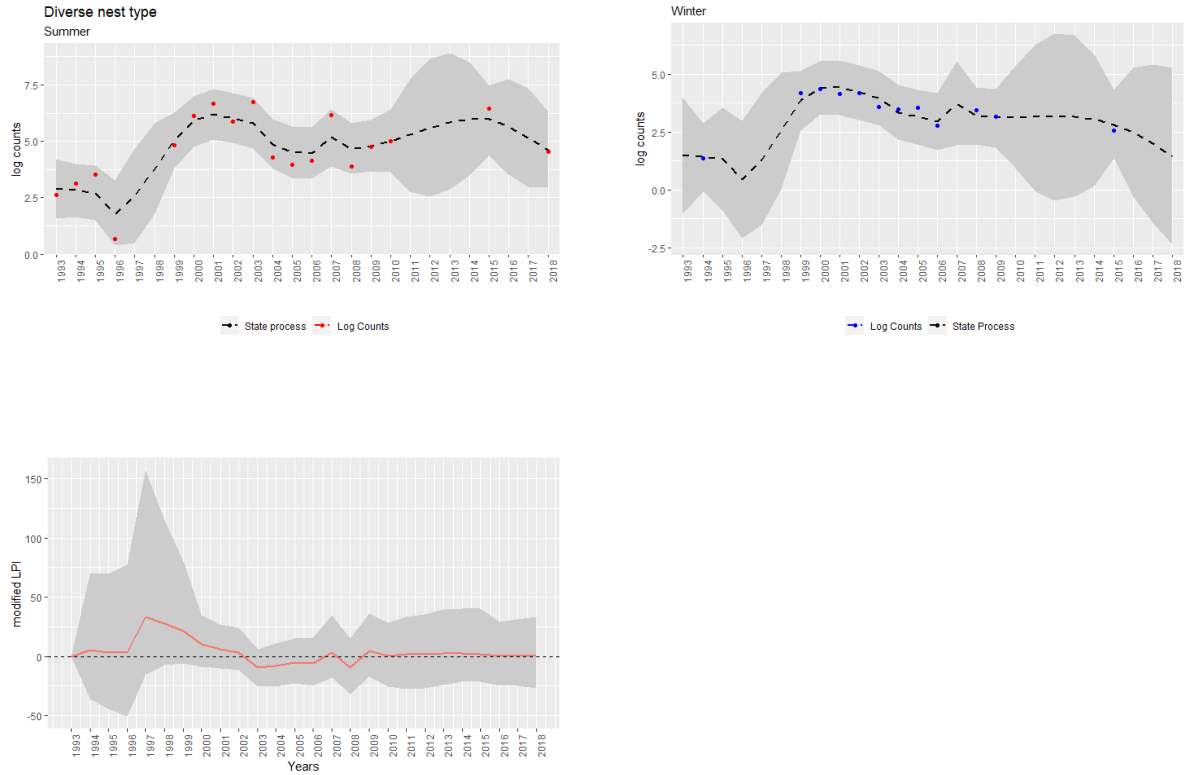
Figure 11: The first two plots are from the SSM output applied to the combined counts of the waterbirds that make their nests in diverse environments, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.
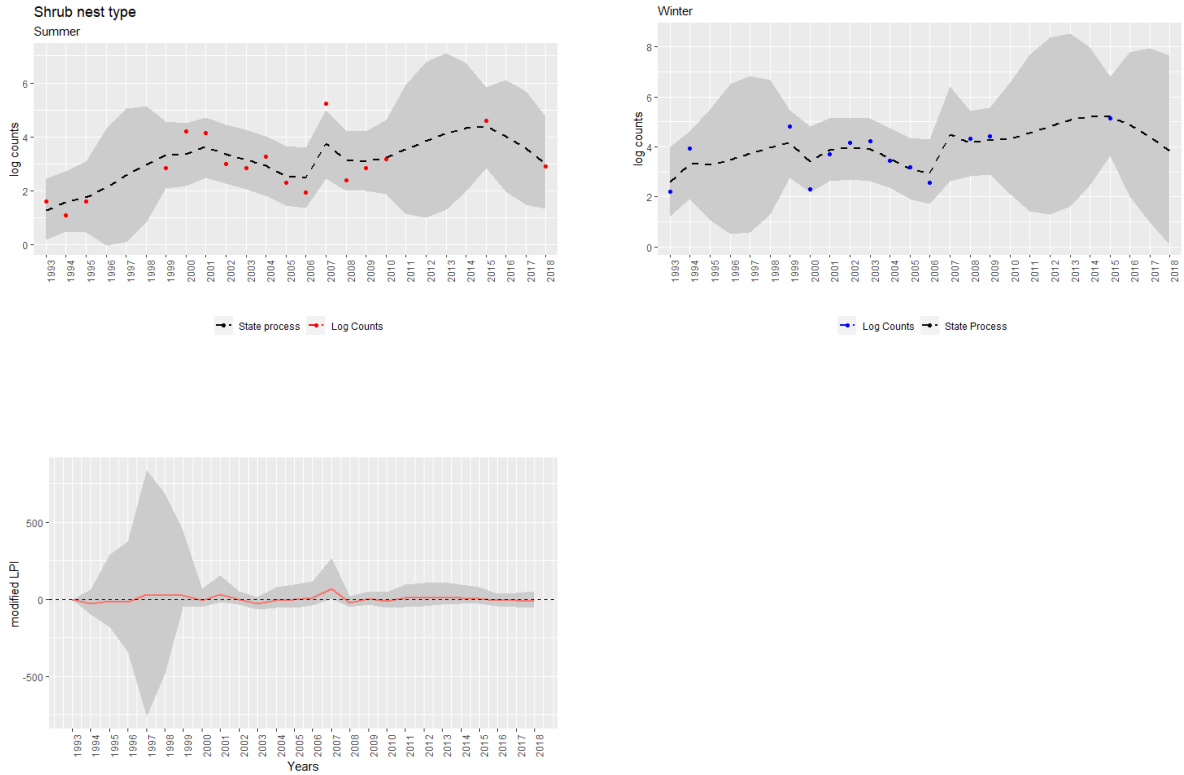
Figure 12: The first two plots are from the SSM output applied to the combined counts of the waterbirds that nest by creating recessions in the ground, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

Figure 13: The first two plots are from the SSM output applied to the combined counts of the waterbirds that make their nests amongst the reeds, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

Figure 14: The first two plots are from the SSM output applied to the combined counts of the waterbirds that nest in shrubs, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

Figure 15: The first two plots are from the SSM output applied to the combined counts of the waterbirds that nest in trees, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

All nest site traits show a positive yearly increase on average. The species with the aquatic or shrub nest type showed the greatest yearly percentage change with an average yearly increase of 16.86% and 12.70% respectively.

The modified LPI displays a sharp increase in trend for waterbirds that nest in an aquatic environment and those that nest in trees, however, these sharp increases occur after the year 2015 and therefore are only based on one count value, thus deeming these sharp increases as unreliable.

3.2.2 Foraging Site Trait

There are five different types of foraging sites used by the waterbirds in Barberspan. Some species use only one site type such as the wader species that often only forage in an aquatic environment. Other species show more diversity in their foraging such as the Cape Wagtail which forages on ground, off-ground, in mud and in aquatic environments. There are many different combinations of foraging sites across the waterbird species. The abundance index was thus applied to species groups

based on how many different foraging sites they utilise. Species that use more foraging sites would be more flexible in their foraging habits compared to those who use just one or two. Most species only exhibited one foraging substratum but some exhibited 2, 3 or 4 different foraging substrata. Figure 17-20 show the abundance index for each foraging site group and their combined counts.
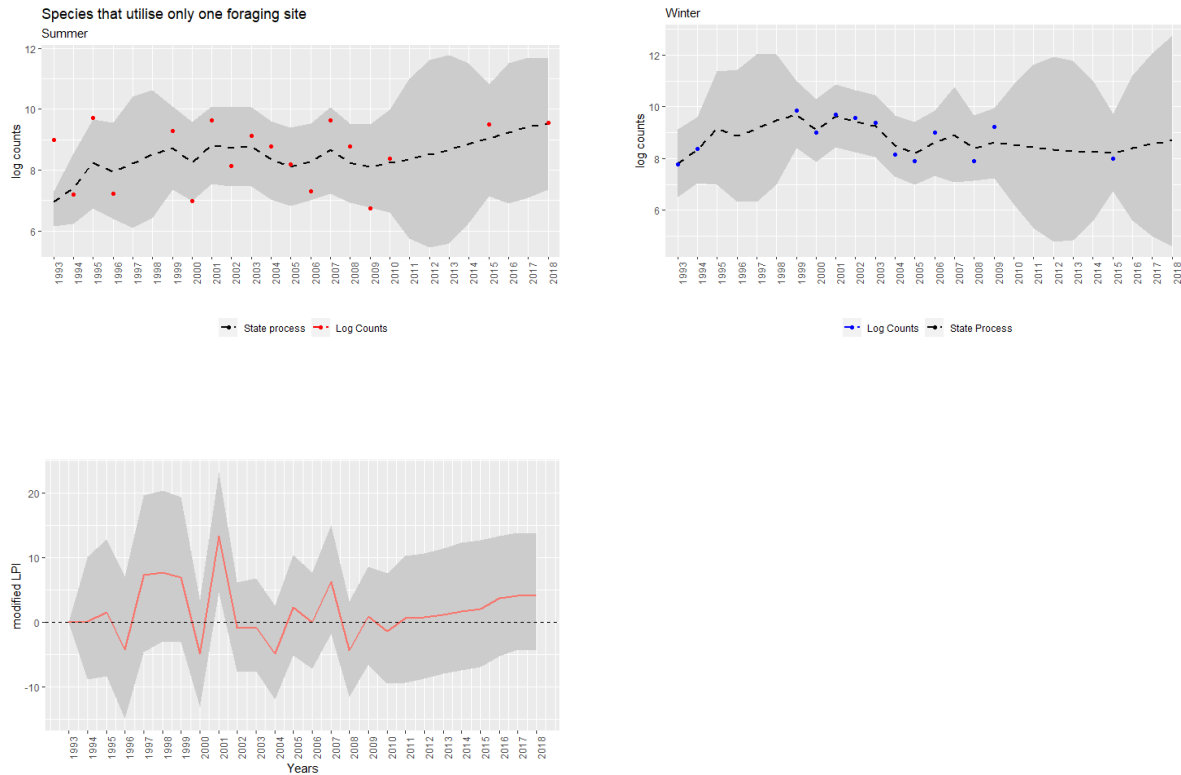
Figure 16: The first two plots are from the SSM output applied to the combined counts of the waterbirds that utilise only one foraging site, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.
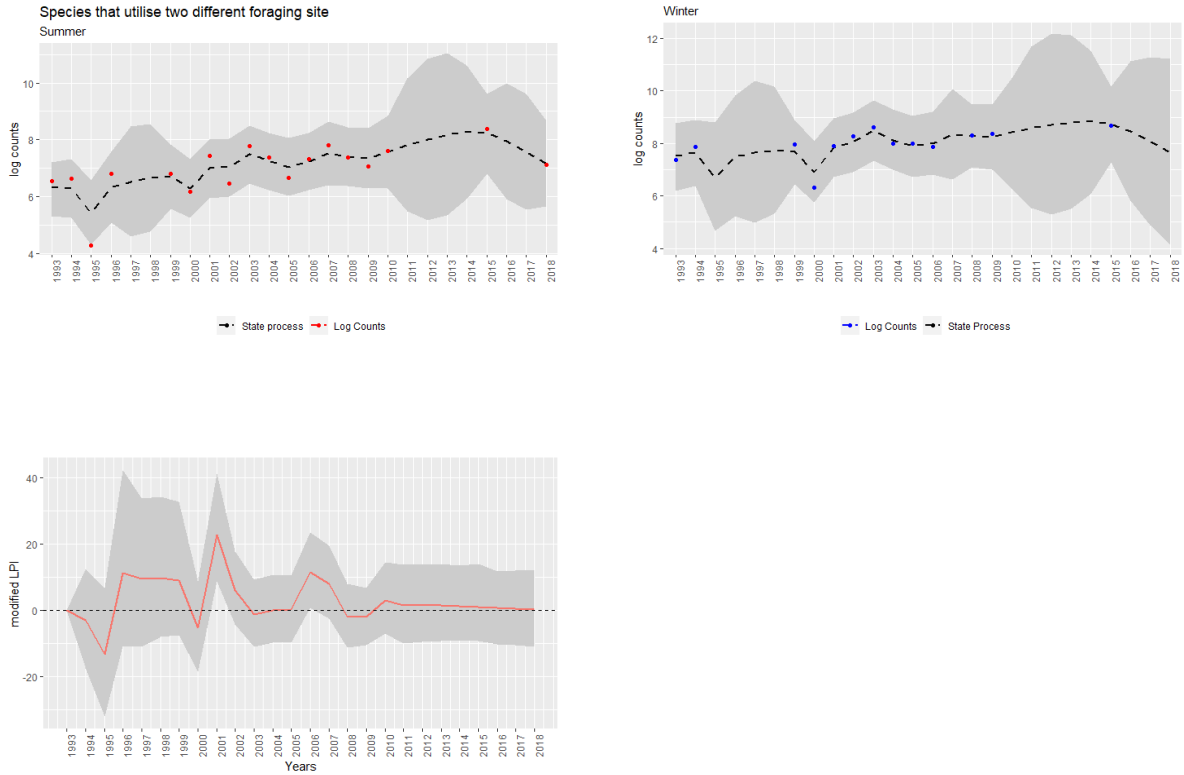
Figure 17: The first two plots are from the SSM output applied to the combined counts of the waterbirds that utilise two different foraging sites, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.
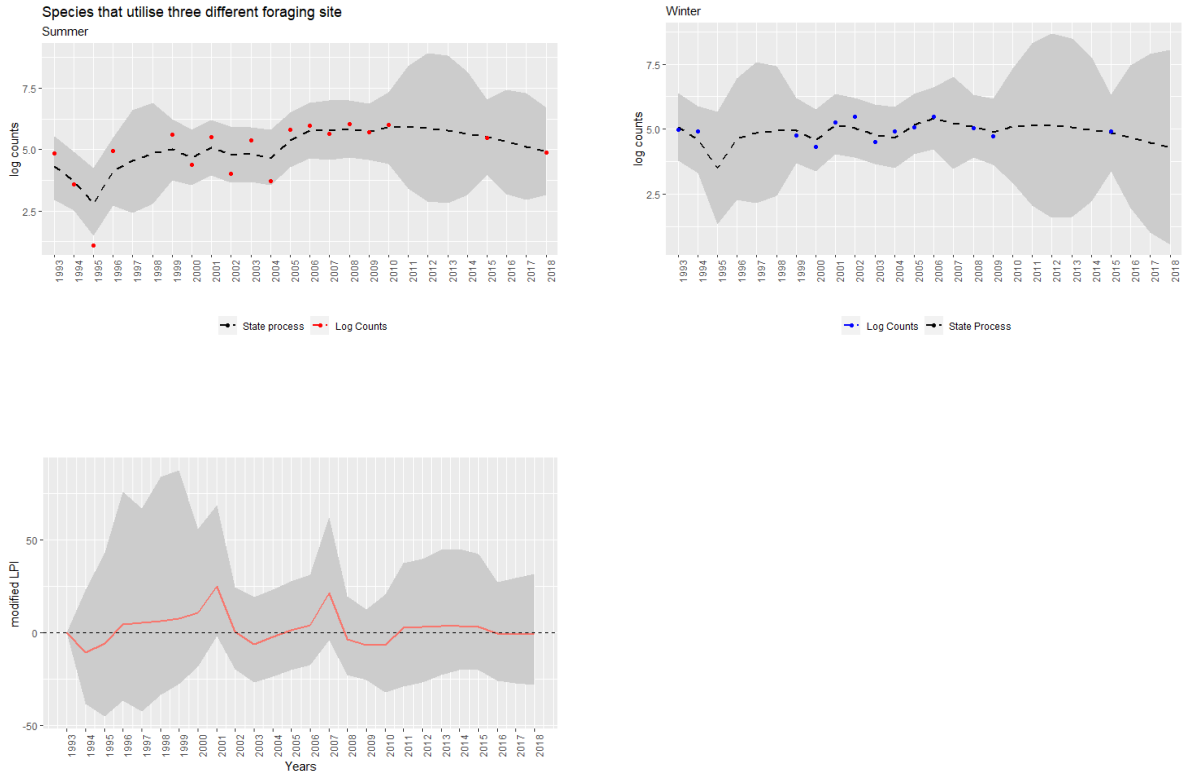
Figure 18: The first two plots are from the SSM output applied to the combined counts of the waterbirds that utilise three different foraging sites, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

Figure 19: The first two plots are from the SSM output applied to the combined counts of the waterbirds that utilise four different foraging sites, separated into summer and winter estimates. The last plot is the average yearly percentage change across those waterbird species.

The average percentage change for each foraging substratum group is similar. There is no evidence to show that a waterbird species that forages in more locations, increases in population faster than waterbirds which utilize fewer foraging types.

Not all waterbird traits will be indicators that determine population dynamics but some are useful. It was useful to analyse the waterbirds separately based on migrant status as the fluctuations in the counts are different due to their migratory patterns. However, the number of foraging substrata and nest site does not seem to play an important role in describing population dynamics for the waterbirds.

3.3 Biodiversity Indices

The underlying level of the state-space model, once generated, are estimates of the underlying population of the analysed bird species. Biodiversity indices are formulated using these values. The indicators used here are the Simpson's index and the exponentiated Shannon's index. The Simpson's

index provides a value representing the evenness of the ecosystem. The value of the Simpson's index varies from zero to one with zero being very little evenness and one being perfect evenness. The exponentiated Shannon's index gives the value of the effective number of species in an ecosystem. The Shannon's and Simpson's index are often used together.

The exponentiated Shannon's index and the Simpson's index were applied to the waterbird counts the same way as the modified LPI. Figure 20 displays the exponentiated Shannon's and Simpson's index each year for Barberspan.
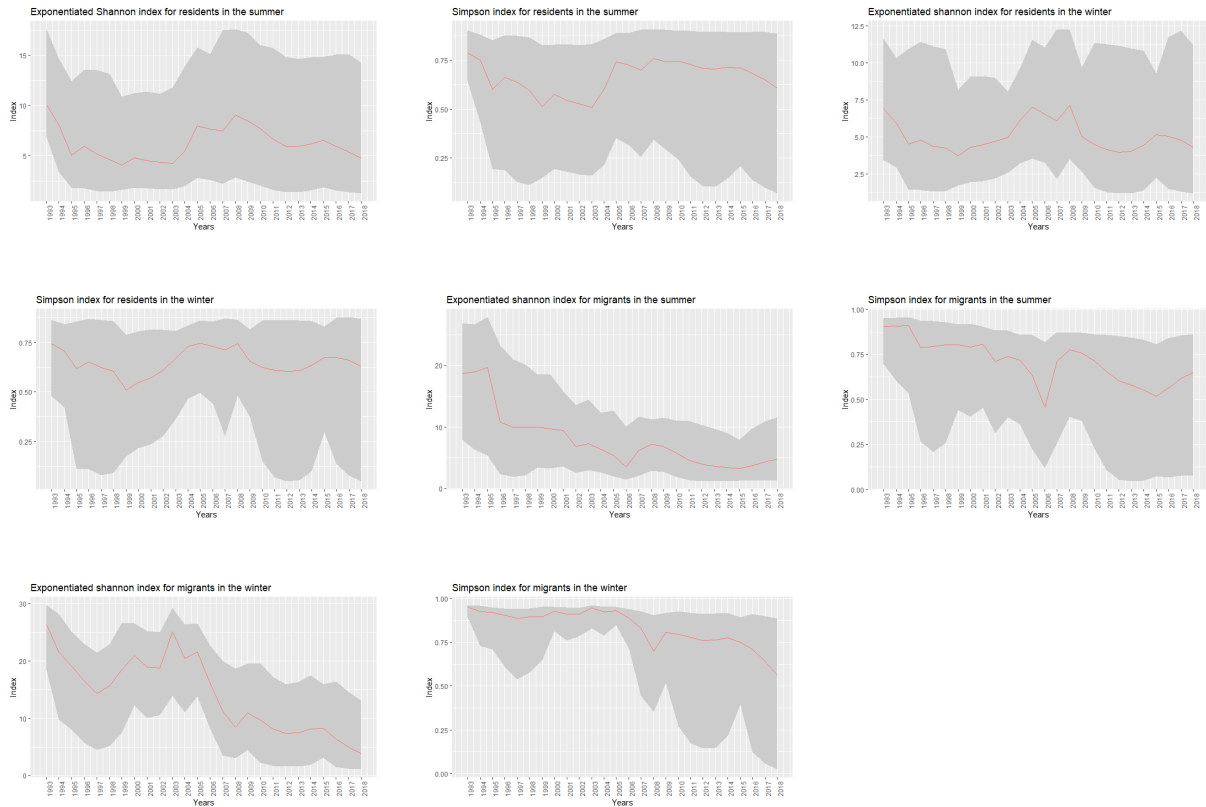
Figure 20: The Shannon and Simpson's indices for resident and migrant species in winter and summer

Due to the high levels of uncertainty of the index, it is difficult to state anything concrete based on these index values. However, it is evident that, on average, there is an overall decrease in the effective number of migratory waterbirds at Barberspan between 1993 and 2018 as displayed by the exponentiated Shannon's index. This is true for migrant waterbirds in the summer and in the winter. Given that migrant population has not changed significantly over time (as seen in figure 7), we can determine that the decrease in effective number of species is not an even decrease across the migrants at Barberspan. The Simpson's index, accordingly, suggests a trend toward lower evenness for the migrants at Barberspan over time.

The exponentiated Shannon's index shows a similar number of effective residents in both summer and winter compared to the migratory waterbirds. This is a reflection of the effect migration plays in the waterbird community in Barberspan. Resident waterbirds rarely move away from Barberspan while migrants show changes in effective number of species depending on the season. Interestingly, migratory waterbirds display a higher effective number of species in winter than in summer despite there being more migrants present at Barberspan in summer compared to winter. This measure is a result of there being a higher evenness amongst migrants in winter compared to summer (displayed by the Simpson's index). For example, 10 waterbird species in a community, each with a similar amount of individuals, will display a higher effective number of species compared to a community with the same number of species present but with one or two dominant species.

4 Discussion

Abundance and Biodiversity Indices

Wetlands are valuable ecosystems for society (Clarkson, Ausseil, and Gerbeaux 2013). Unfortunately, there has been global wetland degradation with about half of the global wetlands being lost to accommodate for agricultural practices and urbanisation. The loss of wetlands has a negative impact on biodiversity, human well-being and has negative long-term impacts on economies (Clarkson, Ausseil, and Gerbeaux 2013). This has given rise to many wetland conservation projects, both locally (Working for Wetlands project) and globally (RAMSAR and AEWA).

Out of the three waterbird attributes investigated in this study (migratory status, nest site and number of foraging sites used), the migratory status seemed to be the most likely to affect population declines, as proportionally more migratory waterbirds displayed declining trends (50%) compared to resident waterbirds (14.6%). The other attributes investigated provided no significant evidence to suggest that they are drivers for population change among the waterbirds in Barberspan.

The higher rate of decline within the migratory waterbirds agrees with similar reports on waterbirds in Southern Africa. A study on migratory waterbirds in South Africa reported that 11 of the 16 palearctic migrants investigated experienced negative trends from 2005-2009 (Barshep et al. 2017). A paper analysing palearctic migrants in Sandwich Harbour and Walvis Bay, Namibia, reported similar findings; four of the 12 palearctic migrants studied experienced declines while only one species experienced an increasing trend (Common Whimbrel) from 1990-2013 (Simmons et al. 2015). Further studies show that Palearctic-Afrotropical migratory waterbirds are experiencing declines in abundance globally (Kirby et al. 2008; Deniau et al. 2022).

The Simpson index displays some evidence that both the migratory and the resident waterbirds of Barberspan are becoming less even over time. This means that there are some waterbirds that are dominating while other species are leaving Barberspan. Investigating the SSM output on the individual migratory waterbirds (Appendix B) we see 6 out of the 14 migratory waterbirds make up over 85% of the total counts for all migratory waterbirds at Barberspan used in this study. These are the Little Stint, Ruff, Curlew Sandpiper, White-winged tern, Whiskered tern and Common Ringed Plover. These 6 waterbirds all displayed fairly positive trends up until year 2013 - 2015, while the rest of the migratory waterbirds displayed decreasing trends or no discernible trend at all. This leads to an increasingly uneven community of waterbirds over time and a decrease in effective number of species over time. After the declining period between the year 2013 and 2015, only the Curlew Sandpiper recovered and started displaying a positive trend again. This leads to further unevenness

in the community and a further decrease in the effective number of migratory waterbirds in Barberspan. We see these aspects reflected in the Simpson's and exponentiated Shannon's index. The Shannon's index displays a decrease in effective number of species over time until it reaches an effective number of approximately four to six migratory waterbirds in Barberspan from 2013 onward. Similarly, the Simpson's index displays a decrease in evenness over time until it reaches a value of 0.6 for the winter counts and 0.66 for the summer counts in 2018. It is interesting to note that the migratory waterbirds mostly experience a higher effective number of species in winter compared to summer, even though there are significantly less migratory waterbirds at Barberspan during the winter. This result is due to the higher degrees of evenness displayed in winter than summer for the migratory waterbirds. There are less migratory birds in winter but higher evenness and therefore higher a effective number of species. Whereas, in summer there are the 6 dominant waterbirds present, as mentioned earlier, which leads to a lower number of effective species.

High measures of unevenness among migratory waterbird species were also presented in a study conducted in the wetlands of Northeastern Algeria. Ali, Ismahan, and Moussa (2016), discovered a high dominance in Eurasian Coots in the wetland studied. The Eurasian Coots made up about 53% of the 39 migratory waterbird species found in the wetland. similarly, A study conducted in a South African riverine habitat, the Shamvura stretch of the Okavango River, also found high levels of dominance among the waterbirds present in the wetland (Kopij and Paxton 2018). In this study there were 6 resident waterbirds out of the 84 recorded waterbirds that were classified as dominant: African reed cormorant, African openbill, cattle egret, wattled lapwing, African darter and white-faced duck.

Among the waterbirds in Barberspan it was also found that resident species were most dominant. The Egyptian Goose and the Red-Knobbed Coot made up 70% of all waterbird counts at Barberspan with the Red-Knobbed Coot being most dominant making up 58% of all counts. The effective number of resident species stayed relatively constant over time, for summer and winter, compared to the migratory birds. Residents displayed a exponentiated Shannon's index of around four to ten regardless of the season. This makes sense as these species do not migrate and so there would be less fluctuation in their abundance compared to the migratory waterbirds.

The outcome of this report is a first step in displaying what can be done using the CWAC dataset. The aspects of biodiversity to monitor were selected based on analysing what needs to be monitored, who needs to monitor it and why it needs to be monitored, thus following the instruction of Yoccoz, Nichols, and Boulinier (2001). The individual indices were selected based on best practices in quantifying biodiversity (Buckland et al. 2005, 2012). The three indices used in conjunction with one another provide a good overview of the waterbird and wetland state. For example, if the modified

LPI displays alarming negative percentage changes for a year or two the user can use the other indices and time series plots to investigate. One could check the exponentiated Shannon's index to see if the effective number of species types has decreased or has all types of species been leaving the wetland at the same rate. One could also check the Simpson's index to identify if there are any dominant species that are using up resources of other species and driving them away as a result. If the Simpson's index displays strong unevenness, the user can then analyse the individual time series plots to identify which species are increasing and which are decreasing. Knowing exactly which waterbird species are decreasing and which are increasing provides valuable insight into which aspects of the wetland may be a problem. For example, increases in Great Crested Grebe can be indicative of increased eutrophication levels (Amat and Green 2010) and decreases in Red-Knobbed Coots can be indicative of increased siltation rates in the water and soil of a wetland (Amat and Green 2010).

The State-Space Model

The state-space model used in a Bayesian context has the potential to quantify uncertainty more thoroughly than the popular methods currently used. Indices such as the LPI, Shannon's index and Simpson's index are most commonly presented with confidence intervals created by bootstrap sampling (McRae, Deinet, and Freeman 2017; Collen et al. 2009; Loh et al. 2005; Fontana et al. 2011; Buckland et al. 2005). These confidence intervals only include uncertainty around the trends, however, the population sizes themselves are also uncertain. Using the SSM in a Bayesian context, as performed in this study, provides a platform to quantify uncertainty around population sizes that can consequently be used to establish uncertainty around biodiversity indices calculated using those population sizes such as the LPI, Shannon's and Simpson's index.

The index outputs were subject to fairly high levels of uncertainty due to the time series being relatively short. Furthermore, we are trying to estimate the observation process independently for every species which leads to high uncertainty around the population sizes. The state-space model models each individual waterbird species with its own observation error, thus when performing operations between the posterior output of individual species we experience an accumulative effect on the error values. The state-space model should ideally be altered to incorporate an observation error per counting session instead of per species. This would be a more realistic model and would, theoretically, produce smaller, and more realistic, credible intervals.

Further benefits of the state-space model is its ability to provide better approximations of the true population based on the bird counts (Auger-Méthé et al. 2021). Popular indices such as the Living Planet Index (LPI) and the Australian Threatened Bird Index, use General Additive Models

(GAMS) based on bird counts to calculate their indices (McRae, Deinet, and Freeman 2017; Bayraktarov et al. 2020). The trends calculated using GAMS are more affected by sampling variation compared to SSMs, which separate the sampling variation from the latent variation.

The SSM can also be altered to incorporate covariates into the analysis of the CWAC data. For example, we see that the effective number of waterbird species in Barberspan are decreasing over time, this is displayed in the exponentiated Shannon's index. Further investigation could be made to identify which factors are affecting the fluctuation of waterbirds in South African wetlands. To aid such an investigation, various auxiliary variables can be monitored and/or obtained such as water level, temperature, climate, foot traffic frequency, etc. These variables could be incorporated into the SSM for a deeper insight into how these variables affect waterbird population fluctuation and, consequently, the state of the wetland. No covariates were used in this dissertation as it was out of the scope of the research. Furthermore, time constraints inhibited obtaining auxiliary datasets for Barberspan.

The SSM can be altered to incorporate various variables into the model by using a multivariate auto-regressive state-space model (MARSS). A similar approach has been taken by Elghafghuf et al. (2018) to model the abundance of sea lice on Atlantic salmon over time. Incorporating temperature (or similar climate change indicators) as a covariate in the analysis of the CWAC data could be beneficial, as an overwhelming number of studies state that climate change is likely the main driver in the declining waterbird populations (Maclean et al. 2007; Kirby et al. 2008; Pavón-Jordán et al. 2015). As a start, one could use a MARSS model and incorporate average seasonal temperature as a covariate in the time series analysis of the CWAC data. This follows a similar approach followed by Oedekoven et al. (2017) in attributing changes in the distribution of species abundance of British breeding birds.

Using population estimates produced by an SSM (calculated in a Bayesian framework) to calculate biodiversity indices is a relatively new concept and literature is limited regarding this methodology. This dissertation provides valuable insight into the limitations and potential of calculating biodiversity indices in this manner.

Furthermore, this dissertation has highlighted the many benefits of using state-space models to model population dynamics and using the output to formulate biodiversity indices. SSMs prove to be flexible models that are intuitive to use in a Bayesian framework when modelling population dynamics (Auger-Méthé et al. 2021). Furthermore, using population estimates obtained from SSMs to calculate biodiversity indices produce biodiversity indices that are less affected by sampling variation.

5 Conclusion

The CWAC dataset proves to be beneficial in displaying the state of waterbirds and wetlands in South Africa. State-space time series models model both the migrant and resident population dynamics well. Using the modified LPI, exponentiated Shannon's entropy and Simpson's index in conjunction provides good insight into the state of the waterbirds and wetland in question. These three indicators can help conservationists develop more targeted approaches in their efforts to conserve waterbirds and wetlands.

We also find strong potential in the use of state-space models for modelling population dynamics and using the population estimates to calculate biodiversity indices. This method of calculating biodiversity indices provide one with the ability to provide credible intervals around the index. Furthermore, the index is less affected by sampling variation.

6 Bibliography

Aeberhard, W. H., E. Cantoni, C. Field, H. R. Künsch, J. Mills Flemming, and X. Xu. 2021. "Robust Estimation for Discrete-Time State Space Models." *Scandinavian Journal of Statistics* 48 (4): 1127–47. https://doi.org/10.1111/sjos.12482.

Ali, E., H. Ismahan, and H. Moussa. 2016. "Diversity Patterns and Seasonal Variation of the Waterbird Community in Mediterranean Wetlands of Northeastern Algeria." *Zoology and Ecology* 26 (2): 85–92. https://doi.org/10.1080/21658005.2016.1163865.

Amat, J. A., and A. J. Green. 2010. "Waterbirds as Bioindicators of Environmental Conditions." In *Conservation Monitoring in Freshwater Habitats: A Practical Guide and Case Studies*, edited by C. Hurford, M. Schneider, and I. Cowx, 45–52. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-1-4020-9278-7_5.

Auger-Méthé, M., K. Newman, D. Cole, F. Empacher, R. Gryba, A. A. King, V. Leos-Barajas, et al. 2021. "A Guide to State-Space Modeling of Ecological Time Series." *Ecological Monographs* 91 (4). https://doi.org/e01470.

Barshep, Y., B. Erni, L. Underhill, and R. Altwegg. 2017. "Identifying Ecological and Life-History Drivers of Population Dynamics of Wetland Birds in South Africa." *Global Ecology and Conservation* 12: 96–107.

Bayraktarov, E., G. Ehmke, A. Tulloch, A. Chauvenet, S. Avery-Gomm, L. McRae, B. Wintle, et al. 2020. "A Threatened Species Index for Australian Birds." *Conservation Science and Practice* 3 (2). https://doi.org/10.1111/csp2.322.

Buckland, S. T., S. R. Baillie, J. M. Dick, D. A. Elston, A. E. Magurran, E. M. Scott, R. I. Smith, P. J. Somerfield, A. C. Studeny, and A. Watt. 2012. "How Should Regional Biodiversity Be Monitored?" *Environmental and Ecological Statistics* 19 (4): 601–26. https://doi.org/10.1007/s10651-012-0202-7.

Buckland, S. T., A. E. Magurran, R. E. Green, and R. M. Fewster. 2005. "Monitoring Change in Biodiversity Through Composite Indices." *Philosophical Transactions of the Royal Society B: Biological Sciences* 360 (1454): 243–54. https://doi.org/10.1098/rstb.2004.1589.

Burgess, H. H. 1969. "Habitat Management on a Mid-Continent Waterfowl Refuge." *The Journal of Wildlife Management* 33 (4): 843–47. https://doi.org/10.2307/3799315.

Camp, R. J., K. W. Brinck, P. M. Gorresen, and E. H. Paxton. 2016. "Evaluating Abundance and Trends in a Hawaiian Avian Community Using State-Space Analysis." *Bird Conservation*

International 26 (2): 225–42. https://doi.org/10.1017/S0959270915000088.

Clarkson, B. R, A. E. Ausseil, and P. Gerbeaux. 2013. "Wetland Ecosystem Services. Ecosystem Services in New Zealand: Conditions and Trends." *Manaaki Whenua Press* Lincoln: 192–202.

Clyde, M., M. Çetinkaya-Rundel, C. Rundel, D. Banks, C. Chai, and L. Huang. 2021. *Chapter 1 the Basics of Bayesian Statistics an Introduction to Bayesian Thinking.* https://statswithr.github.io/book/the-basics-of-bayesian-statistics.html.

Collen, B., J. Loh, S. Whitmee, L. McRAE, R. Amin, and J. E. M. Baillie. 2009. "Monitoring Change in Vertebrate Abundance: The Living Planet Index." *Conservation Biology* 23 (2): 317–27. https://doi.org/10.1111/j.1523-1739.2008.01117.x.

Coro, G. 2017. "Gibbs Sampling with JAGS: Behind the Scenes." https://www.researchgate.net/publication/313905185_Gibbs_Sampling_with_JAGS_Behind_the_Scenes.

Cox, D. R., E. Spjøtvoll, S. Johansen, W. R. van Zwet, J. F. Bithell, O. Barndorff-Nielsen, and M. Keuls. 1977. "The Role of Significance Tests." *Scandinavian Journal of Statistics* 4 (2): 49–70. https://www.jstor.org/stable/4615652.

Deniau, C. P., R. Mathevet, D. Gautier, A. Besnard, G. Cornu, and S. Le Bel. 2022. "Flyways to Hell? An Empirical Assessment of Palearctic Migratory Waterbird Harvest Practices in Key Wetlands of Sahel-Sub-Saharan Africa." *Biological Conservation* 265 (January): 109419. https://doi.org/10.1016/j.biocon.2021.109419.

Dennis, Brian. 1996. "Discussion: Should Ecologists Become Bayesians?" *Ecological Applications* 6 (4): 1095–1103. https://doi.org/10.2307/2269594.

Douc, R., E. Moulines, J. Olsson, and R. van Handel. 2011. "Consistency of the Maximum Likelihood Estimator for General Hidden Markov Models." *The Annals of Statistics* 39 (1). https://doi.org/10.1214/10-AOS834.

Duffy, J. E. 2009. "Why Biodiversity Is Important to the Functioning of Real-World Ecosystems." *Frontiers in Ecology and the Environment* 7 (8): 437–44. https://doi.org/10.1890/070195.

Elghafghuf, A., R. Vanderstichel, S. St-Hilaire, and H. Stryhn. 2018. "Using State-Space Models to Predict the Abundance of Juvenile and Adult Sea Lice on Atlantic Salmon." *Epidemics* 24 (September): 76–87. https://doi.org/10.1016/j.epidem.2018.04.002.

Ellison, A. M. 2004. "Bayesian Inference in Ecology." *Ecology Letters* 7 (6): 509–20. https://doi.org/10.1111/j.1461-0248.2004.00603.x.

FitzPatrick Institute of African Ornithology. 2020. "CWAC Coordinated Waterbird Counts."
https://cwac.birdmap.africa/.

Fontana, S., T. Sattler, F. Bontadina, and M. Moretti. 2011. "How to Manage the Urban Green to
Improve Bird Diversity and Community Structure." *Landscape and Urban Planning* 101 (3): 278–85.
https://doi.org/10.1016/j.landurbplan.2011.02.033.

Gelman, A., J. Hwang, and A. Vehtari. 2014. "Understanding Predictive Information Criteria for
Bayesian Models." *Statistics and Computing* 24 (6): 997–1016.
https://doi.org/10.1007/s11222-013-9416-2.

Gelman, A., and D. B. Rubin. 1992. "Inference from Iterative Simulation Using Multiple Sequences."
Statistical Science 7 (4): 457–72. https://doi.org/10.1214/ss/1177011136.

Goodman, Steven N. 2005. "Introduction to Bayesian Methods I: Measuring the Strength of
Evidence." *Clinical Trials* 2 (4): 282–90. https://doi.org/10.1191/1740774505cn098oa.

Gregory, R. D., D. Noble, R. Field, J. Marchant, M. Raven, and D. W. Gibbons. 2003. "Using Birds
as Indicators of Biodiversity." *Ornis Hungarica* 12 (13): 11–24.

Gregory, R. D., and A. van Strien. 2010. "Wild Bird Indicators: Using Composite Population Trends
of Birds as Measures of Environmental Health." *Ornithological Science* 9 (1): 3–22.
https://doi.org/10.2326/osj.9.3.

Grooten, M., and R. E. A. Almond, eds. 2018. *Living Planet Report 2018: Aiming Higher.* Gland,
Switzerland: WWF international.

Hill, M. O. 1973. "Diversity and Evenness: A Unifying Notation and Its Consequences." *Ecology* 54
(2): 427–32. https://doi.org/10.2307/1934352.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al.
2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge."
Ecological Monographs 75 (1): 3–35. https://doi.org/https://doi.org/10.1890/04-0922.

Hooten, M. B., and N. T. Hobbs. 2015. "A Guide to Bayesian Model Selection for Ecologists."
Ecological Monographs 85 (1): 3–28. https://doi.org/10.1890/14-0661.1.

Hurlbert, S. H. 1971. "The Nonconcept of Species Diversity: A Critique and Alternative
Parameters." *Ecology* 52 (4): 577–86. https://doi.org/10.2307/1934145.

Jonsen, I. D., M. Basson, S. Bestley, M. V. Bravington, T. A. Patterson, M. W. Pedersen, R.
Thomson, U. H. Thygesen, and S. J. Wotherspoon. 2013. "State-Space Models for Bio-Loggers: A

Methodological Road Map." *Deep Sea Research Part II: Topical Studies in Oceanography*, Fourth International Symposium on Bio-logging Science, 88: 34–46. https://doi.org/10.1016/j.dsr2.2012.07.008.

Jost, L. 2006. "Entropy and Diversity." *Oikos* 113 (2): 363–75. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kellner, Ken. 2019. *JagsUI: A Wrapper Around 'Rjags' to Streamline 'Jags' Analyses.* https://CRAN.R-project.org/package=jagsUI.

Kéry, M., and M. Schaub. 2011. "Bayesian Population Analysis Using WinBUGS," 444.

Kirby, J. S., A. J. Stattersfield, S. H. M. Butchart, M. I. Evans, R. F. A. Grimmett, V. R. Jones, J. O'Sullivan, G. M. Tucker, and I. Newton. 2008. "Key Conservation Issues for Migratory Land- and Waterbird Species on the World's Major Flyways." *Bird Conservation International* 18 (S1): S49–S73. https://doi.org/10.1017/S0959270908000439.

Kopij, G., and M. Paxton. 2018. "Seasonal Changes in the Diversity and Numbers of Waterbirds in a Tropical River in Southern Africa." *Polish Journal of Ecology* 66 (3): 257–69. https://doi.org/10.3161/15052249PJE2018.66.3.006.

Lele, S. R., and B. Dennis. 2009. "Bayesian Methods for Hierarchical Models: Are Ecologists Making a Faustian Bargain?" *Ecological Applications* 19 (3): 581–84. https://www.jstor.org/stable/27645998.

Loh, J., R. E. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. "The Living Planet Index: Using Species Population Time Series to Track Trends in Biodiversity." *Philosophical Transactions of the Royal Society B: Biological Sciences* 360 (1454): 289–95. https://doi.org/10.1098/rstb.2004.1584.

Maclean, I. M. D., M. M. Rehfisch, S. Delany, and R. A. Robinson. 2007. "The Effects of Climate Change on Migratory Waterbirds Within the African-Eurasian Flyway." *BTO Research Report* 486.

Magurran, A. E. 2003. *Measuring Biological Diversity.* John Wiley & Sons.

McRae, L., S. Deinet, and R. Freeman. 2017. "The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator." *PLoS One* 12 (1): e0169156. https://doi.org/10.1371/journal.pone.0169156.

Mekonen, S. 2017. "Birds as Biodiversity and Environmental Indicator." *Journal of Natural Sciences Research* 7 (21): 28–34. https://core.ac.uk/reader/234657570.

Morris, E. K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T. S. Maier, T. Meiners, et al. 2014.

"Choosing and Using Diversity Indices: Insights for Ecological Applications from the German Biodiversity Exploratories." *Ecology and Evolution* 4 (18): 3514–24. https://doi.org/10.1002/ece3.1155.

Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, O. Gimenez, and L. Thomas. 2014. "State-Space Models." In *Modelling Population Dynamics: Model Formulation, Fitting and Assessment Using State-Space Methods*, edited by K. B. Newman, S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, O. Gimenez, and L. Thomas, 39–50. Methods in Statistical Ecology. New York, NY: Springer. https://doi.org/10.1007/978-1-4939-0977-3_3.

Niemeijer, D., and R. S. de Groot. 2008. "Framing Environmental Indicators: Moving from Causal Chains to Causal Networks." *Environment, Development and Sustainability* 10 (1): 89–106. https://doi.org/10.1007/s10668-006-9040-9.

Oedekoven, C. S., D. A. Elston, P. J. Harrison, M. J. Brewer, S. T. Buckland, A. Johnston, S. Foster, and J. W. Pearce-Higgins. 2017. "Attributing Changes in the Distribution of Species Abundance to Weather Variables Using the Example of British Breeding Birds." *Methods in Ecology and Evolution* 8 (12): 1690–1702. https://doi.org/10.1111/2041-210X.12811.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. "State–Space Models of Individual Animal Movement." *Trends in Ecology & Evolution* 23 (2): 87–94. https://doi.org/10.1016/j.tree.2007.10.009.

Pavón-Jordán, D., A. D. Fox, P. Clausen, M. Dagys, Bernard Deceuninck, K. Devos, R. D. Hearn, et al. 2015. "Climate-Driven Changes in Winter Abundance of a Migratory Waterbird in Relation to EU Protected Areas." *Diversity and Distributions* 21 (5): 571–82. https://doi.org/10.1111/ddi.12300.

Peet, R. K. 1974. "The Measurement of Species Diversity." *Annual Review of Ecology and Systematics* 5 (1): 285–307. https://doi.org/10.1146/annurev.es.05.110174.001441.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." *3rd International Workshop on Distributed Statistical Computing (DSC 2003); Vienna, Austria* 124.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Remisiewicz, M., and J. Avni. 2011. "Status of Migrant and Resident Waders, and Moult Strategies of Migrant Waders Using African Inland Wetland Habitats, at Barberspan Bird Sanctuary in South

Africa: Reports from BOU-Funded Projects." *Ibis* 153 (2): 433–35.
https://doi.org/10.1111/j.1474-919X.2011.01112_1.x.

Ritchie, H., and M. Roser. 2021. "Biodiversity." *Our World in Data*, April.
https://ourworldindata.org/living-planet-index.

Rothman. 2015. "Barberspan." South Africa's Ramsar Sites. *Barberspan.*
http://www.saramsar.com/2015/06/barberspan.html.

Secretariat of the Convention on Biological Diversity. 2020. "Convention on Biological Diversity."
Aichi Biodiversity Targets. https://www.cbd.int/sp/targets/.

Simmons, R. E., H. Kolberg, R. Braby, and B. Erni. 2015. "Declines in Migrant Shorebird
Populations from a Winter-Quarter Perspective: State-Space Models for Shorebird Trends."
Conservation Biology 29 (3): 877–87. https://doi.org/10.1111/cobi.12493.

Skowno, A. L. 2019. *National Biodiversity Assessment 2018: The Status of South Africa's Ecosystems
and Biodiversity: Synthesis Report.* Pretoria: South African National Biodiversity Institute.

Valpine, P. de. 2012. "Frequentist Analysis of Hierarchical Models for Population Dynamics and
Demographic Data." *Journal of Ornithology* 152 (S2): 393–408.
https://doi.org/10.1007/s10336-010-0642-5.

Watermeyer, K. E., G. Guillera-Arroita, P. Bal, M. J. Burgass, L. M. Bland, B. Collen, C. Hallam, et
al. 2021. "Using Decision Science to Evaluate Global Biodiversity Indices." *Conservation Biology* 35
(2): 492–501. https://doi.org/10.1111/cobi.13574.

Whittaker, R. H. 1965. "Dominance and Diversity in Land Plant Communities." *Science* 147 (3655):
250–60. https://doi.org/10.1126/science.147.3655.250.

Wilson, Howard B., Bruce E. Kendall, Richard A. Fuller, David A. Milton, and Hugh P. Possingham.
2011. "Analyzing Variability and the Rate of Decline of Migratory Shorebirds in Moreton Bay,
Australia." *Conservation Biology* 25 (4): 758–66. https://doi.org/10.1111/j.1523-1739.2011.01670.x.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. "Monitoring of Biological Diversity in Space
and Time." *Trends in Ecology & Evolution* 16 (8): 446–53.
https://doi.org/10.1016/S0169-5347(01)02205-4.

Yoccoz, Nigel G. 1991. "Use, Overuse, and Misuse of Significance Tests in Evolutionary Biology and
Ecology." *Bulletin of the Ecological Society of America* 72 (2): 106–11.
https://www.jstor.org/stable/20167258.