Favorable inland wetland conditions increase apparent survival of migratory shorebirds in Australia

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ABSTRACT

Many migratory shorebird species using the East Asian–Australasian Flyway are declining rapidly. While the loss of staging habitats in East Asia is considered the primary cause, stressors to fitness often occur throughout the geographic range of declining species, and threats in the non-breeding grounds have been comparatively poorly studied. Three species of migratory shorebird, Curlew Sandpiper (Calidris ferruginea), Sharp-tailed Sandpiper (C. acuminata) and Red-necked Stint (C. ruficollis), use Australia’s dynamic temporary wetland systems opportunistically, yet these large wetland systems have become increasingly degraded, with reduced frequency and extent of flooding. Here, we test whether variables related to wetland availability in Australia’s interior can explain annual variation in apparent survival, abundance or immature to adult ratios at three well-monitored coastal shorebird areas in southern Australia (total area > 1315 km²). We show that coastal annual bird abundance and ratios of immatures at the coast were higher when inland Australia was relatively hot and dry. Also, a small but significant amount of variation in annual apparent survival can be explained by annual variation in inland conditions, with higher survival rates in years when inland conditions were relatively wet and cool. For the endangered Curlew Sandpiper, the impacts of Australian environmental conditions may be exacerbating the impacts of conditions experienced in other parts of its range on fitness and survival. While the effects we document here are relatively weak, they do suggest that management of inland wetlands for these shorebirds may positively affect survival rates of these sharply declining species.

Introduction

Habitat loss is the most frequently implicated cause of population declines (Burton et al. 2006; Sanderson et al. 2006; Moores et al. 2008), yet the evidence of the impact of habitat loss on either individuals or populations of migratory species that move widely throughout the landscape can be hard to establish (Carlisle et al. 2009; Alves et al. 2013). For example, migratory shorebirds travelling through the East Asian–Australasian Flyway are in rapid decline, and there is an urgent need to identify causes of the declines and management interventions to reverse them (Amano et al. 2010; Wilson et al. 2011; Clemens et al. 2016). Thus far, these declines have been attributed to the rapid loss of intertidal habitat in the Yellow Sea region of East Asia (Murray et al. 2014; Piersma et al. 2015), with the rate of annual decline on Australasian non-breeding grounds being highest in those species most reliant on Yellow Sea staging areas (Studds et al. 2017). However, shorebirds also face threats in both the arctic breeding areas and the southern non-breeding areas (Pearce-Higgins et al. 2017; Wauchope et al. 2017; Gallo-Cajiao et al. 2020). Indeed, changing arctic conditions have been linked to reduced survival for Red Knot Calidris rufa that breeds in western Siberia (Van Gils et al. 2016), and climatically suitable breeding conditions for arctic-breeding shorebirds are predicted to decline rapidly in the next few decades (Wauchope et al. 2017). In non-breeding areas, declines in shorebird numbers in eastern Australia have been attributed to over-extraction of water (Nebel et al. 2008), and modelling has indicated the potential impacts of Australian habitat degradation on Ruddy Turnstone Arenaria interpres survival (Aharon-Rotman et al. 2016). For migratory shorebirds that...
facultatively use temporary wetlands across the vast inland of Australia during the non-breeding season, it is possible that changing wetland dynamics are also having an impact on migratory shorebirds.

Australia’s interior is characterised by vast wetlands with enormous fluctuations in water availability over time and space (Roshier et al. 2001; Kingsford and Norman 2002). These temporary wetland systems are especially threatened due to river regulation, which has markedly reduced flood frequency and extent in many regions (Kingsford 2000; Finlayson et al. 2013; Bino et al. 2016). The Curlew Sandpiper *Calidris ferruginea*, Sharp-tailed Sandpiper *C. acuminata* and Red-necked Stint *C. ruficollis* are the most numerous migratory shorebird species in Australia’s inland wetlands. These species appear to move from coastal habitats to inland habitats in response to heavy rains, and return to coastal areas as inland wetlands dry (Alcorn et al. 1994; Chambers and Loyn 2006; Loyn et al. 2014). These movements suggest varying suitability of inland wetland habitats and include observations of shorebirds stopping at inland wetlands on their way to southern coastal areas in some years (Alcorn et al. 1994). However, the benefit of these movement patterns is unclear: birds may gain greater condition when foraging at inland wetlands during wet years; birds may reduce the need to travel on to coastal areas; movements may reduce competition experienced at the coast; or birds may escape coastal predation pressure or human disturbance (Glover et al. 2011) by moving. Regardless of the benefit of these movements, degradation of these inland wetlands might adversely affect survival and abundance of shorebirds observed at coastal areas.

Migratory shorebirds experience different energetic costs and gains in different non-breeding habitats often due to temperature and food availability (Piersma and Lindstrom 2004; Colwell 2010), which have increasingly been related to survival rates and breeding success in the following year (Baker et al. 2004; McGowan et al. 2011; Alves et al. 2013; Aharon-Rotman et al. 2016). Studies have generally focused on the impacts of variation in habitat quality in areas that tend to be used regularly, but inland Australia is unusual in that up to 20% of the individuals of a species population can occur at a single
lake in only one of 30 years (Kingsford and Norman 2002). The rarity of such events makes it difficult to predict the consequences of large-scale fluctuations in environmental suitability over time, which may vary in magnitude, frequency or duration.

Here we examined a 30-year dataset to explore whether changing conditions across Australia’s interior wetlands are correlated with (i) total abundance, (ii) immature ratios (an index of reproductive success) and (iii) survival in non-breeding Curlew Sandpipers, Sharp-tailed Sandpipers and Red-necked Stints at three major southern Australian coastal shorebird areas. We further explored these relationships at regional and national scales. We also sought to determine whether environmental conditions predicted population patterns in the current or subsequent year.

### Methods

#### Study area

The three coastal shorebird areas considered in this study are wetlands in Victoria. The shorebird roosts monitored are in Western Port (38.28 S, 145.41 E, 680 km²), Werribee-Avalon (38.00 S, 144.59 E, 37 km²) and Corner Inlet (38.71 S, 146.68 E, 600 km²); the wetlands are separated by large areas that are unsuitable for shorebirds, and movements of banded shorebirds between the three areas rarely occur (Herrod 2010).

Western Port is a large tidal embayment 65 km south-east of Melbourne, and contains two large islands, French and Phillip Island, plus numerous small islets. French Island does include some non-tidal wetlands that are occasionally used by shorebirds. Most of the region is characterised by extensive intertidal mudflats with substantial cover of seagrass and highly diverse fringing saltmarsh habitat accompanied in many locations by mangrove *Avicennia marina* (Hansen et al. 2015). The majority of the embayment is designated as a Ramsar site.

The Werribee-Avalon study area is 30 km west of Melbourne, Victoria. It is dominated by the Western Treatment Plant (WTP), an active sewage treatment plant where shorebirds forage in natural intertidal habitats fringing Port Phillip Bay (Rogers et al. 2013) and in nearby extensive non-tidal freshwater wetlands (converted sewage ponds) that are managed for shorebirds (Rogers and Hulzebosch 2014). Previously, shorebirds of the WTP made occasional movements into adjacent roosts at Avalon Saltfield and Pt. Wilson (Rogers et al. 2013), so shorebird counts from the three areas are carried out concurrently, allowing the data to be pooled as Werribee-Avalon. The wide variety of habitat types within the Werribee-Avalon area has historically supported over 1% of the flyway population of the three migratory shorebird species considered in this study. The Werribee-Avalon area forms part of the larger Port Phillip Bay (Western Shoreline) and Bellarine Peninsula Ramsar Site (Herrod 2010).

Corner Inlet is a large estuary 200 km south-east of Melbourne, with approximately 270 km² of intertidal area. The inlet is formed by extensive fringing mangrove and saltmarsh plus four large coastal barrier islands, and contains 65 islands throughout. Most of the area is designated as a Ramsar site, which regularly supports over 29,000 shorebirds.

While these shorebird areas are relatively close together, evidence suggests they are used by independent groups of birds. For example, at three locations along Port Phillip Bay in Victoria, 98% of all recaptures were from the same coastal shorebird area as previous captures (n = 2710 Red-necked Stint, n = 1655 Curlew Sandpiper and n = 221 Sharp-tailed Sandpiper) (Herrod 2010). Similarly, while there is evidence through resighting of banded birds of regular movements during migration between north-west Australia and south-east Australia, there are few records indicating regional coastal movements during the non-breeding season (Minton et al. 2006).

#### Shorebird data

Data on shorebird abundance, age ratios and apparent annual survival have been collected by volunteers throughout Australia for over three decades (Clemens et al. 2014) and were summarised in each year from 1982 to 2011.

Count data were recently collated from both coastal and inland areas and vetted as part of a national analysis of shorebird population trends (Clemens et al. 2016; Studds et al. 2017). Data from counts included annual surveys generally conducted within two hours of high tide during the peak of the summer non-breeding period from November to February. Counts were fairly consistent at these three shorebird areas, and count coverage was generally complete at both Corner Inlet and Werribee-Avalon (Herrod 2010; Minton et al. 2012; Hansen et al. 2015). The number of roosts within Western Port varied between nine and 14 in any year, so the average number of birds counted per roost, per year was used to represent abundance.

Shorebird mark-recapture data were collected by the Victorian Wader Study Group by cannon-netting birds to obtain morphometric, age and recapture data.
(Minton 2006). Each captured bird was fitted with a metal band inscribed with a unique number (used to generate capture histories), and (after 1992) with a plastic orange leg ‘flag’ (Minton 2006). Individual capture histories were pooled annually by shorebird area, with individuals captured or recaptured between August and July of the following year noted as having been captured at least once in that year. This time frame was selected because most shorebirds arrive in Australia from the breeding grounds after July each year (Rogers et al. 1996).

For each of the three species at each of the three shorebird areas for each summer (December to February) an annual estimate of recruitment was calculated, termed ‘immature ratio’. We have used ‘immature ratio’ throughout as it is somewhat different from immature proportion and is viewed as an unbiased estimate of recruitment. The ratio divides the number of first-year (‘immature’) birds caught by the number of adult birds caught (Rogers et al. 2004). This removes second-year birds which did not migrate the previous year. Age can be reliably estimated throughout the year for each of these species based on plumage characteristics (Higgins and Davies 1996), assuming that age ratios were the same in catches as in non-captured birds; there is some empirical support for this assumption (Rogers et al. 2005). Data were insufficient to estimate ratios for Sharp-tailed Sandpiper at Corner Inlet.

Environmental data

Five variables were selected to capture conditions at inland wetlands that could be associated with the costs and benefits to fitness in the three shorebird species (supplemental Table S1). Each of these five variables was summarised annually for 30 years from 1982 to 2011 at either continental scale or within 500 km of the study area, resulting in a total set of 10 annual environmental variables used to examine the importance of regional or national wetland availability in the same model. Each of these annual dependent variables was compared to the annual response variable in both the same year and in the following year in separate models.

The independent variable ‘predicted inland abundance’ for each of these three shorebird species was derived from separate work which used all available shorebird data and environmental variables to develop species distribution models to predict the abundance of each of these species in each 0.1 degree grid cell across all of inland Australia each month for over 30 years (Clemens 2017). These predictions were then totalled at either the 500 km regional or continental scale over summer months, and monthly totals were averaged resulting in annual estimates of the number of each of these species predicted to be using inland wetlands. Because resulting predictions were not sufficiently precise (Clemens 2017), we selected four additional variables related to dynamic water availability and suitable temperature ranges, based on previous work (Clemens 2017). The variable ‘total stream flow’ was derived from stream flow data collected by the Bureau of Meteorology (BOM) at 3500 Australian locations. Inland flow volumes have been shown to be significantly related to coastal waterbird abundance previously (Chambers and Loyn 2006). The standardised maximum monthly averages of daily maximum flow in cubic metres per second were used as values in a 0.1 degree grid. Missing grid values within each month were filled using simple spatial interpolation with thin plate splines applied to each monthly grid (Hijmans 2014). Variables related to surface wetness (Raupach et al. 2009) reflect the availability of foraging habitat in the form of wet mud or shallow water. Upper soil moisture in the spring was intended to represent the amount of favourable habitat encountered during southward migration, while regional annual surface wetness was expected to influence whether birds remained at the coast after arriving there. The cumulative upper soil moisture over the latest two years was also subtracted from the cumulative soil moisture over the two years prior to that period, creating a variable reflecting longer-term changes in soil moisture intended to reflect the increase in habitat quality for shorebirds as wetland water levels recede (Rehfisch 1994; Sanders 2000). Temperature data (Jones et al. 2009) associated with surface wetness and resulting wetland drawdown included both spring inland temperatures averaged at a continental scale and annual non-breeding season regional temperatures.

Continental or regional totals were drawn from grid data of the five variables with a 0.1 degree resolution within the Geocentric Datum of Australia (GDA 1994) coordinate system. The monthly values in these grids were then summed across one of the two spatial scales (continental or regional) and were then averaged annually during the non-breeding period for migratory shorebirds (October to March), or averaged annually across spring (August to October). All variables were processed using python in ArcGIS (ESRI 2011) and the raster package in R version 3.3.1 (Hijmans 2014; R Development Core Team 2016).

Annual apparent survival estimates

Estimates of annual apparent survival were made independently for each of the three species at each of the
three shorebird areas using a Bayesian analysis to fit a Cormack-Jolly-Seber model with a state-space likelihood reliant on Markov chain Monte Carlo (MCMC) methods for computation (McCarthy and Masters 2005; Gimenez et al. 2007; Royle 2008; Kéry and Schaub 2012). This implementation of a Cormack-Jolly-Seber hierarchical model uses one model for the latent or hidden state process of whether the bird is alive or dead, and a second model for the observations or detections which are conditional on the state process (Royle 2008):

The latent process: $z_{it}\mid z_{it}= Bernoulli(\delta_{z_{it}})$ and detection or recapture probability: $y_{it}\mid z_{it}= Bernoulli(\phi)$

where:

$z_{it} = true state matrix, indicating whether individual i is alive at time t (z = 1)$, or dead $(z = 0)$, $\phi = apparent survival probability for individual i from time t to t + 1$, $y_{it} = is the observed capture history for individual i at time t$,

$P_{it} = recapture probability for individual i at time t$.

Priors on the inverse logit of the annual fixed effects were assumed to be uniform between zero and one.

Models were fitted using WINBUGS (Lann et al. 2000) with the R2WinBUGS package (Sturtz et al. 2005) in R. Model parameters were estimated from three chains thinned by six of 10,000 Monte Carlo iterations with the initial 5,000 discarded as ‘burn-in’. Convergence was assessed visually using trace plots and all simulated chains stabilised at similar values. Credible intervals of 95% were calculated for each parameter estimate. Data were insufficient to estimate apparent survival for Sharp-tailed Sandpiper at Corner Inlet.

The following assumptions were made in these models: (1) marked birds were a random and representative sample of birds visiting each of the three shorebird areas each year, (2) marking was accurate with no loss of bands, no misread bands and no data entry errors, (3) the fate of individual birds was independent, and (4) each individual had the same survival and recapture probability within each year.

Statistical relationship between inland wetland conditions and shorebirds

Multiple linear regression was used to determine whether a significant amount of the variation in shorebird counts, apparent shorebird survival or the estimated number of immatures could be explained by variables related to inland wetland conditions in that year, or in a separate model in the previous year. All analyses were conducted using the MASS package in R (Venables and Ripley 2002), where variables for each model are chosen using sequential evaluation of the (AIC) Akaike information criterion value. All variables were selected after stepwise selection sequentially added variables as in forward selection, and sequentially removed variables which did not improve fit as in backward selection. All variables were standardised by taking the value at each year and subtracting the mean value across all years, and then dividing by the standard deviation across years. All annual variables were analysed over the period when migratory shorebirds are visiting between November and February. For reporting and analyses purposes each summer is reported as the second calendar year in a summer, i.e. the summer of 1987/88 was reported as 1988. Analyses were restricted from 1982 to 2011. Unbalanced data were fully analysed by omitting years without records for a particular species. Results were assessed using residual plots to test assumptions, and log-transformations were used on the dependent variable to rectify residual plots where needed (Table 1). Variance inflation factors were used to test for multicollinearity. Autocorrelation functions and residual plots in R were also used to inspect for autocorrelation in the residuals. Multicollinearity and autocorrelation were not problematic in the variables tested.

Results

Annual counts of each of the species showed considerable variation, with standard deviations ranging from 30 to 95% of the mean. Variation in annual immature ratio estimates was also high (supplemental Table S2), with standard deviations often exceeding the mean and with individual values occasionally being five times greater than the mean value. Survival from the previous year was estimable between 1982 and 2011, but estimates were not precise. For example, at the Western Treatment Plant the average widths of 95% credible intervals were 0.24 for Curlew Sandpiper, 0.58 for Red-necked Stint and 0.71 for Sharp-tailed Sandpiper, with considerable variation in those widths from year to year (supplemental Table S3). Annual apparent survival estimates were not highly correlated between shorebird areas or species ($r < 0.49$, mean $r = 0.17$). Low recapture probability was the probable cause of low precision in survival estimates. At the Western Treatment Plant, for example, average capture probabilities were only 0.098 ± 0.009SD for Curlew Sandpiper, 0.062 ± 0.028 for Red-necked Stint and 0.127 ± 0.099 for Sharp-tailed Sandpiper (Table S3). Variation in predictor variables was also quite high, with standard deviations often greater than the mean.
Table 1. Multiple regression results predicting annual apparent survival (\(\Phi\)), annual abundance (count), or the annual estimated immature ratio related to inland wetland condition in Australia for Curlew Sandpiper (CUSA), Red-necked Stint (RNST) or Sharp-tailed Sandpiper (STSA) at the Western Treatment Plant, Corner Inlet, or Western Port, Victoria

<table>
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<tr>
<th>Regression models</th>
<th>Multiple regression model results</th>
<th>National inland variables</th>
<th>Regional inland variables (&lt; 500 km)</th>
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<tr>
<td>Species</td>
<td>Dependent variable</td>
<td>F-Value</td>
<td>Adjusted R²</td>
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<td></td>
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<td></td>
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<td>STSA Phi</td>
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<td>RNST Phi</td>
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<td>CUSA Immature ratio</td>
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<tr>
<td></td>
<td>STSA Immature ratio</td>
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<td>STSA count</td>
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<td>STSA count next yr ((t))</td>
<td>(F_{2,17} = 2.69)</td>
<td>0.22</td>
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(Continued)
Table 1. Multiple regression model results for each species. The dependent variables were counts of each species at the coast, the regional inland variables were selected, while similar comparisons, only regional variables were important, for example, in regressions of counts against inland condition in the previous year for Curlew Sandpiper at Corner Inlet, only regional variables were selected in the best model, while similar comparisons for Red-necked Stint at Corner Inlet resulted in only one national variable being selected (Table 1). Most comparisons, however, contained both regional and national variables in the best model.

Inland wetland conditions explained significant amounts of variation in apparent survival, with lower survival when inland areas were relatively dry and hot, and higher survival when the inland areas were relatively wet and cool. Comparisons of apparent survival with inland conditions in the same year revealed significant results at two shorebird areas for both Curlew Sandpiper and Red-necked Stint, which explained between 15 and 32% of the variation (Table 1). Results were not significant for Sharp-tailed Sandpiper. When comparing apparent survival with inland conditions the previous year, the results were significant at all three areas for Curlew Sandpiper, at two areas for Red-necked Stint, and at one of two areas for Sharp-tailed Sandpiper with between 22 and 49% of the variation explained (Table 1).

In regression analyses, the annual count of each of the three species at the coast was significantly related to inland wetland conditions, often with hotter, drier inland conditions and fewer predicted inland shorebirds related to greater counts at the coast (Table 1). This was true for all species at all shorebird areas except for Red-necked Stint at Western Port (Table 1). Indeed, variables related to inland wetland conditions explained a fair proportion of the variation in annual shorebird counts in these species ranging from 19% for Red-necked Stint at the Western Treatment Plant to 64% for Curlew Sandpiper at Corner Inlet (Table 1). Inland wetland conditions in one year were also significantly related to
the number of individuals counted the following year at all three areas for Curlew Sandpiper, at two areas for Sharp-tailed Sandpiper and at one area for Red-necked Stint. The amount of variation explained in counts the following year ranged from 20% for Red-necked Stint at Corner Inlet to 71% for Curlew Sandpiper at Western Port (Table 1).

The ratio of immatures present at different shorebird areas was significantly but inconsistently related to inland conditions. Curlew Sandpiper, Red-necked Stint and Sharp-tailed Sandpiper immature ratios were significant at one area. The variation explained in significant findings in these three species ranged from 30% to 30% (Table 1). When comparing immature ratios to wetland conditions the previous year, the relationships were more consistent with significant findings evident for Curlew Sandpiper at all three areas, and Sharp-tailed Sandpiper at both the areas where sufficient data was available. The explained variation for these two species ranged from 25% to 62%, but findings were not significant at any of the three areas for Red-necked Stint (Table 1).

**Discussion**

Identification of factors that affect wildlife populations is important for ensuring that conservation actions can be appropriately targeted to help declining populations recover. Our results indicate that drier and hotter inland conditions in Australia affect migratory shorebird species that stop at inland wetlands. The parameters of coastal shorebird populations explored here have probably always been correlated to the boom and bust cycles in inland wetland availability, but the likelihood of ‘bad’ years is rising because of (1) a decreasing area of wetlands that naturally flood and (2) declining winter rainfall (Finlayson 2013). This suggests that improved interior wetland management in Australia could assist in the recovery of some declining populations. Our findings also serve as a reminder of the importance of conserving migratory species throughout their full annual cycle.

Overall, our findings have potentially important implications for our understanding of migratory shorebird ecology and conservation in Australia. We explore some of the possible interpretations of these results below. While small but significant amounts of variation were explained in these analyses, it is important to note that most of the variation in these parameters appeared to result from unmeasured factors.

**Survival**

A positive impact of inland wetland conditions on survival is consistent with birds moving between coastal and inland areas, perhaps enabling individuals to seek out both spatial and temporal subsidies in resource availability, thereby allowing their populations to persist at higher levels than they would in the absence of such resource pulses (Sears et al. 2004; Holt 2008). Potential negative impacts of inland wetland conditions could be related to mortality associated with crossing a desert continent when conditions are especially hot and dry, which has been observed in migratory birds crossing the deserts of West Africa (Zwarts et al. 2009). The degree to which the survival of these three species appears to be related to inland conditions is somewhat proportional to the rate at which they are decreasing nationally (Clemens et al. 2016).

Curlew Sandpiper is the migratory shorebird showing the most rapid decline in Australia (Clemens et al. 2016; Studys et al. 2017), and was also the species that showed the strongest and most widespread significant association between inland conditions and apparent survival. Previous studies suggest that Curlew Sandpiper cross the continent during southward migration (Minton et al. 2006). We suggest the stronger significant correlations between apparent survival and wetland conditions in the same year relate to the greater risk of crossing the desert during migration when coming from degraded habitats in the Yellow Sea. Similarly, correlations between apparent survival and inland conditions the previous year suggest that inland wetland conditions encountered during the non-breeding season are increasingly related to their capacity to survive their northward migration.

There was an association between Australian inland wetland conditions and apparent survival in both Sharp-tailed Sandpiper and Red-necked Stint, but these correlations were inconsistent across the three shorebird areas. There are two possible explanations for these differences. First, different conditions within each of the coastal shorebird areas might compensate for the effects of inland condition on survival to varying degrees. Second, it is possible that the network of inland wetlands used by individuals at each shorebird area is sufficiently different to lead to different effects on survival. Further, Sharp-tailed Sandpiper is much less reliant on East Asia’s disappearing intertidal habitats (Bamford et al. 2008) than Curlew Sandpiper, which may explain why Sharp-tailed Sandpiper survival appears not to be affected by Australian inland wetland conditions during southward migration, because unlike Curlew Sandpiper, Sharp-tailed Sandpiper are less likely to be in poor condition upon arrival in Australia. It is also possible that deteriorating conditions in Australia do leave Sharp-tailed Sandpiper in poor enough condition to have a lower chance of surviving northward migration.
Results from Red-necked Stint suggest impacts of inland condition are felt during southward migration as well as during the rest of the non-breeding season.

**Abundance**

Our finding that coastal shorebird abundance varied with inland conditions is similar to studies that show that other waterbirds are known to move back and forth between coastal and inland areas as inland conditions change (Alcorn et al. 1994; Chambers and Loyn 2006; Wen et al. 2016). This suggests that similar to resident waterbirds (Wen et al. 2016), some non-breeding migratory shorebird species may be adapted to take advantage of the temporary expansions of suitable habitat found within Australia’s highly dynamic wetland systems. It seems reasonable to suppose that conditions at coastal sites are not changing sufficiently rapidly to cause this variation in counts.

**Immature ratio**

Breeding success is related to conditions experienced on the non-breeding grounds in migratory birds in general (Norris et al. 2004), and possibly shorebirds in particular (Aharon-Rotman et al. 2016). In our results, shorebird immature ratios showed significant relationships with inland conditions both in the previous year and in the current year, with the ratio of immatures lower at the coast when the interior was wet and cool. This suggests that immatures mirror adult patterns, but larger proportions of immatures stay away from the coast than adults when the interior is suitable. It has been hypothesised that immature shorebirds, which tend to conduct their first migration independent of adults and therefore lack prior information on where to go, would be more flexible in their selection of non-breeding habitats (Cresswell 2014).

**Limitations**

Several other factors might explain the lack of uniform causes of variation in response variables. First, the variables we used here are coarse surrogates of wetland availability and condition. Second, there are interspecific differences in optimal wetland conditions among these three species, with each preferring different water depths (Rogers and Hulzebosch 2014), and species such as Sharp-tailed Sandpiper are more likely to occur in areas with short vegetation such as saltmarsh or sedges (Higgins and Davies 1996). Third, it is also likely that these three species employ different migration and movement strategies, which may help explain why records of tens of thousands of individuals (of these species) at inland wetlands infrequently come from mixed species flocks (Barrett et al. 2003; Bertzeletos et al. 2012). We suspect that a better understanding of movement patterns through tracking work and restig of leg flags could explain variation in both abundance and survival data. Some populations of these individuals are believed to return to the same coastal shorebird area annually, while others are thought to use inland wetlands annually, but return to the same coastal refuge in times of drought. On present knowledge it would be very difficult to distinguish ‘transient’ birds from ‘resident’ birds, but that distinction could explain much of the variation in these data.

It would be useful to validate our results in other locations, to increase the precision of dependent variable estimates and also to identify predictors more closely tied to interspecific habitat requirements and the availability of shallow water, wet mud and wetland invertebrate densities. Future validation work could focus first on survival estimates for these three species and their relationship with inland wetland conditions, since our study is the first time this relationship has been reported. For example, one of the assumptions made in these survival analyses was that each individual had the same survival and recapture probability within each year. Both trap response and non-random temporary emigration can bias annual apparent survival estimates (Kendall et al. 1997; Fujiwara and Caswell 2002; Sandercock 2003; Schaub et al. 2004). This may explain why survival estimates are unrealistically low, especially for Sharp-tailed Sandpiper. Trap response can be modelled within the framework we have used here (Kéry and Schaub 2012). It is possible that further work within an integrated population model framework, which draws on additional population data and could estimate annual emigration (Kéry and Schaub 2012), could then be used to inform a multi-state Bayesian model (Gilroy et al. 2012).

**Conservation implications**

Our results suggest that enhanced management of Australian inland wetlands could be important to conserve declining shorebird populations, but further investigation will be required to make more prescriptive recommendations for management. Recent efforts towards wetland management in coastal or near coastal areas in South Australia’s Gulf of St. Vincent and near Victoria’s Port Phillip Bay may help mitigate shorebird declines (Clemens et al. 2016), notably the degradation of the Coorong wetland (Paton et al. 2018). However, our results suggest that efforts further afield could also
be productive, such as those being considered in the Murray-Darling Basin (Pittock and Finlayson 2011), or regionally within Victoria at wetlands with environmental water allocations.

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References


expert knowledge for a group of declining migratory birds. *Bird Conservation International* 27(1), 6–34. doi:10.1017/S0959270916000678


