## Response models for key waterbird species of the Coorong

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Table 1. Details of the ten key waterbird species considered in this report. For each species, the following is shown: an estimate (and/or estimated range) of the size of the Australian population (for non-migratory

### **Respect and reconciliation**

Aboriginal people are the First Peoples and Nations of South Australia. The Coorong, connected waters and surrounding lands have sustained unique First Nations cultures since time immemorial.

The Goyder Institute for Water Research acknowledges the range of First Nations' rights, interests and obligations for the Coorong and connected waterways and the cultural connections that exist between Ngarrindjeri Nations and First Nations of the South East peoples across the region and seeks to support their equitable engagement.

Aboriginal peoples' spiritual, social, cultural and economic practices come from their lands and waters, and they continue to maintain their cultural heritage, economies, languages and laws which are of ongoing importance.

## **Executive summary**

The diverse and abundant waterbird community of the Coorong and Lakes Albert and Alexandrina has played a central role in the region being listing as a Wetland of International Importance under the Ramsar Convention. The Coorong is an important site for migratory shorebird species of the East Asian–Australasian Flyway, many species of which have suffered population declines. The Coorong also provides important foraging and breeding habitat for non-migratory waterbird species and acts as a refuge habitat for many species during summer and drought conditions. To develop ongoing management strategies that support this diverse waterbird assemblage, the response of waterbirds to physical and biological characteristics of the Coorong must be understood.

This report details the development and validation of quantitative response models for representative waterbird species that link the occupancy (i.e., probability of presence) and abundance of these species, and the proportion of birds observed foraging, to abiotic drivers (e.g., water level and salinity) and biotic drivers (e.g., density of fish, chironomid larvae, *Ruppia* seagrass community). Using data from the annual, spatially stratified Coorong waterbird monitoring program conducted in January each year, the models were formulated for ten key waterbird species: two piscivorous species (Australian pelican and fairy tern), two waterfowl (black swan and chestnut teal) and six shorebirds (common greenshank, curlew sandpiper, red-capped plover, red-necked stint, red-necked avocet and sharp-tailed sandpiper).

The maximum proportion of variation in the abundance of these species that could be explained by these models was relatively high for some species such as the Australian pelican (0.51), black swan (0.45) and common greenshank (0.48) but was lower for others including the red-necked avocet (0.16), fairy tern (0.19) and curlew sandpiper (0.20). The predictive capacity of different candidate models of waterbird abundance was evaluated by cross-validation to compare the ability of models to predict hold-out years of data which were not used for the model-fitting process. When predictive performance was measured against hold-out data aggregated to the level of the Coorong South or North Lagoon, the minimum normalised Root Mean Square Error of models with the top predictive power was reasonable at around 0.5 (approximately representing a prediction error of  $\pm$  50 % of the true species count) for the Australian pelican (0.59), chestnut teal (0.58) and common greenshank (0.39). However, predictive performance was poorer even at this lagoon level for the curlew sandpiper (1.24) and sharp-tailed sandpiper (2.26).

Given correlations between possible drivers of waterbird responses in the Coorong, and because different model formulations often yielded similar performance, we used Akaike's information criterion (AIC) to rank candidate models of species abundance and the proportion of individuals foraging, and to develop a framework for generating model-averaged predictions. First, using the top-AIC ranked model for each species we explored how waterbird responses changed with variation in important covariates. The primary drivers of waterbird abundance and proportion foraging identified were water level and salinity, while overall the biological variables tested proved to have limited explanatory power.

In the South Lagoon, the abundance and foraging rate of the piscivorous species declined with increasing salinity. Foraging by Australian pelicans also increased substantially for water levels above 1 m Australian Height Datum (AHD) in the South Lagoon. Fairy tern were more abundant when the density of small fish was higher, and more abundant in the North Lagoon when small fish were rare in the South Lagoon. Of the two waterfowl, the abundance of the black swan declined with increasing salinity, while the chestnut teal was tolerant of high salinity and a higher proportion of this species was observed foraging as the density of *Ruppia* seagrasses increased. Of the shorebirds, only the common greenshank, a generalist feeder, exhibited strong declines in abundance with increasing salinity, while curlew sandpiper, red-necked stint, sharp-tailed sandpiper and red-capped plover were most abundant at low water levels (when mudflat extent was greatest). However, foraging rate of curlew sandpiper and red-capped plover, a resident shorebird adapted to using saltpans, was highest at extreme salinities, as was foraging by red-necked avocet which can specialise on abundant brine shrimp when available. Avocet foraging was also high when water levels were low in either Coorong lagoon.

Our models also indicated that the sharp-tailed sandpiper uses the Coorong as a drought refuge, with occupancy of this species in both lagoons declining as the availability of inland water increased, while this effect was less obvious but in the same direction for black swan, red-necked avocet and red-necked stint.

To illustrate the use of these models for predicting waterbird responses under different management scenarios, we generated spatial predictions of waterbird counts (total and number foraging) in January assuming a year of average abiotic and biotic conditions. Taken together, our results demonstrate the difficulty of managing the Coorong South Lagoon for waterbird species with different foraging requirements but suggest maintaining water levels between *c*. 0.2 and 0.4 m AHD in January would produce foraging habitat useful to a range of shorebirds (including three species which likely use the Coorong as a drought refuge), while also providing some useful habitat for fairy terns, chestnut teal and black swan. Although foraging by Australian pelicans in the South Lagoon was highest when water levels exceeded this range, this species is highly mobile and pelicans breeding in the South Lagoon regularly travel to the North Lagoon to feed in January. Of course, summer water-level targets for the South Lagoon should consider impacts on other components of the Coorong system, including densities of fish and *Ruppia* seagrasses which are positively correlated with abundance and/or foraging in some key waterbird species considered here (e.g., fairy tern, common greenshank, red-necked avocet).

# **Acknowledgments**

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# **1** Introduction

### 1.1 Background

The diverse and abundant waterbird community of the Coorong, Lower Lakes (Alexandrina and Albert) and Murray Mouth (CLLMM) played a central role in the international recognition of the site as a Wetland of International Importance under the Ramsar Convention in 1985 (O'Connor et al. 2012). The site continues to support significant numbers of migratory and non-migratory waterbird species during parts of their life histories, and the wetland meets all five Ramsar Criteria pertaining to bird abundance and distribution (O'Connor et al. 2012). The site supports high bird species richness, with 307 bird species recorded within 1 km of the site (O'Connor et al. 2012); 119 of which use or are reliant on wetland habitat (Ecological Associates 2010). The site regularly supports 100,000 to 300,000 waterbirds and in some years has accounted for > 90 % of the waterbird abundance found across all six of The Living Murray icon sites within the Murray-Darling Basin (Kingsford and Porter 2008; 2009).

The CLLMM provides important habitat for threatened waterbird species that are formally listed under national and/or and state legislation (e.g., the curlew sandpiper *Calidris ferruginea*; and the fairy tern *Sterna nereis nereis*); and supports the key waterbird life-history stages of reproduction (15 species, particularly colonial- and beach-nesting birds) and moulting (56 species) (O'Connor et al. 2012; Paton 2010). The system also provides a refuge from drought for many species by supporting waterbird reproduction and/or survival when inland wetlands are dry (O'Connor et al. 2012), provides critical foraging habitat for migratory shorebirds of the East Asian–Australasian Flyway (EAAF) (Clemens et al. 2019; Clemens et al. 2016) and has regularly supported > 1% of the total flyway population size for three shorebird species (O'Connor et al. 2012). An important driver of waterbird abundance and diversity in the CLLMM is the range of wetland habitat types, including the freshwater habitats of Lakes Alexandrina and Albert, the tidal mudflats of the Murray estuary, and extensive hypermarine mudflats that are found over the Coorong lagoons, especially the South Lagoon (Phillips and Muller 2006).

The waterbird assemblage of the Coorong, and particularly the Coorong South Lagoon, is distinct from those found in other parts of the CLLMM (Paton et al. 2009; Rogers and Paton 2009), and contributes substantially to the overall abundance and diversity of waterbirds across the entire Ramsar site. Annual waterbird monitoring indicates that, in summer, the Coorong supports approximately twice as many waterbirds as the Lower Lakes (Paton et al. 2020). However, the Coorong has experienced a long-term decline in its ecological condition, primarily due to reductions in River Murray inflows. In particular, basin-wide extraction and regulation of water for human uses in combination with the period of the Millennium Drought from 2001 to 2010 resulted in very low freshwater input from the Lower Lakes for an extended period (Aldridge et al. 2017; Montazeri et al. 2011). This negatively impacted the ecological condition of the entire Coorong system, and modified the composition of the waterbird assemblage (Ecological Associates 2010; Gosbell and Grear 2005; Paton et al. 2020; Prowse 2020).

Anthropogenic modification of the Coorong's natural flow regime now sees water levels declining in the South Lagoon rapidly during spring and summer along with periods of extreme salinity (>100 g/L) and/or excessive phytoplankton and filamentous algal growth. These changes have impacted the structure and function of Coorong food webs (Ye et al. 2020) and influenced the availability of resources and foraging habitat for waterbirds in the Coorong South Lagoon (Paton et al. 2020). Although species-level responses to drought-driven conditions in the Coorong South Lagoon varied substantially, the Millennium Drought during the period 2001 to 2010 produced more 'losers' than 'winners' (Prowse 2020). While the abundance of some species in the Coorong South Lagoon has recovered in the decade since the drought broke in 2010 (e.g., black swan, great-crested grebe, grey teal, white-faced heron), other species remain at low abundance (e.g., chestnut teal, common greenshank, fairy tern) in comparison to long-term medians (Paton and Paton 2020).

Appropriate management of hydrological conditions in the Coorong to maintain resilient waterbird populations relies upon an understanding of how waterbird distribution and abundance respond to environmental conditions (including water levels and salinities). To date, most analyses based on the

historical Coorong waterbird monitoring datasets have focused on understanding long-term population trends (Gosbell and Grear 2005; Paton et al. 2009). Research to understand habitat selection based on occurrence data has also been conducted for a small number of waterbird species (O'Connor et al. 2013) as well as preliminary tracking studies to determine characteristic patterns of movement and habitat use for shorebirds (Mott et al. 2021a). However, comprehensive statistical modelling of the relationships between waterbird abundance and various abiotic drivers has not yet been undertaken.

In this final report, waterbird response models are developed and validated using data collected during annual waterbird censuses conducted by the University of Adelaide (Associate Professor David Paton) every January between 2000 and 2020. The data set spans approximately one medium term (20 year) dry-wet cycle, with the Millennium Drought and associated poor flows and rising salinities towards the end of the drought, followed by a decade of increased freshwater input. As such, over this 21-year monitoring period the Coorong has experienced extremes in physical, hydrological and chemical conditions (Paton et al. 2015), which enables the models to access data on waterbird responses to a range of conditions experienced in mid-summer over this period. Although the abundance of waterbird species in the Coorong is undoubtedly impacted by processes operating at a range of scales (Clemens et al. 2016; Prowse 2020), this report focuses on understanding the relationship between local abiotic and biotic conditions and the distribution, abundance and foraging of ten key waterbird species.

### 1.2 Aims

The aim of the Healthy Coorong, Healthy Basin (HCHB) Program Trials and Investigations (T&I) Activity 4.1 "Habitat suitability models for key waterbird species of the Coorong" was to develop response models for ten key waterbird species which were chosen to be representative of the ecology of the Coorong waterbird assemblage, and because many have undergone demonstrable declines in the Coorong South Lagoon since the year 2000 (Paton et al. 2020; Prowse 2020). These species comprise two piscivorous species (Australian pelican *Pelecanus conspicillatus*; fairy tern *Sterna nereis nereis*), two waterfowl (black swan *Cygnus atratus*; chestnut teal *Anas castanea*), and six shorebirds (common greenshank *Tringa nebularia*, curlew sandpiper *Calidris ferruginea*; red-capped plover *Charadrius ruficapillus*; red-necked stint *Calidris ruficollis*; red-necked avocet *Recurvirostra novaehollandiae*; sharp-tailed sandpiper *Calidris acuminata*). Estimated population sizes and the conservation status of each of these species is provided in Table 1.

The primary aim of this Activity is to develop waterbird response models for these species and to develop an improved understanding of the key abiotic and biotic drivers for these species. A further aim is to produce models that will allow prediction of waterbird distribution and abundance under a range of management and environmental scenarios identified by the HCHB Program. In conducting this modelling, the project will contribute to informing how hydrological management of the Coorong is expected to influence the distribution of habitat for the waterbird community.

This final technical report presents the results of work completed during the period from January 2021 to April 2022.

Table 1. Details of the ten key waterbird species considered in this report. For each species, the following is shown: an estimate (and/or estimated range) of the size of the Australian population (for non-migratory species) or EAAF population (migratory species), the federal conservation status and the South Australian conservation status.

SPECIES	AUSTRALIAN/EAAF POPULATION	FEDERAL CONSERVATION STATUS	SOUTH AUSTRALIAN CONSERVATION STATUS
Australian pelican	70,000-300,000 <sup>a</sup>	Not listed	Not listed
Black swan	100,000-1,000,000 °	Not listed	Not listed
Chestnut teal	110,000 °	Not listed	Not listed
Common greenshank	110,000 <sup>b</sup>	Not listed	Not listed
Curlew sandpiper	90,000 <sup>b</sup>	Critically Endangered	Endangered
Fairy tern (S. n. neris.)	7,450 (range 6,800–8,100) <sup>c</sup>	Vulnerable	Endangered
Red-capped plover	95,000 ª	Not listed	Not listed
Red-necked avocet	107,000 (range 25,000-1,000,000) <sup>a</sup>	Not listed	Not listed
Red-necked stint	475,000 <sup>b</sup>	Not listed	Not listed
Sharp-tailed sandpiper	85,000 <sup>b</sup>	Not listed	Not listed

<sup>a</sup> Estimate from Wetlands International (2012)

<sup>b</sup> East Asian Australasian Flyway population estimate from Hansen et al. (2022)

<sup>c</sup> Estimate from Commonwealth of Australia (2020)

# 2 Methods

### 2.1 Long-term monitoring data for key waterbird species

Annual, spatially stratified, waterbird monitoring has been conducted in the Coorong every year since 2000 (Gosbell and Grear 2005; Paton 2010; Paton et al. 2020). These surveys are conducted in January when the abundance of waterbirds using the Coorong wetlands is generally at its greatest. The annual monitoring data are spatially explicit, with the shoreline of each lagoon divided into 1 km sections, and all waterbirds are counted within the western, central, and eastern portions of each of these sections (hereafter termed 'sites'). Between 2000 and 2020, bird surveys were conducted annually at 355 sites within the Coorong lagoons and surrounds. To provide a consistent basis for spatiotemporal modelling, we retained data for 307 Coorong sites that were surveyed in every year of this 21-year timeframe (Figure 1a), which retained 98.8 % of the total waterbird abundance (across the 10 waterbird species modelled). Birds that were observed flying over the survey site were excluded from subsequent analyses.

To increase the computational feasibility of the model-fitting approach (see Section 2.3), we then aggregated waterbird species counts across *c*. 3-4 km-long stretches of shoreline whilst maintaining the western, central and eastern divisions, which yielded data for 90 derived 'locations' (Figure 1b). These locations were then stratified into eight 'zones' from north to south. We ensured that the first (most northerly) zone matched the extent of the area defined as the Murray Estuary in previous HCHB reports (Ye et al. 2019). Finally, we also stratified locations by their 'lagoon', with the Coorong South and North Lagoons defined as separated by the narrow constriction at Parnka Point (Figure 1). For each key waterbird species, the proportion of occupied locations and the total species' abundance is illustrated at the lagoon level in Figures 2 and 3.



Figure 1. (a) The survey sites from the long-term waterbird monitoring program that were retained for developing models in this report. (b) Survey locations and zones after aggregating the data prior to analysis. In (a), sites in the Coorong South and North Lagoons are separated at Parnka Point.



Figure 2. Proportion of occupied locations (see main text) for each key waterbird species in the Coorong South and North Lagoons, for the period between 2000 and 2020.



Figure 3. Abundance (i.e., total number of birds observed at the 307 surveys sites included for analysis, excluding flyovers) of each key waterbird species in the Coorong South and North Lagoons, for the period between 2000 and 2020.

### 2.2 Covariate processing and derivation

#### 2.2.1 Abiotic covariates

To prepare for the development of waterbird response models, required abiotic covariates were collated across a common  $50 \times 50$  m raster grid. The following spatial data were prepared using the R (v. 4.2) environment for statistical computing (R Core Team 2020):

**Digital elevation model.** We used a digital elevation model (DEM) representing the height (m) of substrate relative to the Australian Height Datum (AHD) for the entire Coorong (Hobbs et al. 2019). This DEM was created from three data sources and therefore has variable vertical precision across its extent (Hobbs et al. 2019) but has a nominal  $1 \times 1$  m spatial resolution (i.e., each cell represents an area of  $1 \text{ m}^2$ ). We aggregated the DEM to a 50-metre resolution by averaging all DEM values within each new 50 × 50 m cell.

**"1-dimensional" (1D) time-varying water level, salinity and water depth.** Although there are several fixed water-monitoring points distributed throughout the Coorong, data were not available for each site in every year covered by the waterbird monitoring dataset. Therefore, we used daily outputs from the 1-dimensional Coorong Hydrodynamic Model (Jöhnk and Webster 2014; Webster 2007) which consisted of daily water level (metres AHD) and salinity (ppt) at 104 sites separated by 1 km along the length of the Coorong. Given these were daily data, water-level variation in the North Lagoon due to tidal movement was not captured by the model outputs. For each point location modelled, we averaged the daily values across January each year (when the waterbird census is conducted) and then interpolated these average values across the grid cells representing the Coorong using an inverse-distance weighted interpolation function (function 'idw' in the R package 'phylin') (Tarroso et al. 2019). Hence this approach did not attempt to use the model to estimate hydrological conditions on the exact day waterbird surveys were conducted but to broadly characterise conditions experienced in January of each year, as was recommended by the Department for Environment and Water (M. Gibbs, pers. comm.). To derive an average water depth in each grid cell in January of each year, we subtracted the DEM values from the interpolated water level data.

"2-dimensional" (2D) time-varying water level, salinity and water depth. As an alternative source of hydrological data, we used outputs from the TUFLOW coarse hydrodynamic model developed for the Coorong (BMT 2021) that has been calibrated to real hydrological data from fixed monitoring sites. These outputs consisted of simulated 2-hourly observations for a spatial mesh of units across the entire Coorong and Murray Mouth for the last c. 23 years, which were then averaged over all depths and each individual day to produce a daily time series provided for analysis. Again, tidal variation was not captured by these daily data. Further, preliminary visualisation of the modelled datasets revealed many unrealistically low salinity values (particularly when simulated depths were close to zero), and that the waterbird survey sites were not completely covered by the TUFLOW mesh. Further, comparison of these 2D modelled salinity values to salinity data collected as part of The Living Murray program suggested some large differences between the model and field measurements (Appendix A, Table A.1). To facilitate cleaning of these data, we calculated the median survey date for each waterbird census and assumed the 2D model output for that day was representative of conditions experienced during each census (this approximation was considered reasonable given strong temporal correlation in the model outputs). All salinity values for simulated depths < 1 cm were then removed, as were any remaining salinity values < 1 ppt or > 300 ppt as these were deemed unrealistically extreme. In these cases, salinity values were imputed with the nearest remaining salinity estimate. Extracted and imputed values from the mesh were then rasterised to a 250-m resolution grid, and spread out to cover a larger extent using a moving-average smoother (i.e., missing values around the edge of the mesh extent were imputed in this way). As above, a raster layer of water depth was produced by subtracting the DEM values from the interpolated water level data.

**Australian "wetness" index.** Variation in the distribution and abundance of waterbird species in the Coorong at least partially depends on the distribution of available habitat across the regional and continental range of each species. Furthermore, the Coorong is believed to be used as a drought refuge by some species. Therefore, we wished to control for these effects in our analyses and also test the relationship between waterbird distribution in the Coorong and conditions elsewhere in Australia. Therefore, we digitally captured

data from a summary figure published by Krause et al. (2021) who used Digital Earth Australia's Water Observations from Space (WOfS) product to calculate the proportional contribution of surface water over time within 295,906 Australian waterbodies ranging in size from 3,125 m<sup>2</sup> to 4,820 km<sup>2</sup>. These data were available up to summer 2020, and we averaged spring and summer values to produce an Australian "wetness" index for testing within the waterbird response models.

#### 2.2.2 Spatial stratification

Each raster cell representing the Coorong lagoon and immediate surrounds was classified as belonging to a discrete location (90 levels), zone (8 levels) and lagoon (2 levels) (Figure 1). Average water level and salinity values for each location, zone and lagoon in each year were then calculated from the raster datasets detailed above. The mean water level and salinity at the lagoon level (calculated from the 1-dimensional model) are illustrated in Figure 4. Further, for each stratification level we used the water depth rasters to calculate the area (hectares) of habitat within the following depth ranges: (1) minus 5 to 5 cm, representing mudflat likely to permit foraging by shorebirds; (2) 5 to 20 cm, representing shallow water likely used for foraging by chestnut teal and red-necked avocet; and (3) 20 to 100 cm, representing foraging habitat likely used by black swans.



Figure 4. Mean water level and salinity in January for the Coorong South and North Lagoons for the period between 2000 and 2020. These values were calculated by averaging interpolated hydrological model outputs for the area of the Coorong covered by the annual monitoring program. Water level is presented as metres above the Australian Height Datum (AHD).

#### 2.2.3 Biotic covariates

Where available, we sourced time-series data on biological components of the Coorong system with likely relevance to waterbird abundance and distribution, from which we generated model-based estimates for use as covariates within the waterbird response models.

**Fish.** Catch per unit effort data from dedicated fish surveys throughout the Coorong was provided by SARDI and is documented elsewhere (Ye et al. 2020). These data covered the period from 2007 to 2020. To ensure a consistent approach to fish density estimation, we: (1) used surveys done using a seine net only; (2) removed surveys conducted within Boundary Creek (which separates Mundoo Island from Ewe Island in the Murray Estuary), and (3) removed survey sites with fewer than five years surveyed. From the retained surveys, fish density in the calendar year preceding the January census was estimated for three regions separately: the Murray Estuary (i.e., waterbird 'Zone 1'; Figure 1), and the North and South Lagoons. To generate these estimates, we used a generalised linear mixed-effect model with the random effects of year and region, assumed fish counts arose from a negative binomial distribution to account for overdispersion in these data, and used the log(number of seine nets) as the offset term to account for variable effort invested

in sampling in each site and year. Hence, output from this model produced the desired time series of expected fish caught per seine net (i.e., density) for every region and year available. Furthermore, these analyses were repeated to generate density estimates for small fish only (i.e., fish of a size suitable for predation by fairy terns), using the same definition as reported in Ye et al. (2020).

**Ruppia community.** Ruppia seagrasses provide an important structural habitat component supporting the Coorong food web (Ye et al. 2020) and comprise part of the diet of herbivorous waterfowl (Giatas et al. 2022). Winter monitoring of *Ruppia* shoot density was available over the period 2000 to 2018 and provided the greatest temporal overlap with the waterbird monitoring data available; however, the majority of non-zero shoot counts occurred in the South Lagoon. As detailed further in Jackson et al. (2022), generalised linear mixed-effect modelling was used to estimate annually averaged shoot density for the entire South lagoon. Therefore, this variable was used as a covariate for waterbird responses in the South Lagoon only.

*Chironomid larvae.* Macroinvertebrate data were collected annually from 22 transects (1 km sections) from 2001 to 2020 across the North and South Lagoons (Paton et al. 2020). Data were collected from both the east and west sides of the channel in South Lagoon transects, but only the east side of the North Lagoon. At each sampling 'site', 10-25 core samples were collected at each of four depths along a transect ('dry', 'waterline', '30 cm' and '60 cm'). However, only data from 22 transects along the east side of the Coorong were available for the full time series (summer 2001- summer 2020), and only sampling at the waterline and 30 cm depth was available. Further, only data on chironomid fly larvae were sufficiently comprehensive across both lagoons and all sampling years to allow a reasonable time series of density to be estimated. Chironomids form an important part of the diet of shorebirds in the Coorong (Paton et al. 2020) including for two focal species of this report: the red-capped plover and sharp-tailed sandpiper (Giatas et al. 2022). Chironomid DNA has also been detected in the scats of waterfowl (Giatas et al. 2022). Therefore, and as detailed further in Jackson et al. (2022), the chironomid count data were analysed using a generalised linear mixed-effect model to produce a time-series of density estimates (chironomids per core) for each lagoon.

### 2.3 Waterbird response modelling and validation

#### 2.3.1 Hurdle models for species occupancy and abundance

Since 2009, evaluation of the status of waterbird populations in the Coorong has been guided by waterbirdrelated ecological targets first specified within the CLLMM Icon Site Monitoring Plan (Maunsell 2009) and subsequently updated in Paton et al. (2017). These targets form the basis for reporting and evaluation for The Living Murray program, and South Australia's Long-term Watering Plan. For 40 waterbird species that are regularly observed in the annual Coorong waterbird (Table 1), two of these targets are currently:

- to exceed the long-term (2000-2015) median abundance in 2 out of every 3 years; and
- to exceed the 75% threshold for the long-term area of occupation and extent of occurrence.

Therefore, to link the waterbird species-level counts to this suite of spatio-temporal covariates, we adopted a hurdle modelling approach suitable for these count data. Hurdle models simultaneously model the probability of a species' presence (i.e., occupancy), and the species' abundance conditional on occurrence, as a function of covariates that can impact either of these levels. As reviewed in Prowse (2020), hurdle models were chosen because they allow simultaneous prediction of presence-absence and abundance responses, so these predictions are directly relatable to the targets detailed above.

We adopted a generalised linear mixed-effects modelling approach to fitting hurdle models for each species to accommodate both fixed and random effects and non-standard error distributions. Preliminary modelling for each species indicated that non-zero counts for many species were substantially over dispersed (i.e., variance greater than the mean). Therefore, we assumed these non-zero counts arose from a negative binomial distribution with overdispersion parameter estimated from the data and adopted the standard binomial model for the probability of species' presence. The hurdle models were fitted using function 'glmmTMB' from the R package of the same name (Brooks et al. 2017).

#### 2.3.2 Binomial models of proportion of waterbirds foraging

Since 2006, the January waterbird census has recorded the behaviour of (almost) every bird counted, which allowed the proportion of foraging individuals to be linked to variation in abiotic and biotic conditions. We therefore developed binomial mixed-effects models for this response variable, using data at the location level, which were again fitted using 'glmmTMB'.

#### 2.3.3 Candidate model sets

A candidate set of hurdle and binomial foraging models was developed for each species (Tables 1 and 2). Depending on the waterbird species, different combinations of the following fixed effects were tested: (1) a lagoon effect; (2) water level at each location or averaged across each lagoon (both the 1D and 2D model output were tested, but never included in the same models); (3) salinity at each location or averaged across each lagoon (from the 1D or 2D model output); area of habitat within certain depth ranges (-5 to 5 cm, 5 to 20 cm, 20 to 100cm) at each location or summed across each lagoon (from the 1D or 2D model output); (4) density of all fish or small fish only (fish per seine net); (5) density of chironomid larvae (per core); and (6) density of *Ruppia* seagrass shoots (per core, South Lagoon only). Given differences in the utilised foraging depths between waterbird species (O'Connor et al. 2015), we decided *a priori* to consider the habitat area within the -5 to 5 cm depth range as a covariate for five shorebird species that preferentially feed on exposed or shallow mudflat (curlew sandpiper, common greenshank, red-capped plover, red-necked stint, sharp-tailed sandpiper), areas within the 5 to 20 cm depth range as covariates for chestnut teal and red-necked avocet, and habitat areas within the 20 to 100 cm depth range for black swan.

To allow quadratic non-linearity in the fixed effects of water level and salinity, we constructed second-order orthogonal polynomials from the raw covariate values using the function 'poly' in R package 'stats' and used these derived variables in the model-fitting process.

To account for unexplained spatiotemporal correlation in waterbird responses, all models were initially fitted with a completely specified random effects structure that included the follow random terms: year, zone, location, lagoon × year, and zone × year. In the case of the hurdle models, this same model structure (fixed and random effects) was adopted for both the hurdle (presence-absence) and abundance model components. Where models proved too complex to permit convergence, the variance components associated with each random effect was examined, and terms with the lowest estimated variance were dropped from the model recursively until convergence was obtained.

Note that, due to the differing temporal availability of the covariate datasets, we adopted a restricted dataset for each species to ensure a consistent basis for model comparison. Specifically, we only modelled data from 2007 to 2020 for the two piscivores (Australian pelican and fairy tern) which reflected the period over which fish density estimates were available. For the remaining eight key waterbird species, we modelled data for the period 2001 to 2019 over which *Ruppia* and chironomid density estimates could be calculated.

#### 2.3.4 Model assessment and cross-validation

To assess the performance of candidate hurdle and foraging models fitted to the location-level data for each species, we considered Akaike's Information Criterion (AIC) which considers model fit but adds a penalty term that increases with increasing model complexity (lower AIC values indicate higher ranked models).

As a measure of the structural goodness-of-fit for the hurdle models, we also calculated the coefficient of determination ( $R^2$ ) to quantify the proportion of the variance in the count data that was explained by each candidate model. To provide a detailed assessment of the predictive capacity of each candidate hurdle model, we used temporal-block cross-validation. Briefly, we constructed new model-training datasets by removing data for each available year in turn and evaluated the ability of models to predict these hold-out years of data when they were excluded from the model-fitting stage. Specifically, we calculated the mean cross-validation deviance (i.e., the average of -2 × the log-likelihood of the hold-out count data assuming the

parameters estimated by the model) where lower values indicate models producing better predictions. Further, we calculated the Normalised Root Mean Square Error (NRMSE) for each cross-validation fold as

$$NRMSE = \frac{\sqrt{\frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{n}}}{\frac{n}{\overline{y}}}$$

where *n* is the number of hold-out values, *y* is the hold-out data vector and  $\hat{y}_i$  is the vector of predicted values from the model. The mean NRMSE across the cross-validation folds provides a measure of the expected variance of the predictions as a proportion of the hold-out sample mean.

Since the distribution and abundance of waterbirds in the Coorong is likely affected by processes operating from the location to lagoon scales (Paton et al. 2015; Prowse 2020), we conducted the cross-validation procedure for candidate models fitted to the location-level data and also for the same model formulations but fitted to the data aggregated to the zone and lagoon levels. This approach evaluated whether modelling the waterbird counts at a fine spatial resolution improved predictions at larger spatial scales. To increase the computational efficiency of this approach, models were run in parallel on the University of Adelaide's High Performance Computing Cluster.

#### 2.3.5 Model selection and partial response curves

Candidate hurdle and foraging models were ranked by AIC and the top-ranked model was used to explore waterbird responses to important environmental and biotic drivers. The selected models were used to produce partial response curves for each species illustrating the probability of species' presence and abundance conditional on presence (assuming an 'average' location) as a function of these covariates.

#### 2.3.6 Waterbirds predictions

To illustrate the use of these models for predicting waterbird responses under different management scenarios, we generated spatial predictions of waterbird counts (total and number foraging) in January assuming a year of average abiotic and biotic conditions. To account for uncertainty in the true models of waterbird responses, a model-averaging approach was used to generate these example predictions. That is, predictions were generated from all fitted models and then those predictions were combined into a single prediction by weighting the contribution of each model using AIC weights.

## **3 Results**

### 3.1 Hurdle model fit and predictive performance

For all species, the top few AIC-ranked models from the candidate set of hurdle models included a random effect of location, illustrating that allowing waterbird presence and abundance to vary at a fine spatial resolution improved the fit of the models to the complete datasets (Appendix B, Table B.1). However, the structural fit of the models varied substantially between the 10 key waterbird species (Table B.1). R<sup>2</sup> for the top AIC-ranked model (i.e., the proportion of variation explained by the model) was relatively high for some species including the Australian pelican (0.51), common greenshank (0.48) and black swan (0.45). R<sup>2</sup> values were lower for other species including the red-necked avocet (0.16), fairy tern (0.19) and curlew sandpiper (0.20). Note that these R<sup>2</sup> values include the contribution of the random effects to model fit, and that they are calculated for data at the location level. After aggregating fitted values from location-level models to the lagoon level, however, model fit is substantially improved.

Reflecting the previous point, the predictive performance of the waterbird response models (as measured by cross-validation) was low (i.e., mean NRMSE values were high) at the location level, but increased when validation was conducted at the zone and lagoon levels (Figure 5). For eight of the ten species considered,

models developed using the location-level data produced better cross-validation results (i.e., lower mean NRMSE values) when validation was conducted at the zone or lagoon level (Figure 5). The two exceptions were the black swan and the fairy tern, for which models developed using survey counts aggregated to the zone level could produce marginally improved cross-validation results at these levels (Figure 5).

For cross-validation performed against hold-out data aggregated to the lagoon level, the minimum recorded mean NMRSE was relatively low at around 0.5 (approximately representing a prediction error of  $\pm$  50 % of the true species count) for the Australian pelican (0.59), chestnut teal (0.58) and common greenshank (0.39). However, predictive performance was poor even at this lagoon level for the curlew sandpiper (1.24) and sharp-tailed sandpiper (2.26).

### 3.2 Model selection and partial response curves

The primary drivers of waterbird abundance and foraging identified were abiotic drivers - water level and salinity - while overall the biological variables tested proved to have limited explanatory power. Model rankings are presented in Appendix B for the hurdle models (Table B.1) and foraging models (Table B.2), and partial response curves for the top AIC-ranked models for each species are illustrated in Figures 6 to 22.

#### 3.2.1 Piscivores

In the South Lagoon, the abundance and foraging rate of the Australian pelican declined strongly with increasing salinity in the South Lagoon, while foraging by this species also increased sharply for water levels above 1 m AHD (Figures 6 & 7). A negative impact of high salinity on fairy terns was also evident, but confidence intervals on response curves were generally wide for this species (Figures 8-9). Although positive relationships between the density of small fish and fairy tern occupancy/abundance were estimated (Figure 8), confidence intervals for these effects overlapped zero. There was a strong negative relationship between fairy tern occupancy/abundance in the North Lagoon and small fish density in the South Lagoon.

#### 3.2.2 Waterfowl

The abundance of the black swan declined with decreasing water level and increasing salinity in both Coorong lagoons (Figure 10), and although the top-AIC ranked hurdle model included *Ruppia* shoot density in the South Lagoon for this species, confidence intervals overlapped zero for these terms. The proportion of black swans foraging in the South Lagoon declined substantially with decreases in the availability of the habitat within the 20 to 100 cm depth range, whereas foraging also decreased with increasing chironomid density in the South Lagoon, potentially due to a positive correlation between chironomid abundance and unfavourable conditions for swans (Figure 11).

In contrast, chestnut teal abundance and foraging behaviour was more tolerant of high salinities, and while the abundance of this species in the South Lagoon was relatively unresponsive to water level, occupancy and abundance in the North Lagoon dropped substantially as water levels rose (Figure 12). A positive relationship between *Ruppia* shoot density and the occupancy/abundance of chestnut teal was estimated (but again parameter confidence intervals overlapped zero). However, the proportion of teal foraging increased strongly with increasing *Ruppia* shoot density (estimate [95% confidence interval]: 0.32 [0.07, 0.57], Figure 13).



Figure 5. Predictive performance of the hurdle models fit and validated against waterbird count data aggregated to different levels (i.e., the location, zone or lagoon level). Predictive performance is quantified via cross-validation, as the mean Normalised Root Mean Square Error (NRMSE) calculated across hold-out years of data. Results are shown for models producing the lowest mean NRMSE within each model level × cross-validation level combination. The dotted horizontal guideline indicates an NRSME of 1, an arbitrary value chosen to highlight variation in the models' ability to predict the abundance of different species.

#### 3.3.1 Shorebirds

Of the shorebirds, only the common greenshank, a generalist feeder, exhibited strong declines with increasing salinity, while curlew sandpiper, red-capped plover, red-necked stint and sharp-tailed sandpiper were most abundant at low water levels. However, foraging behaviour by curlew sandpiper and red-capped plover was most intense in the South Lagoon at intermediate water levels (c. -0.2 to 0.6 m AHD). Foraging by the red-capped plover was highest at extreme salinities (Figure 19), as was foraging by red-necked avocet (Figure 20). Avocet foraging was also high when water levels were low in either Coorong lagoon (Figure 21) and increased alongside the density of *Ruppia* shoots in the South Lagoon (estimate: 0.37 [0.16,0.59]).

#### 3.3.2 Influence of water availability across Australia

Our models also indicated that the sharp-tailed sandpiper uses the Coorong as a drought refuge, with occupancy of this species in both lagoons declining as the availability of inland water increased, while this effect was less obvious but in the same direction for black swan, red-necked avocet and red-necked stint (Figure 26).

#### **3.3.3 Model-averaged predictions**

Model-averaged spatial predictions of waterbird counts (total and number foraging) in January assuming a year of average conditions demonstrated that the model outputs captured important features of waterbird responses in the Coorong (Figures 27 and 28). For example, predictions for Australian pelican correctly identified the location of high abundance over North Pelican Island in the South Lagoon, where pelicans aggregate to breed through spring and summer (Figure 28a). Despite this, the foraging model for this species correctly predicted that most pelican foraging occurs within the Murray Estuary and adjacent to the barrage structures. Similarly, the models captured the high abundance and foraging rate of many shorebird species in the shallow mudflats around Parnka Point and nearby islands.



Figure 6. Summary of the selected hurdle model for the Australian pelican. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table 1.



Figure 7. Summary of the selected foraging model for the Australian pelican. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 6.



Figure 8. Summary of the selected hurdle model for the fairy tern. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 9. Summary of the selected foraging model for the fairy tern. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. Missing values in (a) reflect the fact that no fairy terns were observed at the included South Lagoon sites in January 2007, 2009 and 2011. For more details on the selected model, see Table 2. All other details are as for Figure 8.



Figure 10. Summary of the selected hurdle model for the black swan. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 11. Summary of the selected foraging model for the black swan. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. Missing values in (a) reflect the fact that no black swans were observed at the included South Lagoon sites in January 2009 and 2010. For more details on the selected model, see Table 2. All other details are as for Figure 10.



Figure 12. Summary of the selected hurdle model for the chestnut teal. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 13. Summary of the selected foraging model for the chestnut teal. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 12.



Figure 14. Summary of the selected hurdle model for the common greenshank. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 15. Summary of the selected foraging model for the common greenshank. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 14.



Figure 16. Summary of the selected hurdle model for the curlew sandpiper. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 17. Summary of the selected foraging model for the curlew sandpiper. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 16.



Figure 18. Summary of the selected hurdle model for the red-capped plover. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 19. Summary of the selected foraging model for the red-capped plover. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 18.



Figure 20. Summary of the selected hurdle model for the red-necked avocet. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 21. Summary of the selected foraging model for the red-necked avocet. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. Missing values in (a) reflect the fact that no red-necked avocets were observed at the included South Lagoon sites in January 2009. For more details on the selected model, see Table 2. All other details are as for Figure 20.



Figure 22. Summary of the selected hurdle model for the red-necked stint. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 23. Summary of the selected foraging model for the red-necked stint. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 22.



Figure 24. Summary of the selected hurdle model for the sharp-tailed sandpiper. (a) Fit of the model (lines represent the model estimate, ribbons represent 95% confidence intervals) to the proportion of occupied locations (points) over time for the Coorong South and North Lagoons; (b) fit of the the model to the raw abundance counts; and (c) partial response curves showing changes in the expected probability of presence and abundance (for an 'average' location) as a function of spatiotemporal covariates. For more details on this selected model, see Table B.1.



Figure 25. Summary of the selected foraging model for the sharp-tailed sandpiper. (a) Fit of the model to the proportion of birds foraging over time for the Coorong South and North Lagoons; and (b) partial response curves showing changes in the expected proportion foraging as a function of spatiotemporal covariates. For more details on the selected model, see Table 2. All other details are as for Figure 24.



Figure 26. Effect of the Australian Wetness Index on the probably of presence for each key waterbird species in the Coorong South and North Lagoon. Negative estimates indicate probability of presence decreases for a species as the water availability increases across Austalia.





(c) Black Swan





600

400

200

(e) Common Greenshank





75

50

25

1600

1200

800

400

#### (g) Red-capped Plover



#### (i) Red-necked Stint



(b) Fairy Tern



15

10

5

100

50

#### (d) Chestnut Teal



(f) Curlew Sandpiper



#### (h) Red-necked Avocet



#### (j) Sharp-tailed Sandpiper



Figure 27. Spatial abundance predictions from the selected hurdle model for each key waterbird species. These predictions assume a hypothetical census during a period of average conditions (i.e., all covariates set to their mean values). Points represent the centroid of each defined location (encompassing three or four 1-km transect segments), and point size and shading illustrate the expected species count in January under these conditions.





#### (c) Black Swan



## Ī

20

10

20

10

#### (e) Common Greenshank



## - 10 - 5

60

40

20

500

400

300

200

100

#### (g) Red-capped Plover



#### (i) Red-necked Stint



#### (b) Fairy Tern



#### (d) Chestnut Teal



#### (f) Curlew Sandpiper



#### (h) Red-necked Avocet



#### (j) Sharp-tailed Sandpiper



Figure 28. Spatial predictions of the number of foraging individuals for each key waterbird species. These predictions assume a hypothetical census during a period of average conditions (i.e., all covariates set to their mean values). Points represent the centrold of each defined location (encompassing three or four 1-km transect segments), and point size and shading illustrate the expected number of foraging birds in January under these conditions.

# **4** Discussion

### 4.1 Correlates of waterbird occupancy, abundance and foraging

For nine of the ten key waterbird species, the hurdle model selected based on AIC rankings included the fixed effects of water level and salinity. For the two piscivorous species, foraging rates were suppressed when water level dropped too low. The effect of salinity was clearest for the Australian pelican, with estimates of occupancy and abundance both declining sharply with increasing salinity, whilst the salinity response was in the same direction but less clear for the fairy tern. It is probable that the salinity relationships for these piscivorous species reflect the negative impact of periods of extremely high salinity on the abundance and distribution of their fish prey (Wedderburn et al. 2008; Ye et al. 2020).

The two waterfowl species showed subtly different responses. The abundance of the black swan increased with increasing water level, and declined with increasing salinity, in both Coorong lagoons, while the proportion of black swans foraging in the South Lagoon declined substantially with the decreases in the availability of habitat within the 20 to 100 cm depth range. This is as expected, since black swans do not usually forage beyond *c*. 1 metre of water depth (Marchant and Higgins 1990). In contrast, chestnut teal were more tolerant of high salinities, and the occupancy and abundance of this species in the North Lagoon dropped substantially as water levels rose, probably reflecting the loss of relatively shallow dabbling habitat (Figure 12). The proportion of teal foraging increased strongly with increasing *Ruppia* shoot density in the South Lagoon, and recent DNA metabarcoding of chestnut teal scats has confirmed *Ruppia* seagrass in the diet of this herbivore (Giatas et al. 2022).

The most obvious relationship for shorebirds was an increase in occupancy and abundance when water levels were low (most clearly for curlew sandpiper, red-capped plover, red-necked stint and sharp-tailed sandpiper) or the availability of shallow foraging habitat was high (red-necked avocet). Partial response curves generally indicated a monotonic decrease in the probability of location occupancy and abundance with increasing water level for these species. This is not unexpected for shorebirds that forage in shallow water, and agrees with results from other aspects of the HCHB T&I Component 4 waterbird project which suggest that availability of mudflat habitat is the primary driver of shorebird abundance in the Coorong (Jackson et al. 2022). However, foraging behaviour by curlew sandpiper and red-capped plover was most intense in the South Lagoon at intermediate water levels (c. -0.2 to 0.6 AHD). A decline in foraging habitat at very high water levels makes sense for these species because food availability is maximised on shallow mudflats which are lost from the Coorong when water levels rise too high (Prowse 2020). For example, although significant freshwater input in spring 2010 promoted the recovery of some elements of the Coorong system following extended drought conditions, the Coorong mudflats were inundated to such an extent that wading waterbirds could not use them (Aldridge et al. 2017; Paton et al. 2015; Waycott et al. 2020; Ye et al. 2019; Ye et al. 2020). This is presumably one driver of the low occupancy and abundance of many waterbird species in January 2011 (Figures 3 and 4) when Coorong water levels were unusually high (Figure 5). The proportion of red-capped plover foraging also increased with salinity in both lagoons; however, this relationship might reflect a correlation between salinity and the availability of mudflat, since red-capped plovers consume a high proportion of terrestrial arthropods which will have limited relationship with salinity.

Previous waterbird research for the Coorong has assumed that, at the scale of the entire Coorong system, the proportion of birds foraging should increase as habitat quality decreases. Under this view, the proportion of birds foraging reflects how much time must be allocated to foraging and is therefore negatively related to the ease with which individuals can acquire food (Paton et al. 2015; Paton et al. 2020). As such, a threshold of no more than 70 % of individuals foraging has been proposed as a useful target to guide management (Paton et al. 2015; Paton et al. 2020). In apparent contrast, our foraging-rate models generally demonstrate positive relationships between the proportion of birds foraging rate in red-necked avocets increased at lower water levels (when the availability of shallow wading habitat is higher) and higher salinities (when brine shrimp can proliferate). While our results might seem to contradict the previous hypothesis, it is important to note that the foraging-rate models were developed at a location scale. At this scale, it is likely that foraging rates increase where habitat quality is higher (e.g., food is more available) because waterbirds are mobile and can select where to invest energy into foraging. Therefore, we suggest that the foraging-rate models

could be used to consider how habitat quality at a fine spatial scale might change under different management scenarios, but do not preclude the possibility that foraging rates across the whole system might increase with overall decreases in foraging habitat quality.

Taken together, our results demonstrate the difficulty in managing the Coorong South Lagoon for multiple waterbird species that have different foraging requirements. However, our models suggest maintaining water levels between c. 0.2 and 0.4 m AHD in January would produce foraging habitat useful to a range of shorebirds (including three species which likely use the Coorong as a drought refuge), while also providing some useful habitat for fairy terns, chestnut teal and black swan. It is also noteworthy that, in January, fairy terns are somewhat tied to suitable nesting habitat (primarily on Coorong islands) so their distribution is bound by proximity to these nesting locations. However, fairy terns successfully bred in the Coorong South Lagoon in the 2015/2016 breeding season when the lagoon averaged water levels reached -0.42 m AHD (Paton et al. 2016), and the water depths in the range 0.2 to 0.4 m are sufficient to afford protection from foxes which can access and predate nesting colonies on South Lagoon islands if water levels fall too low. Although foraging by Australian pelicans in the South Lagoon was highest when water levels exceeded 0.4m AHD, this species is highly mobile and pelicans breeding in the South Lagoon regularly travel to the North Lagoon to feed in January (Mott et al. 2022). Of course, summer water-level targets for the South Lagoon should consider impacts on other components of the Coorong system, including densities of fish and Ruppia seagrasses which are positively correlated with abundance and/or foraging in some key waterbird species (e.g., fairy tern, common greenshank, red-necked avocet).

Given the abundance of waterbird species in the Coorong is impacted by processes operating at a range of scales (Clemens et al. 2016; Prowse 2020), it is important to consider covariates relating to conditions beyond the Coorong itself (e.g., proxies of wetland availability in the broader landscape). Waterbirds are highly mobile, so it is feasible that some species preferentially inhabit the Coorong during drought conditions when wetland availability elsewhere is low, which could contribute to the observed negative relationship between occupancy/abundance and water level for some species. Our models provide some evidence that the sharp-tailed sandpiper uses the Coorong as a drought refuge, with occupancy of this species in both lagoons declining as the availability of inland water increased. Our results also suggest the same could be true for three other species: black swan, red-necked avocet and red-necked stint.

For migratory shorebirds, off-site impacts such as the degradation of breeding and foraging habitat at international sites along the EAAF (particularly within East Asia's Yellow Sea region) are also impacting flyway population sizes (Bamford et al. 2008) and will naturally have flow-on impacts on the waterbird abundance recorded in the Coorong. For example, global declines in the population of curlew sandpiper are reflected by decreasing trends for this species in Australia generally (Clemens et al. 2019; Clemens et al. 2016) and the Coorong specifically (Paton et al. 2020). Curlew sandpiper abundance in the Coorong has not improved since the Millennium Drought ended in 2010 (Figure 4) and it is likely that statistical relationships with local environmental conditions are confounded by the global population trend for this species.

Our study has demonstrated that: (1) models with the best predictive performance always included a random effect of location; and (2) the predictive performance of response models was lowest at the location level but higher at the zone and lagoon levels. Together, these results suggest that fine-scale spatial variation in habitat is an important driver of waterbird abundance, but also that obtaining data on the covariates important to waterbird responses at fine temporal and spatial scales presents a substantial challenge. For shorebirds in particular, one important component that cannot be captured by the response modelling is the high variability in Coorong water levels over short time-scales, in that water levels change quickly and sometimes dramatically in response to a complex interplay of factors including wind speed and direction, inputs of water over the barrages, water surges from storm events and tidal fluctuations (Gibbs et al. 2017). Importantly for shorebirds, water level and water-level history (i.e., whether the waterline is advancing or receding) both affect the accessibility of macroinvertebrate prey, such that site-level habitat suitability for shorebirds probably varies substantially over daily and even hourly timescales. Such variability cannot be captured by the waterbird response models detailed in this report; however, consistent location effects can be usefully incorporated as spatial random effects to improve predicted waterbird abundances.

### 4.2 Future directions and linkages

The models presented for waterbird species occupancy, abundance and foraging rate can be used to generate quantitative predictions of waterbird responses under scenarios. In particular, these models can be used in combination with scenario tests being developed with hydro-ecological models to test the likely responses of waterbird species under different management and infrastructure scenarios. As detailed above, however, the models presented in this report are unable to consider fine-scale temporal variation in habitat suitability for the key waterbird species. Moreover, abundance is only one of multiple measures used to assess waterbird habitat quality (Mott et al. 2021b); since an increase in waterbird abundance does not necessarily indicate local habitat improvement in the Coorong, it follows that abundance should not be used as the sole index of habitat quality. The abundance modelling detailed in this report is therefore complemented by separate models for foraging rate, as well as other aspects of HCHB T&I Component 4's project plan. Specifically, under Activity 4.2 (Measures of habitat quality for Key Waterbird Species), fieldwork has investigated the response of shorebirds to fine-scale habitat variation at sites throughout the Coorong North and South Lagoons, through the simultaneous assessment of multiple variables including waterbird abundance, macroinvertebrate sampling at shallow depths near the waterline (where shorebirds can access prey), foraging observations, body-condition assessments and measurements of abiotic conditions (salinity, water level, wind). The results from these studies are being reported coincidentally in Jackson et al. (2022).

# List of shortened forms and glossary

AIC	Akaike's Information Criterion, a metric for comparing different statistical models fitted to the same dataset
AHD	Australian Height Datum, the official reference surface for vertical mapping, which passes through mean sea level
CLLMM	Coorong, Lower Lakes (Alexandrina and Albert) and Murray Mouth
DEM	Digital Elevation Model
EAAF	EAAF East Asian–Australasian Flyway
Hold-out data	Data that is withheld from the model-fitting phase, and used for validation of the model predictions.
Hypermarine	Having a salinity exceeding that of marine (sea) water.
Fixed effect	A variable in a statistical model for which a single fixed value is estimated.
Key Waterbird Species	Waterbirds selected as Key Waterbird Species for the purposes of Component 4 of the Healthy Coorong, Healthy Basin Program's Trials and Investigations Project. The ten Key Waterbird Species (sharp-tailed sandpiper, red-necked avocet, chestnut teal, Australian pelican, red- necked stint, curlew sandpiper, common greenshank, red-capped plover, fairy tern, and black swan) were selected because each represents a different ecological group (e.g., foraging guild, migratory strategy, abundance) within the Coorong.
Millennium Drought	An Australian drought which impacted the Murray-Darling Basin over the period 1996-2010, and substantially impacted the Coorong over the period 2001-2010.
Monotonic	Used to describe a function that never decreases (i.e., increases or remains stable over its whole range) or never increases (i.e., decreases or remains
	stable over its whole range).
NRMSE	stable over its whole range). Normalised Root Mean Square Error
NRMSE Partial response curve	stable over its whole range). Normalised Root Mean Square Error The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant.
NRMSE Partial response curve Piscivorous waterbirds	stable over its whole range). Normalised Root Mean Square Error The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant. These species are solely or primarily fish-eating and have specialised bills and/or talons for catching underwater prey.
NRMSE Partial response curve Piscivorous waterbirds Random effect	stable over its whole range). Normalised Root Mean Square Error The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant. These species are solely or primarily fish-eating and have specialised bills and/or talons for catching underwater prey. A variable in a statistical model which is assumed to be random; that is, derived from a probability distribution defined by parameters that are also estimated by the model.
NRMSE Partial response curve Piscivorous waterbirds Random effect <i>Ruppia</i> community	<ul> <li>stable over its whole range).</li> <li>Normalised Root Mean Square Error</li> <li>The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant.</li> <li>These species are solely or primarily fish-eating and have specialised bills and/or talons for catching underwater prey.</li> <li>A variable in a statistical model which is assumed to be random; that is, derived from a probability distribution defined by parameters that are also estimated by the model.</li> <li>The multi-species assemblage that has become established across the southern Coorong and includes <i>Ruppia tuberosa</i>, <i>Althenia cylindrocarpa</i> along with an as yet unresolved species of <i>Ruppia</i>.</li> </ul>
NRMSE Partial response curve Piscivorous waterbirds Random effect <i>Ruppia</i> community Shorebirds	<ul> <li>stable over its whole range).</li> <li>Normalised Root Mean Square Error</li> <li>The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant.</li> <li>These species are solely or primarily fish-eating and have specialised bills and/or talons for catching underwater prey.</li> <li>A variable in a statistical model which is assumed to be random; that is, derived from a probability distribution defined by parameters that are also estimated by the model.</li> <li>The multi-species assemblage that has become established across the southern Coorong and includes <i>Ruppia tuberosa</i>, <i>Althenia cylindrocarpa</i> along with an as yet unresolved species of <i>Ruppia</i>.</li> <li>These bird species forage on intertidal areas and/or the margins of wetlands, and typically they do not swim. Australia is home to nonmigratory shorebirds which remain in Australia year-round, and also provides habitat for migratory shorebirds of the East Asian–Australasian Flyway, which inhabit the northern hemisphere in the austral winter and migrate to the southern hemisphere for the austral summer.</li> </ul>
NRMSE Partial response curve Piscivorous waterbirds Random effect <i>Ruppia</i> community Shorebirds	<ul> <li>stable over its whole range).</li> <li>Normalised Root Mean Square Error</li> <li>The modelled change in a response variable as a function of a single covariate, while all other covariates are held constant.</li> <li>These species are solely or primarily fish-eating and have specialised bills and/or talons for catching underwater prey.</li> <li>A variable in a statistical model which is assumed to be random; that is, derived from a probability distribution defined by parameters that are also estimated by the model.</li> <li>The multi-species assemblage that has become established across the southern Coorong and includes <i>Ruppia tuberosa</i>, <i>Althenia cylindrocarpa</i> along with an as yet unresolved species of <i>Ruppia</i>.</li> <li>These bird species forage on intertidal areas and/or the margins of wetlands, and typically they do not swim. Australia is home to nonmigratory shorebirds which remain in Australia year-round, and also provides habitat for migratory shorebirds of the East Asian–Australasian Flyway, which inhabit the northern hemisphere in the austral winter and migrate to the southern hemisphere for the austral summer.</li> <li>Trials and Investigations</li> </ul>

have webbed feet and a flattened bill for crushing their plant- or algaebased foods.

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## **Appendix A – Comparison of modelled and field salinity values**

Table A.2. Comparison of modelled salinity values (from the 2-dimensional TUFLOW model) and field salinity measurements collected as part of The Living Murray Research program, at 17 waterbird survey sites. Modelled salinity values are generally higher than the field measurements over the period between 2001 and 2014, but lower thereafter.



## **Appendix B – Model selection tables**

Table B.3. Evaluation of the candidate hurdle models for each of the ten key waterbird species, using models fitted to location-level bird count data which were assessed with Akaike's Information Criterion (AIC) and temporal-block cross-validations. Shown for each model are: the number of parameters fitted (k); the log-likelihood of the model (logLik), AIC for which lower numbers indicate higher ranked models; the change in AIC relative to the top AIC-ranked model for each species ( $\Delta$ AIC); the coefficient of determination (R<sup>2</sup>), the mean predictive deviance obtained by cross-validation (CV Deviance) and its standard error calculated across the cross-validation folds; the mean normalised Root Mean Square Error (RMSE) obtained by cross-validation and calculated at the location level (Location NRMSE), the mean NRMSE at the zone level (Zone RMSE), and the mean NRMSE at the lagoon level. In the model formula, second-order polynomial terms for covariate *X* are denoted poly(*X*, 2). For brevity, only the top ten AIC-ranked candidate models are presented and the random-effect structure is omitted from the model specification. For each species, the selected model with the lowest AIC score is shown in bold.

Species	Model	k	logLik	AIC	ΔΑΙC	R <sup>2</sup>	CV Deviance [SE}	Location NRMSE [SE]	Zone NRMSE [SE]	Lagoon NRMSE [SE]
Australian pelican	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2)	28	-4503.7	9063.4	0.0	0.512	0.62 [0.05]	10.11 [1.1]	3.15 [0.33]	1.17 [0.12]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:All fish	32	-4500.9	9065.8	2.5	0.509	0.66 [0.06]	10.52 [1.43]	3.34 [0.35]	1.25 [0.12]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:All_fish + NorthLagoon:All_fish_SL	36	-4499.7	9071.3	7.9	0.506	0.66 [0.07]	10.59 [1.5]	3.34 [0.34]	1.25 [0.12]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:All_fish + NorthLagoon:All_fish_SL	36	-4504	9079.9	16.6	0.507	0.66 [0.07]	9.33 [0.44]	3.31 [0.34]	1.21 [0.13]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:All_fish	33	-4509	9084.0	20.6	0.516	0.69 [0.08]	9.25 [0.44]	3.26 [0.35]	1.25 [0.13]
	Lagoon:AustWeiness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:All_fish	35	-4508	9086.1	22.7	0.517	0.74 [0.08]	9.4 [0.46]	3.35 [0.34]	1.3 [0.12]
	$Lagoon: Aust Wetness + Lagoon + Lagoon: poly(Lagoon_Waterlevel_1D, 2) + Lagoon: poly(Lagoon_Salinity_1D, 2$	31	-4515.6	9093.2	29.8	0.505	0.64 [0.07]	18.8 [9.35]	3.15 [0.36]	1.16 [0.12]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Salinity_1D,2)	24	-4523.1	9094.3	30.9	0.519	0.6 [0.06]	9.49 [0.53]	3.03 [0.37]	1.08 [0.12]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:All fish + NorthLagoon:All fish SL	37	-4510.9	9095.9	32.5	0.502	0.7 [0.09]	19.34 [9.95]	3.39 [0.4]	1.27 [0.15]
	$Lagoon: AustWetness + Lagoon + Lagoon: poly(Lagoon_Salinity_1D, 2) + Lagoon: All_fish$	28	-4521.1	9098.3	34.9	0.519	0.61 [0.09]	9.34 [0.41]	3.1 [0.39]	1.11 [0.15]
Fairy tern	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Small_fish + northLagoon:southLagoon.S fish1	28	-1350.2	2756.4	0.0	0.189	0.86 [0.07]	4.12 [0.25]	5.13 [0.44]	1.67 [0.13]
	Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Small_fish + northLagoon:SouthLagoon.S_fish1	30	-1349.4	2758.9	2.5	0.187	0.86 [0.08]	4.16 [0.25]	5.16 [0.46]	1.67 [0.14]
	$Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2)$	23	-1356.6	2759.3	2.9	0.171	0.99 [0.08]	4.54 [0.41]	5.22 [0.44]	1.75 [0.13]
	Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2)	26	-1356.2	2764.5	8.1	0.179	1.01 [0.11]	4.25 [0.29]	5.34 [0.51]	1.78 [0.17]
	$Lagoon: poly (Location\_Waterlevel\_1D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Small\_fish$	27	-1356.1	2766.1	9.7	0.174	0.95 [0.09]	5.21 [0.89]	5.16 [0.42]	1.71 [0.13]
	Lagoon + Lagoon:poly(Lagoon_Salinity_1D,2)	16	-1368.9	2769.9	13.5	0.193	0.92 [0.07]	4.38 [0.43]	5 [0.35]	1.71 [0.12]
	Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2)	24	-1361.5	2771.0	14.6	0.184	1.16 [0.28]	5.8 [1.15]	5.89 [0.96]	2.06 [0.43]
	$Lagoon + Lagoon: poly (Location_Waterlevel\_1D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Small\_fish$	30	-1355.6	2771.2	14.8	0.18	0.96 [0.11]	5.25 [0.88]	5.24 [0.47]	1.73 [0.15]
Species	Model	k	logLik	AIC	ΔΑΙC	R <sup>2</sup>	CV Deviance	Location NRMSE	Zone NRMSE	Lagoon NRMSE

							[SE}	[SE]	[SE]	[SE]
Fairy tern	Lagoon:location.mean_waterlevel1 + Lagoon:location.mean_waterlevel2 + Lagoon:poly(Location_Salinity_ID,2)	22	-1363.8	2771.5	15.2	0.179	1.4 [0.47]	5.95 [1.57]	6.76 [1.77]	2.44 [0.76]
(cont.)	Lagoon:location.mean_waterlevel1 + Lagoon:location.mean_waterlevel2 + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Small_fish + northLagoon:southLagoon.S_fish1	29	-1357.5	2773.1	16.7	0.191	1.88 [1.06]	6.49 [1.57]	9.04 [4.1]	3.4 [1.74]
Black swan	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) +	33	-4064.3	8194.6	0.0	0.453	2.96 [2.43]	7.17 [0.33]	6.83 [4.21]	4.36 [3.24]
	Lagoon: AustWetness + Lagoon: poly(Location_Waterlevel_1D,2) + Lagoon: poly(Location_Salinity_ID,2) + Lagoon: Chironomids + southLagoon: Runnia	37	-4060.6	8195.3	0.7	0.454	1.16 [0.56]	7.25 [0.31]	3.47 [0.83]	1.86 [0.68]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:Poly(Location_Salinity_ID,2) + Lagoon:Chironomids	34	-4063.8	8195.6	1.0	0.45	0.63 [0.11]	7.16 [0.27]	2.62 [0.18]	1.22 [0.14]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:Chironomids + southLagoon:Ruppia	38	-4065.8	8207.6	13.0	0.461	1.31 [0.64]	7.31 [0.37]	3.97 [1.23]	2.19 [0.91]
	Lagoon:AustWetness + Lagoon:location.depth_20_100cm + Lagoon:poly(Location_Salinity_ID,2)	26	-4078.4	8208.7	14.1	0.442	0.92 [0.32]	6.95 [0.36]	3.01 [0.47]	1.58 [0.41]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Lagoon_Salinity_1D,2) + southLagoon:Ruppia	31	-4074.9	8211.9	17.2	0.463	1 [0.33]	7.08 [0.45]	3.28 [0.53]	1.71 [0.43]
	Lagoon:AustWetness + Lagoon:location.depth_20_100cm + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids	30	-4076.1	8212.3	17.7	0.444	0.87 [0.27]	7.2 [0.43]	2.93 [0.39]	1.52 [0.35]
	$Lagoon: AustWetness + Lagoon + Lagoon: poly(Lagoon_Waterlevel_1D, 2) + Lagoon: poly(Lagoon_Salinity_1D, 2)$	34	-4072.3	8212.6	18.0	0.457	0.58 [0.09]	7.16 [0.35]	2.59 [0.16]	1.14 [0.12]
	Lagoon:AustWetness + Lagoon:spatial.location.depth_20_100cm + Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia	27	-4080	8213.9	19.3	0.448	1.5 [0.7]	7.08 [0.42]	3.89 [1]	2.24 [0.84]
	$Lagoon: AustWetness + Lagoon: poly(Location_Waterlevel_1D, 2) + Lagoon: poly(Location_Salinity_2D, 2) + Lagoon: poly(Location_Salinity_Sal$	29	-4078.1	8214.3	19.7	0.451	0.66 [0.19]	6.76 [0.35]	2.71 [0.27]	1.23 [0.2]
Chestnut	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) +	35	-6594.8	13259.5	0.0	0.339	1.07 [0.51]	10.78 [0.67]	2.95 [0.63]	1.55 [0.59]
tear	Lagoon: poly(Location_satinity_2D,2) + sountLagoon: Kappua Lagoon: AustWetness + Lagoon + Lagoon: poly(Location_Waterlevel_1D,2) + Lagoon: poly(Location_Satinity_2D,2) + Lagoon: Chiranomids	38	-6592.1	13260.2	0.7	0.339	0.56 [0.07]	10.77 [0.65]	2.38 [0.2]	0.99 [0.09]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids	35	-6595.1	13260.2	0.7	0.359	0.6 [0.07]	12.46 [1.4]	2.4 [0.18]	1.06 [0.09]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + southLagoon:Ruppia	33	-6597.5	13261.0	1.4	0.352	20.59 [20.01]	12.13 [1.2]	28.09 [25.72]	25.32 [24.31]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	37	-6594.3	13262.6	3.1	0.358	11.8 [11.18]	12.74 [1.47]	16.71 [14.34]	14.74 [13.68]
	Lagoon:AustWetness + Lagoon:location.depth_5_20cm + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	33	-6598.7	13263.3	3.8	0.346	1.44 [0.78]	10.99 [0.65]	3.39 [0.97]	2.02 [0.93]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Salinity_1D,2)	24	-6609.4	13266.8	7.3	0.347	0.58 [0.07]	10.62 [0.58]	2.37 [0.21]	1 [0.09]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2)	32	-6602.4	13268.7	9.2	0.343	0.57 [0.06]	12.24 [1.7]	2.38 [0.2]	0.98 [0.07]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:Chironomids	36	-6599.9	13271.8	12.3	0.346	0.62 [0.08]	17.65 [6.81]	2.44 [0.19]	1.05 [0.08]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2) + southLagoon:Ruppia	35	-6601.3	13272.6	13.1	0.342	17.52 [16.94]	12.63 [1.86]	24.12 [21.77]	21.7 [20.73]

Species	Model	k	logLik	AIC	ΔΑΙC	R <sup>2</sup>	CV Deviance [SE}	Location NRMSE [SE]	Zone NRMSE [SE]	Lagoon NRMSE [SE]
Common	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) +	31	-3096.5	6255.0	0.0	0.484	0.66 [0.22]	5.15 [0.24]	2.07 [0.32]	0.99 [0.26]
Greenshank	sounLagoon:Auppia Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	35	-3096.3	6262.5	7.6	0.484	0.74 [0.26]	5.35 [0.29]	2.16 [0.39]	1.1 [0.32]
	Lagoon: Aust Wetness + Lagoon + Lagoon: poly(Location_Waterlevel_1D,2) +	32	-3101.9	6267.9	12.9	0.479	0.52 [0.06]	5.02 [0.23]	1.82 [0.12]	0.83 [0.1]
	Lagoon: Poly(Location_Salinity_2D,2) + SouthLagoon: Poly(Location_Waterlevel_1D,2) +	34	-3101.8	6271.7	16.7	0.479	0.54 [0.07]	5.05 [0.23]	1.83 [0.12]	0.84 [0.1]
	Lagoon: Naby(Location_Salinity_2D,2) + sound2goon: Nabpat Lagoon: Naby(Location_Salinity_2D,2) + Lagoon: Poby(Location_Waterlevel_1D,2) +	37	-3100	6273.9	18.9	0.478	0.58 [0.07]	5.36 [0.38]	1.85 [0.12]	0.9 [0.12]
	Lagoon: AustWetness + Lagoon + Lagoon: poly(Location_Waterlevel_1D,2) + Lagoon: noly(Location_Salinity_2D,2) + Lagoon: Chironomids + southLagoon: Runnia	39	-3099.8	6277.6	22.7	0.478	0.62 [0.09]	5.44 [0.39]	1.89 [0.13]	0.94 [0.13]
	Lagoon: Noty(Locanon_Salinity_LD,2) + Lagoon. Chronomas + sounLagoon. Kappia Lagoon: AustWetness + Lagoon + Lagoon: poly(Lagoon_Waterlevel_1D,2) +	33	-3110.9	6287.7	32.8	0.477	0.5 [0.09]	4.95 [0.23]	1.83 [0.15]	0.83 [0.13]
	Lagoon:Poly(Lagoon_Jaumy 10,2) Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + southLagoon:Punnia	34	-3111.4	6290.7	35.8	0.475	0.57 [0.07]	5.4 [0.38]	1.85 [0.13]	0.88 [0.12]
	Lagoon:Poly(Location_Salinity_20,2) + Lagoon:Chronomas + sounLagoon.Ruppid Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Salinity_1D,2)	25	-3120.4	6290.8	35.9	0.478	0.38 [0.04]	4.99 [0.24]	1.74 [0.11]	0.68 [0.07]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon_Depth_2D([-5]-5cm) + Lagoon:poly(Lagoon_Salinity_1D,2) + southLagoon:Ruppia	31	-3115.2	6292.5	37.5	0.478	0.43 [0.06]	4.98 [0.22]	1.8 [0.11]	0.74 [0.08]
Curlew	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2)	29	-2592.9	5243.7	0.0	0.204	2.12 [1.14]	9.19 [3.19]	6.11 [1.47]	3.08 [1.34]
sandpiper	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	32	-2591.9	5247.8	4.0	0.217	3 [1.67]	6.7 [1.07]	7.88 [2.76]	4.96 [2.66]
	Lagoon:AustWetness + Lagoon:location.depth_min5_5cm + Lagoon:poly(Location_Salinity_ID,2) + southLagoon:Ruppia	28	-2596.8	5249.5	5.8	0.283	2.17 [1.14]	6.77 [1.27]	6.91 [1.74]	3.23 [1.21]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids	33	-2591.8	5249.6	5.9	0.205	2.22 [1.14]	9.79 [3.36]	6.14 [1.47]	3.22 [1.34]
	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia	30	-2595.3	5250.7	7.0	0.218	3.01 [1.67]	6.46 [0.92]	7.88 [2.72]	4.97 [2.66]
	Lagoon:AustWetness + Lagoon:location.depth_min5_5cm + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids	30	-2595.6	5251.1	7.4	0.283	2.22 [1.17]	7.04 [1.34]	6.92 [1.76]	3.32 [1.22]
	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + southLagoon:Ruppia	34	-2591.6	5251.2	7.4	0.216	3.01 [1.66]	6.85 [1.09]	7.87 [2.74]	4.96 [2.65]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon_Depth_2D([-5]-5cm)	20	-2605.8	5251.6	7.9	0.219	1.25 [0.39]	6.13 [0.91]	5.12 [0.66]	2.33 [0.58]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	35	-2591.2	5252.3	8.6	0.205	2.22 [1.14]	9.75 [3.35]	6.14 [1.46]	3.22 [1.33]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon_Depth_2D([-5]-5cm) + Lagoon:Chironomids	24	-2602.3	5252.6	8.9	0.219	1.34 [0.43]	6.65 [1.13]	5.21 [0.71]	2.48 [0.64]
Red-capped plover	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	31	-3738.6	7539.2	0.0	0.378	0.84 [0.18]	6.26 [0.33]	3.22 [0.42]	1.34 [0.25]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2)	33	-3739	7544.0	4.9	0.383	0.81 [0.14]	6.74 [0.47]	2.98 [0.32]	1.22 [0.18]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location Salinity 2D,2)	32	-3740.1	7544.2	5.1	0.393	1.33 [0.42]	6.24 [0.37]	4.59 [1.28]	2.03 [0.66]

Species	Model	k	logLik	AIC	ΔΑΙC	R <sup>2</sup>	CV Deviance [SE}	Location NRMSE [SE]	Zone NRMSE [SE]	Lagoon NRMSE [SE]
Red-capped	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D_2) + Lagoon:Chironomids	36	-3736.7	7545.3	6.2	0.387	1.09 [0.35]	6.92 [0.52]	3.63 [0.81]	1.56 [0.42]
(cont.)	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:Poly(Location_Salinity_2D,2) + southLagoon:Ruppia	34	-3739.3	7546.7	7.5	0.394	1.38 [0.45]	6.24 [0.37]	4.65 [1.32]	2.09 [0.69]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2) + southLagoon:Ruppia	35	-3738.4	7546.7	7.6	0.383	0.83 [0.15]	6.79 [0.47]	3 [0.33]	1.24 [0.18]
	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia	30	-3743.5	7547.1	7.9	0.363	2.48 [0.96]	6.44 [0.42]	7.14 [2.66]	3.56 [1.37]
	Lagoon:AustWetness + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia	29	-3744.8	7547.7	8.5	0.366	3.02 [1.33]	6.41 [0.4]	7.42 [2.5]	4.05 [1.65]
	Lagoon:AustWetness + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	31	-3743.3	7548.5	9.4	0.365	1.9 [0.77]	6.47 [0.5]	6.07 [2.22]	2.79 [1.09]
	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_min5_5cm + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	32	-3742.3	7548.5	9.4	0.363	3.19 [1.88]	6.56 [0.54]	11.45 [7.45]	5.03 [3.16]
Red-necked	Lagoon:AustWetness + Lagoon + Lagoon:spatial.location.depth_5_20cm +	31	-4368.5	8799.0	0.0	0.159	2.62 [1.37]	7.87 [0.56]	6.08 [2.18]	3.3 [1.5]
avocet	Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids Lagoon:AustWetness + Lagoon + Lagoon:spatial location depth 5 20cm +	32	-4367.9	8799.8	0.7	0.158	2.66 [1.36]	7.93 [0.55]	6.09 [2,18]	3.34 [1.5]
	Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + southLagoon:Ruppia	32	1507.5	0777.0	0.7	0.150	2.00 [1.50]	1.55 [0.55]	0.09 [2.10]	5.51[1.5]
	Lagoon:AustWetness + Lagoon:spatial.location.depth_5_20cm + Lagoon:poly(Location_Salinity_2D,2) +	30	-4370.2	8800.4	1.4	0.159	2.72 [1.47]	7.94 [0.56]	6.31 [2.4]	3.41 [1.62]
	Lagoon:AustWetness + Jagoon:spatial.location.depth_5_20cm + Lagoon:poly(Location_Salinity_2D,2) +	29	-4371.7	8801.4	2.4	0.137	2.75 [1.47]	7.89 [0.56]	6.43 [2.43]	3.44 [1.61]
	Lagoon: Chironomias Lagoon: AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon: poly(Location_Salinity_2D,2) + Lagoon: Chironomids	36	-4366.9	8805.7	6.7	0.175	2.74 [1.41]	8.14 [0.61]	5.97 [2.03]	3.38 [1.51]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon Salinity 1D,2) + Lagoon:Chironomids	34	-4369.8	8807.6	8.6	0.169	2.18 [0.75]	9.28 [1.2]	5.35 [1.22]	2.84 [0.85]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon_Depth_2D(5-20cm) + Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:Chironomids	30	-4374.4	8808.8	9.8	0.171	1.81 [0.68]	8.08 [0.57]	4.71 [1.05]	2.41 [0.78]
	Lagoon:AustWetness + Lagoon + Lagoon:Lagoon_Depth_2D(5-20cm) + Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:Chironomids + southLagoon:Ruppia	32	-4372.6	8809.3	10.3	0.17	1.76 [0.63]	8.11 [0.57]	4.63 [0.99]	2.35 [0.73]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) +	35	-4369.9	8809.8	10.8	0.172	2 [0.62]	9.34 [1.27]	5.01 [1.01]	2.63 [0.7]
	Lagoon:poly(Lagoon_Salinity_1D,2) + Lagoon:Chironomids + southLagoon:Ruppia Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	33	-4372.9	8811.7	12.7	0.176	2.85 [1.55]	8.25 [0.61]	6.15 [2.27]	3.47 [1.67]
Red-necked	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2)	31	-7106.7	14275.3	0.0	0.233	0.79 [0.1]	11.48 [0.42]	3.5 [0.36]	1.42 [0.21]
stint	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) +	33	-7106	14277.9	2.6	0.231	0.9 [0.13]	11.71 [0.49]	3.6 [0.37]	1.56 [0.22]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) +	35	-7105.5	14280.9	5.6	0.231	0.91 [0.13]	11.81 [0.49]	3.62 [0.38]	1.57 [0.22]
	Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) +	35	-7105.7	14281.3	6.0	0.231	0.8 [0.09]	11.63 [0.47]	3.51 [0.36]	1.43 [0.2]
	Lagoon:Chironomias Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2)	29	-7112.5	14282.9	7.6	0.259	0.64 [0.07]	20.23 [8.92]	3.24 [0.32]	1.19 [0.14]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + southLagoon:Ruppia	37	-7104.9	14283.8	8.5	0.229	0.92 [0.13]	11.91 [0.59]	3.62 [0.37]	1.57 [0.22]

Species	Model	k	logLik	AIC	ΔΑΙC	R <sup>2</sup>	CV Deviance [SE]	Location NRMSE [SE]	Zone NRMSE [SE]	Lagoon NRMSE [SE]
Red-necked	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) +	33	-7110.6	14287.3	11.9	0.256	0.65 [0.09]	21.89 [10.51]	3.26 [0.32]	1.22 [0.15]
(cont.)	southLagoon:Ruppta Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:Poly(Location_Salinity_ID,2) + Lagoon:Chironomids	33	-7111.3	14288.6	13.3	0.261	0.62 [0.07]	20.25 [8.62]	3.18 [0.29]	1.15 [0.11]
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2)	31	-7114.1	14290.1	14.8	0.272	0.59 [0.08]	47.97 [36.56]	3.15 [0.29]	1.14 [0.11]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	36	-7109.3	14290.6	15.3	0.259	0.62 [0.09]	21.69 [10.03]	3.21 [0.3]	1.19 [0.12]
Sharp-tailed	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_1D,2) +	33	-6634.1	13334.2	0.0	0.273	3.42 [2.55]	10.69 [0.66]	7.33 [4.07]	5.08 [3.48]
sandpiper	Lagoon:poly(Location_Salinity_2D,2)									
	Lagoon:AustWetness + Lagoon + Lagoon:poly(Location_Waterlevel_ID,2) +	39	-6630.9	13339.7	5.5	0.263	3.07 [2.26]	11.3 [1.06]	6.64 [3.6]	4.46 [3.02]
	Lagoon: Poly(Location_Salinity_2D,2) + Lagoon: Chironomids + southLagoon: Ruppia	20	6640.0	12241 6	7.4	0.005	2.96 [2.26]	10 54 50 571	10 12 15 201	5 45 52 021
	Lagoon:AustWetness + Lagoon:location.deptn_min5_5cm + Lagoon:poly(Location_Salinity_ID,2) +	30	-6640.8	13341.6	7.4	0.285	3.86 [2.36]	10.54 [0.57]	10.13 [5.29]	5.45 [3.03]
	Lagoon: AustWetness + Lagoon: poly(Location_Waterlevel_1D,2) + Lagoon: poly(Location_Salinity_ID,2) +	34	-6637.2	13342.4	8.2	0.286	3.23 [2.38]	13.42 [1.96]	6.41 [3.53]	4.27 [2.91]
	Lagoon: Chironomids									
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + southLagoon:Ruppia	34	-6637.4	13342.8	8.6	0.276	3.21 [2.39]	10.87 [0.7]	7.08 [3.91]	4.84 [3.32]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	36	-6636.1	13344.3	10.1	0.286	3.26 [2.37]	13.64 [1.96]	6.46 [3.5]	4.31 [2.9]
	Lagoon:AustWetness + Lagoon:location.depth_min5_5cm + Lagoon:poly(Location_Salinity_ID,2) + Lagoon:Chironomids + southLagoon:Ruppia	33	-6639.4	13344.8	10.6	0.284	4.19 [2.6]	10.66 [0.6]	10.65 [5.58]	5.87 [3.33]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_ID,2) + southLagoon:Runpia	32	-6641.3	13346.6	12.4	0.299	3.23 [2.64]	12.82 [1.49]	6.57 [3.96]	4.41 [3.31]
	Lagoon:AustWetness + Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + southLagoon:Runpia	38	-6635.3	13346.6	12.4	0.269	2.88 [2.18]	12.13 [1.54]	6.46 [3.52]	4.29 [2.94]
	$Lagoon: Aust Wetness + Lagoon + Lagoon: poly(Lagoon_Waterlevel_1D, 2) + Lagoon: Chironomids$	29	-6648.6	13355.2	21.0	0.291	2.48 [1.83]	14.89 [3.17]	5.19 [2.48]	3.35 [2.12]

Table B.4. Evaluation of the candidate probability of foraging models for each of the ten key waterbird species, using binomial models fitted to location-level bird count data which were assessed with Akaike's Information Criterion (AIC). Shown for each model are: the number of parameters fitted (k); the log-likelihood of the model (logLik), AIC for which lower numbers indicate higher ranked models; and the change in AIC relative to the top AIC-ranked model for each species ( $\Delta$ AIC). In the model formula, second-order polynomial terms for covariate *X* are denoted poly(*X*, 2). For brevity, only the top ten AIC-ranked candidate models are presented and the random-effect structure is omitted from the model specification. For each species, the selected model with the lowest AIC score is shown in bold.

Species	Model	k	logLik	AIC	ΔΑΙC
Australian	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	13	-4675.9	9377.8	0.0
penean	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	15	-4675.7	9381.3	3.5
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:All_fish	16	-4675.1	9382.2	4.4
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:All_fish	17	-4675.0	9384.1	6.2
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon. All\_$	17	-4675.1	9384.2	6.4
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon. All\_fish$	18	-4675.0	9386.1	8.2
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:All_fish	15	-4684.7	9399.4	21.6
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	13	-4687.0	9400.1	22.2
	$Lagoon: poly (Location\_Waterlevel\_1D, 2) + Lagoon: poly (Location\_Salinity\_1D, 2) + Lagoon: All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon: SouthLagoon. All\_fish + NorthLagoon. All\_fi$	16	-4684.6	9401.2	23.4
	Lagoon + Lagoon:poly(Lagoon_Waterlevel_1D,2) + Lagoon:poly(Lagoon_Salinity_1D,2)	14	-4843.0	9714.0	336.2
Fairy tern	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	12	-473.5	971.0	0.0
	$Lagoon + Lagoon: spatial. location. depth\_exc\_20cm1 + Lagoon: poly(Location\_Salinity\_2D, 2) + Lagoon: Small\_fish$	14	-472.1	972.2	1.2
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	14	-473.2	974.4	3.4
	Lagoon:Small_fish + NorthLagoon:Small_fish_SL	6	-481.9	975.8	4.8
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Small_fish	15	-472.9	975.8	4.8
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Small\_fish + NorthLagoon: Small\_fish\_SL$	16	-472.5	977.0	6.0
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Small_fish	16	-472.6	977.2	6.3
	Lagoon + Lagoon:Small_fish	7	-482.0	978.0	7.0
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Small\_fish + NorthLagoon: Small\_fish\_SL$	17	-472.1	978.3	7.3
	Lagoon:Small_fish	7	-482.3	978.7	7.7
Black swan	Lagoon + Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	12	-3698.2	7420.4	0.0
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	16	-3695.1	7422.2	1.7
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Ru$	17	-3695.1	7424.2	3.7
	$Lagoon + Lagoon: Lagoon\_Depth\_2D(20-100cm) + Lagoon: poly(Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Ruppia + L$	14	-3698.1	7424.2	3.7
Species	Model	k	logLik	AIC	ΔΑΙΟ
Black swan	Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2)	9	-3703.3	7424.6	4.2

(cont.)	Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	13	-3699.6	7425.1	4.7
	Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	14	-3699.2	7426.4	6.0
	Lagoon + Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	12	-3701.3	7426.6	6.2
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	14	-3699.6	7427.2	6.8
	Lagoon:Lagoon_Depth_2D(20-100cm) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	12	-3701.6	7427.3	6.9
Chestnut teal	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	16	-5555.8	11143.6	0.0
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	15	-5557.8	11145.5	1.9
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	18	-5554.9	11145.8	2.2
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	17	-5556.7	11147.5	3.9
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	15	-5559.0	11147.9	4.3
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	14	-5560.1	11148.3	4.6
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	15	-5559.2	11148.3	4.7
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	14	-5561.0	11150.1	6.5
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	15	-5566.3	11162.6	19.0
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	14	-5567.9	11163.9	20.3
Common Greenshank	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	15	-1225.0	2480.0	0.0
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	11	-1229.4	2480.8	0.9
	Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	17	-1224.9	2483.9	3.9
	Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	15	-1229.4	2488.8	8.9
	Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	13	-1235.2	2496.3	16.4
	Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	11	-1237.3	2496.7	16.7
	Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	12	-1236.8	2497.6	17.6
	Lagoon + Lagoon:Lagoon_Depth_2D([-5]-5cm) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	13	-1235.9	2497.7	17.8
	Lagoon:Lagoon_Depth_2D([-5]-5cm) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	12	-1237.2	2498.4	18.4
	Lagoon:Lagoon_Depth_2D([-5]-5cm) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	10	-1239.4	2498.9	18.9
Curlew sandpiper	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	13	-1055.2	2136.3	0.0
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	14	-1054.6	2137.2	0.9
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	14	-1055.5	2138.9	2.6
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	15	-1054.5	2139.0	2.7
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + SouthLagoon: Ruppia + Lagoon: Poly (Location\_Salinity\_2D, 2) + Lagoon: Poly (Location\_Salinity\_2D, 2) + SouthLagoon: Ruppia + Lagoon: Poly (Location\_Salinity\_Sa$	15	-1055.0	2140.1	3.8
Species	Model	k	logLik	AIC	ΔΑΙC

Curlew sandpiper	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	16	-1054.3	2140.6	4.3
(cont.)	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Chironom$	15	-1055.7	2141.4	5.1
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Rupp$	17	-1054.7	2143.3	7.0
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	12	-1081.0	2186.0	49.7
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	13	-1080.9	2187.9	51.6
Red-capped plover	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	12	-2128.0	4280.0	0.0
_	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	13	-2127.8	4281.6	1.6
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	14	-2127.9	4283.9	3.9
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	15	-2127.7	4285.4	5.4
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + South Lagoon: Ruppia + Lagoon:$	15	-2149.6	4329.2	49.2
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Chironomids + SouthLagoon$	18	-2148.0	4332.1	52.0
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	12	-2154.1	4332.3	52.3
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + Lagoon: Chironomida + Lagoon: Chirono$	16	-2150.6	4333.2	53.2
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	15	-2152.6	4335.3	55.2
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Rupp$	16	-2151.7	4335.4	55.4
Red-necked avocet	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	16	-4850.1	9732.2	0.0
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + SouthLagoon: Ruppia + Lagoon: Ruppia + $	14	-4855.8	9739.6	7.4
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	15	-4855.8	9741.5	9.4
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chirono$	16	-4855.3	9742.7	10.5
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Rupp$	17	-4854.6	9743.2	11.0
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Ru$	15	-4859.8	9749.6	17.4
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	14	-4861.2	9750.4	18.3
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chironomida + La$	16	-4859.4	9750.7	18.6
	Lagoon:location.depth_5_20cm1 + Lagoon:poly(Location_Salinity_1D,2)	10	-4889.6	9799.1	67.0
	Lagoon:location.depth_5_20cm1 + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	12	-4887.6	9799.2	67.0
Red-necked stint	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2)	12	-18275.6	36575.1	0.0
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	15	-18272.7	36575.3	0.2
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	16	-18272.2	36576.3	1.2
	Lagoon:poly(Location_Waterlevel_1D,2) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	14	-18275.5	36578.9	3.8
	Lagoon:Location_Depth_1D([-5]-5cm) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	10	-18595.9	37211.9	636.7
Species	Model	k	logLik	AIC	ΔΑΙC

Red-necked stint	Lagoon:Location_Depth_1D([-5]-5cm) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids + SouthLagoon:Ruppia	14	-18594.6	37217.2	642.1
(cont.)	Lagoon:Location_Depth_1D([-5]-5cm) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	13	-18596.5	37219.0	643.9
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	13	-18673.7	37373.4	798.3
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + South Lagoon: Ruppia + Lagoon:$	14	-18673.6	37375.3	800.1
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	14	-18674.4	37376.7	801.6
Sharp-tailed sandpiper	Lagoon:Location_Depth_1D([-5]-5cm) + Lagoon:poly(Location_Salinity_1D,2) + Lagoon:Chironomids	12	-14051.4	28126.8	0.0
	$Lagoon: Location\_Depth\_1D([-5]-5cm) + \ Lagoon: poly(Location\_Salinity\_1D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Ruppia + Lagoon$	13	-14051.4	28128.8	2.0
	Lagoon:Location_Depth_1D([-5]-5cm) + Lagoon:poly(Location_Salinity_1D,2) + SouthLagoon:Ruppia	11	-14056.0	28134.1	7.3
	$Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Rupp$	15	-14245.9	28521.8	395.0
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chironomida + Lagoon: Chirono$	16	-14246.7	28525.4	398.6
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + Lagoon:Chironomids	16	-14246.7	28525.5	398.7
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Chironomids + SouthLagoon: Ruppia + Lagoon: Ruppia + $	18	-14245.8	28527.6	400.9
	Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2) + SouthLagoon:Ruppia	14	-14251.4	28530.8	404.0
	$Lagoon + Lagoon: poly (Location\_Waterlevel\_2D, 2) + Lagoon: poly (Location\_Salinity\_2D, 2) + SouthLagoon: Ruppia + Lagoon: $	15	-14251.1	28532.3	405.5
	Lagoon + Lagoon:poly(Location_Waterlevel_2D,2) + Lagoon:poly(Location_Salinity_2D,2)	13	-14253.2	28532.4	405.6





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