



# Analyzing Variability and the Rate of Decline of Migratory Shorebirds in Moreton Bay, Australia

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**Abstract:** *Estimating the abundance of migratory species is difficult because sources of variability differ substantially among species and populations. Recently developed state-space models address this variability issue by directly modeling both environmental and measurement error, although their efficacy in detecting declines is relatively untested for empirical data. We applied state-space modeling, generalized least squares (with autoregression error structure), and standard linear regression to data on abundance of wetland birds (shorebirds and terns) at Moreton Bay in southeast Queensland, Australia. There are internationally significant numbers of 8 species of waterbirds in the bay, and it is a major terminus of the large East Asian-Australasian Flyway. In our analyses, we considered 22 migrant and 8 resident species. State-space models identified abundances of 7 species of migrants as significantly declining and abundance of one species as significantly increasing. Declines in migrant abundance over 15 years were 43–79%. Generalized least squares with an autoregressive error structure showed abundance changes in 11 species, and standard linear regression showed abundance changes in 15 species. The higher power of the regression models meant they detected more declines, but they also were associated with a higher rate of false detections. If the declines in Moreton Bay are consistent with trends from other sites across the flyway as a whole, then a large number of species are in significant decline.*

**Keywords:** migratory species, population declines, shorebirds, state-space models, variability

Análisis de la Variabilidad y Tasa de Declinación de Aves Vadeadoras Migratorias en la Bahía Moreton, Australia

**Resumen:** *La estimación de la abundancia de especies migratorias es difícil porque las fuentes de variabilidad difieren sustancialmente entre especies y poblaciones. Modelos de estado-espacio desarrollados recientemente abordan el tema de la variabilidad mediante la modelación directa de los errores ambientales y de medición, aunque su eficacia para la detección de declinaciones no ha sido probada con datos empíricos. Aplicamos modelos estado-espacio, mínimos cuadrados generalizados (con estructura de autorregresión de error), y regresión lineal estándar a datos sobre abundancia de aves de humedales (aves vadeadoras y golondrinas de mar) en la Bahía Moreton en el sureste de Queensland, Australia. En la bahía hay números significativos internacionalmente de 8 especies de aves acuáticas, y es un importante punto final del Corredor Asia-Australasia Oriental. En nuestros análisis, consideramos 22 especies migratorias y 8 residentes. Los modelos estado-espacio identificaron que las abundancias de 7 especies migratorias declinaron significativamente y que la abundancia de una especie aumentó significativamente. Las declinaciones en la abundancia de especies migratorias a lo largo de 15 años comprendieron entre 43 y 79%. Los mínimos cuadrados generalizados con estructura de autorregresión de error mostraron cambios en la abundancia de 11 especies, y la regresión lineal estándar indicó la declinación en 15 especies. El mayor poder de los modelos de regresión significa que*

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*detectaron más declinaciones, pero también se asociaron con una mayor tasa de detecciones falsas. Si las declinaciones en la Bahía Moreton son consistentes con las tendencias en otros sitios en el corredor, entonces un gran número de especies están declinando significativamente.*

**Palabras Clave:** aves veadoras, declinaciones poblacionales, especies migratorias, modelos estado-espacio, variabilidad

## Introduction

Long-term monitoring programs typically encompass many species within an assemblage (e.g., Thomas & Martin 1996; Link & Sauer 1998; Hewson & Noble 2009); thus, their design is often a compromise that allows monitoring of diverse life histories. For example, detection of trends in abundance of rare species requires more investment in survey effort, whereas common species require more stringent survey design. Identifying and understanding population trends in migratory species pose an additional challenge. Abundances and estimates of abundances of migratory species may be expected to be particularly variable because the animals are highly mobile, different stages of their life cycle occur in different places, and their wide spatial extent and high abundance create logistical difficulties in coordinating abundance estimation and monitoring (Piersma & Baker 2000; Piersma 2007). All these sources of variability make the robust detection of trends difficult because it is challenging to eliminate noise, and unless monitoring or analysis methods account for this variability, changes in abundance may go undetected. When the abundance of different species in an assemblage of both migrants and nonmigrants has different sources of variability, identifying trends can be extremely difficult.

Addressing variability in abundance requires a method that explicitly identifies and estimates the different forms and degrees of variability among species in an assemblage. Variability in abundance stems principally from measurement error and natural environmental variability (process error) (Wilson et al. 2011). Both of these types of variability are expected to be high for migratory birds. Although there are a number of good approaches for analyzing counts of bird abundance (e.g., Gregory et al. 2007; Soldaat et al. 2007), we expected a state-space approach (DeValpine & Hastings 2002; Holmes 2004; Staudenmayer & Buonaccorsi 2006) to be well suited to measuring abundances of co-occurring species with high variation in abundance and different life histories.

Abundances of multiple species of wetland birds are often monitored simultaneously with a single method (e.g., Skagen et al. 2003). We analyzed a time series of data on abundances of wetland birds collected at Moreton Bay, southeast Queensland, Australia (Milton & Driscoll 2006). Intercontinental migrants and Australian resident species occur at Moreton Bay, which is one terminus of the East Asian–Australasian Flyway and a Ramsar site. It supports up to 40,000 shorebirds in the summer and has interna-

tionally important numbers (>1% of the total flyway population) of 8 migratory shorebird species (Bamford et al. 2008; Oldland et al. 2008). There are numerous threats to migrant shorebird populations in Moreton Bay, and more generally in the flyway, including climate change, which may affect wetland breeding habitat in the Arctic (Klein et al. 2005); loss of stopover sites in mainland Asia (Barter 2002; Moores 2006), and reduction in area and quality of nonbreeding grounds, primarily in Australia (Environment Australia 1997). Migrant shorebirds worldwide seem particularly vulnerable to decline. Of 237 populations of migrant shorebirds for which data on trends in abundance exist, 52% are decreasing and 8% increasing (Wetlands International 2006). Two long-distance migrants endemic to the East Asian–Australasian Flyway and present in Moreton Bay have been listed recently as globally threatened by the International Union for Conservation of Nature (IUCN) (Great Knot [*Calidris tenuirostris*] and Eastern Curlew [*Numenius madagascariensis*]). There is an urgent need, therefore, to identify which species are declining and the principal causes of their decline (Kirby et al. 2008).

We used stochastic, state-space models to analyze the species assemblage from Moreton Bay. The data we used were composed of monthly estimates of abundance obtained over 15 years. We sought to identify abundance trends in the species that occur at Moreton Bay. An important consideration in selecting survey methods, however, is the trade-off between the statistical power gained to detect trends by collecting more years of data and the extra effort and cost involved in intensive sampling. Thus, we also compared the power obtained when analyzing all the within-year data with the power obtained when analyzing only one count per year. We also compared population trends and variability in abundance of resident and migrant species to help determine whether the causes of any trends might have been local or reflected conditions elsewhere.

Although the data we used required considerable effort to collect, 15 years is not a long time series in the context of state-space models. These models are computationally demanding because they fit more parameters than standard methods such as linear regression (Hovestadt & Nowicki 2008). State-space models also have lower power than linear regression to detect declines but at a lower probability of falsely detecting a decline (Wilson et al. 2011). Selecting 1 of the 2 approaches requires a choice between fitting more realistic, more complex, mechanistic models and fitting simpler models

with fewer parameters. Furthermore, state-space models are still relatively new and their efficacy in detecting declines in real data has been relatively untested. Consequently, we compared the results from the state-space model with a simple model of linear regression and also with generalized least squares with an autoregressive error structure because process noise tends to introduce autocorrelation into the residuals, which biases  $p$  values associated with results from a linear regression (e.g., Myers 1990).

## Methods

### Data Collection

Waterbirds were systematically counted by volunteers at 180 coastal sites in Moreton Bay between 1992 and 2008 (Milton & Driscoll 2006). Each month, approximately 40 of these sites were visited at the same time by different observers. Visits were concentrated around high tide (80% of visits made within 2 hours of the time of high tide), when birds are concentrated at roost sites, such as claypans and sand spits (Zharikov & Milton 2009). The number of sites visited per year increased between 1992 and 1995 and remained relatively stable thereafter. The spatial extent of survey effort was also greater in summer months (January–March) when nonbreeding migrants are most abundant. To account for this variation in sampling effort, we used the average number of birds counted per site per month as an index of abundance. We then log transformed the data and because some visits detected no birds, we used  $Y_t = \log(N_t + 0.5)$ , where  $N_t$  is the average number of birds counted per site at time  $t$  and  $Y_t$  is the observed log abundance index.

We analyzed data on the 30 most common waterbird species. In 21 of these species, the majority of the population leaves Australia during the austral winter and migrates northward to East Asian breeding grounds. One species, the Double-Banded Plover (*Charadriusbicinctus*), migrates to New Zealand in the austral summer to breed. We designated these 22 species as migrants (Table 1). The remaining 8 species are resident within Australia, and all but one species (Red-Necked Avocet [*Recurvirostranovaehollandiae*]) breeds within Moreton Bay. We designated these species as residents to distinguish them from species using the East Asian–Australasian Flyway (Table 1), even though the abundance of many of these residents varies seasonally as a function of local movements and inland breeding events (Higgins & Davies 1996).

### Annual Abundance Index

Within any 1 year, there was strong seasonal variation in abundance at Moreton Bay (Fig. 1). To avoid confounding different sources of variability, we modeled the

within-year seasonal variation in abundance and the annual change in abundance separately by reducing the monthly data to an annual abundance index. Use of the abundance observed at a given time of year (e.g., January) may confound interannual abundance fluctuations with interannual variability in the timing of migration, whereas the maximum observed abundance in each year has poor statistical properties. Both approaches do not use all the within-year data. Instead, we fitted a within-year periodic model, which can be represented with trigonometric terms (e.g., Flury & Levri 1999; Cannon et al. 2005):

$$Y_t = \beta_0 + \beta_1 \cos(2\pi t) + \beta_2 \sin(2\pi t) + \gamma_t, \quad (1)$$

where  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$  are estimated coefficients,  $t$  is time (in years), and  $\gamma_t$  has a normal distribution with mean zero and variance  $\sigma^2$ . Two terms are needed to represent seasonal periodicity, one for the amplitude of the oscillation and one for the phase. For 23 species the peak abundance was in the summer (January–March), so we defined their year as running from August to the end of July. The abundance of 7 species peaked in the winter (July–September), so we defined their year as running from January to the end of December. Because data were available for August 1992 to August 2008, there was one less estimate of abundance for species in the latter group. Different definitions of year did not alter results, but they allowed a more rigorous fitting procedure.

We fitted Eq. 1 to the abundance data for each year (12 points) for each species. We then used the maximum abundance from the fitted model from each year as the annual abundance estimate for each species. This process gave us an index of abundance proportional to the average peak-season abundance, but applied information from an entire year's sampling and resulted in 16 estimates of abundance covering 15 years. For each year, we generated parametric bootstrap samples of the betas in Eq. 1 with the estimated variance–covariance matrix from the regression. Thus, for each new sample set of  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$ , we calculated the maximum abundance on the basis of Eq. 1. The among-sample variance of these maxima gave an estimate of the error variance in the annual abundance estimate in year  $t$ , the within-year measurement (WYM) error variance ( $\hat{\sigma}_{\text{WYM}}^2(t)$ ) (where the hat represents an estimated parameter). We then calculated a mean value of this variance over the 15 years of data ( $\hat{\sigma}_{\text{WYM}}^2$ ) and used this value in the state-space models.

An alternative to collecting data every month is to collect data once in summer and once in winter (as in Shorebirds 2020, the Australian national monitoring program [Oldland et al. 2008]). Therefore, we also constructed a second time series of annual abundance indexes with only the raw January data on abundance of migrants (Fig. 1c) and only the raw July data for resident species. There was no within-year fitting, so we could not estimate a value for the WYM-error variance.

**Table 1. Trends in abundance of 30 waterbird species from Moreton Bay, Queensland, grouped into migrants and residents and arranged in increasing order of annual change in abundance.**

Species	Migrant or resident status	LR, annual change (%) <sup>a</sup>	p <sup>b,c</sup>	GLS p <sup>c,d</sup>	SS, annual change (%) <sup>e</sup>	AIC <sub>c</sub> weights (stable, declining or increasing, random walk)
White-winged Black Tern <i>Cblidoniasleucopterus</i>	M	-10.6	0.038*		-10.4	0.06, 0.55, 0.39
Red Knot <i>Calidriscanutus</i>	M	-9.1	0.001**		-8.9	0.1, 0.71, 0.18
Crested Tern <i>Sterna bergii</i>	R	-6.4	0.04*	= 0.19		0.08, 0.12, 0.80
Bar-tailed Godwit <i>Limosalapponica</i>	M	-6.4	<0.001**		-6.9	0.14, 0.67, 0.19
Ruddy Turnstone <i>Arenariainterpres</i>	M	-6.1	0.003**		-6.8	0.19, 0.53, 0.27
Greater Sand Plover <i>Charadriusleschenaultii</i>	M	-6.0	0.04*			0.83, 0.09, 0.08
Greenshank <i>Tringanebularia</i>	M	-5.9	<0.001**		-5.8	0.03, 0.7, 0.27
Great Knot <i>Calidristenuirostris</i>	M	-4.4	0.01*		-4.5	0.09, 0.5, 0.41
Grey Plover <i>Pluvialisquatarola</i>	M	-4.4	0.12			0.5, 0.14, 0.36
Curlew Sandpiper <i>Calidrisferruginea</i>	M	-4.0	0.13			0.36, 0.09, 0.55
Whimbrel <i>Numeniusphaeopus</i>	M	-3.8	<0.001**	<0.001**	-4.1	0.11, 0.64, 0.24
Lesser Sand Plover <i>Charadriusmongolus</i>	M	-3.8	0.28	= 0.17		0.04, 0.24, 0.73
Australian Pied Oystercatcher <i>Haematopuslongirostris</i>	R	-3.7	0.02*	= 0.15		0.08, 0.15, 0.76
Little Tern <i>Sterna albifrons</i>	R	-2.5	0.49			0.02, 0.14, 0.84
Eastern Curlew <i>Numeniusmadagascariensis</i>	M	-2.4	0.037*			0.45, 0.33, 0.22
Marsh Sandpiper <i>Tringastagnatilis</i>	M	-2.0	0.23			0.08, 0.18, 0.74
Terek Sandpiper <i>Xenuscinereus</i>	M	-1.6	0.58			0.98, 0, 0.02
Grey-tailed Tattler <i>Heteroscelusbrevipes</i>	M	-0.8	0.65			0.21, 0.15, 0.64
Black-winged Stilt <i>Himantopusbimantopus</i>	R	-0.8	0.71			0.02, 0.13, 0.85
Black-tailed Godwit <i>Limosalimosa</i>	M	-0.4	0.88			0.05, 0.14, 0.82
Caspian Tern <i>Hydroprogneaspia</i>	R	-0.3	0.83			0.07, 0.11, 0.82
Masked Lapwing <i>Vanellus miles</i>	R	-0.05	0.96			0.04, 0.12, 0.84
Common Tern <i>Sterna hirundo</i>	M	+0.4	0.96			0.33, 0.09, 0.58
Red-necked Avocet <i>Recurvirostranovaebollandiae</i>	R	+0.8	0.91			0.07, 0.12, 0.81
Red-capped Plover <i>Charadriusruficapillus</i>	R	+1.8	0.10			0.03, 0.16, 0.80
Double-banded Plover <i>Charadriusbicinctus</i>	M	+3.4	0.30			0.03, 0.21, 0.76
Gull-billed Tern <i>Gelochelidonnilotica</i>	M	+4.7	0.019*	= 0.13		0.09, 0.04, 0.88
Red-necked Stint <i>Calidrisruficollis</i>	M	+10.5	<0.001**		+9.5	0.05, 0.59, 0.36
Sharp-tailed Sandpiper <i>Calidrisacuminata</i>	M	+10.7	0.01*	= 0.13		0.04, 0.15, 0.81
Pacific Golden Plover <i>Pluvialisfulva</i>	M	+12.3	<0.001**			0.04, 0.24, 0.73

<sup>a</sup>Slope from a standard linear regression.<sup>b</sup>The p value from each regression.<sup>c</sup>Significance: \*p<0.05, \*\*p<0.01.<sup>d</sup>The p value for 6 species for which a generalized least squares regression (where the residuals follow an AR[1] correlation structure) provided a better fit to abundance data than standard linear regression (smaller AIC<sub>c</sub>). In all other species, linear regression was a better fit to the data.<sup>e</sup>Best state-space model was stochastic decline or increase. The estimated annual percentage change is given.

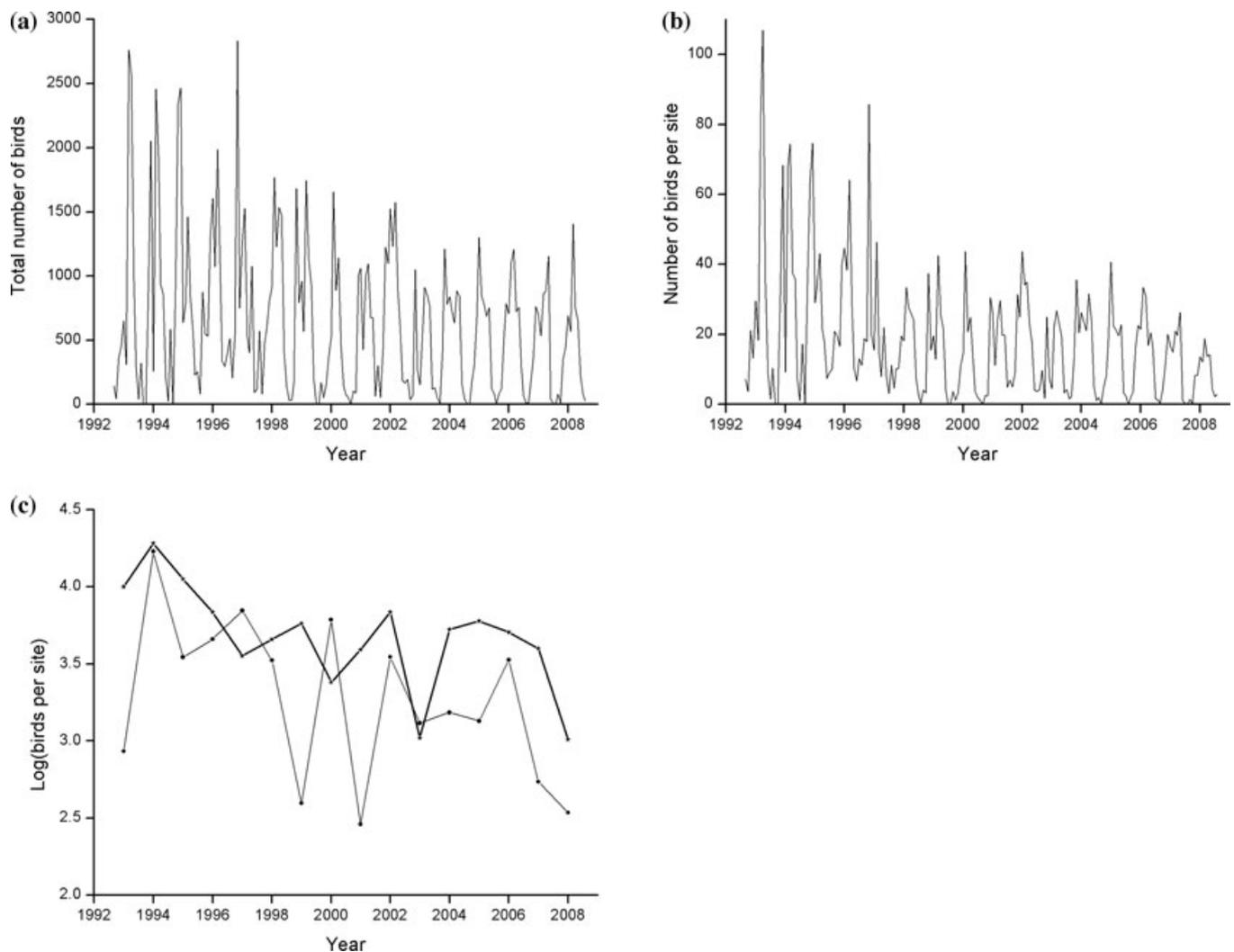


Figure 1. Times series of abundance data for Great Knot from Moreton Bay: (a) total number counted in each month in the entire Bay, (b) number counted in each month per site visited, (c) January count (thin line with circle symbols) and the fitted within-year periodic model (solid line with star symbols).

### State-Space Model

As in Wilson et al. (2011), we used a simple stochastic Gompertz model that represents deterministic factors, such as density dependence, and stochastic factors, such as process and measurement error. We used maximum likelihood to fit the state-space model to the time series of annual abundance indexes (Dennis et al. 2006). One problem with this approach is that the maximum likelihood estimates are frequently zero for one of the noise parameters. This is biologically unlikely and can be overcome by constraining the parameter-fitting process by imposing a nonzero minimum value for both parameters (Dennis et al. 2006; Knappe 2008). We used the estimate of WYM error ( $\hat{\sigma}_{\text{WYM}}^2$ ) as a minimum value for the total measurement error ( $\hat{\sigma}_M^2 \geq \hat{\sigma}_{\text{WYM}}^2$ ). For the process error, we set an arbitrary, but small, minimum value

( $\hat{\sigma}_M^2 \geq 0.0025$ ). When using a single count per year, we also used an arbitrary, but small, minimum value for the measurement error ( $\hat{\sigma}_p^2 \geq 0.0025$ ). As in Wilson et al. (2011), we fitted 3 nested models of decreasing complexity: quasi stable, density-dependent stability, stochastic exponential decrease or a random walk. We used a likelihood-ratio test to determine which model best represented the data.

For all species with abundances identified as declining, we also inspected the likelihood profile for  $\hat{a}$ , the growth rate. This was calculated by fixing a value of  $a$ , and then maximizing the log likelihood over the remaining parameters. By choosing values for  $a$  above and below  $\hat{a}$  and calculating the resultant likelihood, we determined a profile of the likelihood in the vicinity of  $\hat{a}$ . All the profiles were unimodal and parabolic (maximum at  $\hat{a}$ ), which suggests

this parameter can be estimated robustly (Dennis et al. 2010).

### Linear Regression

We fitted the following standard linear regression model to the data:

$$Y_t = \beta_0 + \beta_1 t + \delta_t, \quad (2)$$

where  $Y_t$  is the observed value of log abundance at time  $t$ ,  $\beta_0$  is the intercept,  $\beta_1$  is the trend parameter, and  $\delta_t$  is the error term. We used a significance level of 0.05 in a 2-tailed test to calculate the probability that the value for  $\beta_1$  was significantly different from zero.

The validity of the  $p$  values in the linear regression depended on whether the residuals ( $\delta_t$ ) were independent, identically distributed, and normal. In our linear-regression model we assumed abundance follows an exponential trend with no process noise. The latter tends to introduce autocorrelation into the residuals, which biases both the  $p$  values and the parameter estimates. To control for these biases, we also used a generalized least-squares regression, in which we assumed the residuals follow an AR(1) correlation structure. We retained only the model (either standard linear regression or generalized least squares) that minimized the Akaike information criterion ( $AIC_c$  was used to correct for small sample size). We refer to this approach as GLS/LR.

### Power Analyses

We calculated the power of the state-space model to detect declines by fitting the model to the annual abundance indices. We estimated  $\sigma_p^2$ ,  $\sigma_M^2$ , and  $X_0$  separately for each species. We then used a model of stochastic exponential decline with these parameters and a given trend ( $a$ ) to generate 1000 simulated time series all of 15-year length. We used a 50% and 80% decline in abundance over the 15 years ( $a = -0.046$  and  $a = -0.107$ ) because these were equivalent to a 4% and 10% decline per year, the maximum and minimum statistically significant decline rates identified in the data. We then fitted the 3 state-space models to the bootstrapped data and determined the best model with a likelihood-ratio test. The power was the proportion of times the best model indicated abundance was declining. We averaged the power over all species. For linear regression, we calculated the power by first estimating all the parameters in Eq. 2 and then generating bootstrapped time series. For GLS/LR, we performed a generalized least-squares regression, but only to generate the bootstrapped time series if the  $AIC_c$  value was less than for linear regression alone. Otherwise we used only the linear regression model. The power was the proportion of the bootstrapped time series for which abundance was identified as declining by linear regression or GLS/LR, respectively.

## Results

The state-space model identified abundances of 7 of the 30 most common species as significantly declining and the abundance of 1 species as increasing. Linear regression identified abundances of 11 species as declining and 4 as increasing (Table 1). All the species for which trends in abundance were identified with the state-space model were also identified with linear regression. The percentage change for all the decreasing species identified by the state-space model was between  $-4.1\%$  and  $-10.4\%$  per year, equating to a 46–79% decline over 15 years (62% on average). The state-space model identified abundances of 8 species as significantly changing (27%), abundances of 4 species as significantly stable and density dependent (13%), and the abundances of 18 species (60%) were best modeled as a random walk.

With the state-space model, all 8 species with significantly changing abundance were migrants. The abundances of all resident species were best modeled as a random walk. For linear regression, 9 out of 11 of the species with declining abundance and all 4 species with increasing abundance were migrants. The power of the state-space model to detect declines in abundances of migrants and residents was similar; for a 50% decline in abundance power was 0.35 for residents and 0.34 for migrants, and for an 80% decline power was 0.77 for residents and 0.72 for migrants.

With use of only a single estimate of abundance from either January or July, the state-space model identified the abundances of 4 migrant species as decreasing significantly (Bar-tailed Godwit [*Limosalapponica*], Green-shank [*Tringanebularia*], Whimbrel [*Numeniusphaeopus*], and Eastern Curlew [*Numeniusmadagascariensis*]) and no species' abundance as increasing. The power (averaged over all species) to detect a 50% and 80% decline in abundance was 0.20 and 0.48, respectively. For all the monthly data, power averaged over all the species was 0.35 and 0.73, respectively (Fig. 2). Linear regression with only a single estimate of abundance identified decreases in abundance of the same 4 species. The power to detect a 50% and 80% decline was 0.33 and 0.76, respectively, compared with 0.59 and 0.91 with all the monthly data (Fig. 2).

The  $AIC_c$  for the GLS/LR models was less than the  $AIC_c$  for the linear-regression model alone for 6 species: Crested Tern (*Sterna bergi*), Whimbrel, Lesser Sand Plover (*Charadriusmongolus*), Australian Pied Oystercatcher (*Haematopuslongirostri*), Gull-billed Tern (*Gelochelidonnilotica*), and Sharp-tailed Sandpiper (*Calidrisacuminata*). For 4 of these species, linear-regression model identified significant declines in abundance, whereas GLS/LR models did not. For one species both models identified a significant decline and for one species neither model identified such a decline (Table 1).

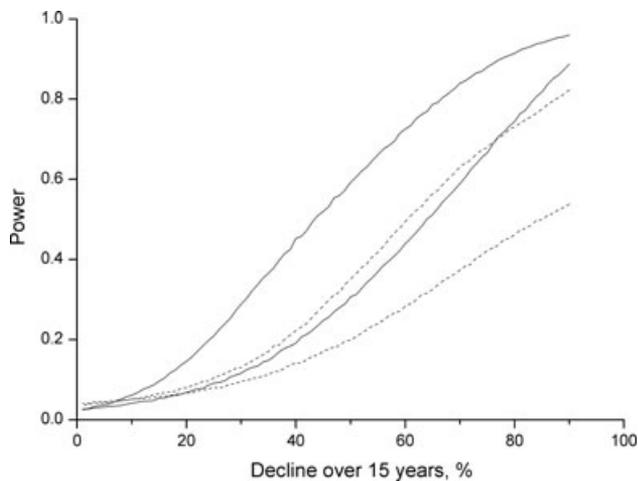


Figure 2. Difference in the power to detect declines between use of a single annual estimate of abundance and 12 monthly estimates (solid lines, standard linear regression; dashed lines, state-space model). In each case the upper solid or dashed line is the monthly abundance and the lower line is the single winter or summer abundance (see text for details). The power is averaged over 1000 time series, and the declines are for over 15 years (16 points).

The GLS/LR models identified no significant changes in abundance for any species that was not also identified with linear regression only. No GLS/LR models identified statistically significant changes in abundance for resident species.

A probability threshold for GLS/LR that would result in a rate of false detections equivalent to the state-space model ( $p = 0.05$  in the likelihood ratio test) was 0.005, 10 times smaller (see Wilson et al. 2011 for methods). Equivalently, the probability threshold for GLS/LR was kept at  $p = 0.05$ , and the probability threshold in the state-space approach increased to  $p = 0.15$ , or  $\chi^2 > 2.0$ . When we analyzed the Moreton Bay data with GLS/LR and  $p = 0.005$ , the abundances of 5 species were declining and 2 were increasing. All 5 declining species and one of the increasing species were identified by the state-space model ( $p = 0.05$ ). The GLS/LR also identified the abundance of the Pacific Golden Plover (*Pluvialisfulva*) as increasing.

## Discussion

State-space models identified many more declines than increases in species' abundances (7 declines, 1 increase). The observed magnitude of declines over 15 years were 43–79%, and those species with significant trends in abundance were all migrants. These results were consistent whether the state-space or linear-regression models

were used. Process noise in abundance data causes an overestimation of the rate of declines, but also results in declines of small magnitude (30–50% over 15 years) being undetected (Wilson et al. 2011). This indicates that some of the declines in abundance may be of smaller magnitude than reported, but also that the number of species with declining abundances may be higher. There was little difference in the statistical power to detect changes in abundances of migrant and resident species, and the bias in detecting declines in the abundance of migrant species remained if the within-year model was not fitted. If these declines in abundance in Moreton Bay are indicative of the global population trend, then the observed declines mean classifying 2 species as endangered and 5 as vulnerable (on the basis of IUCN criterion A2, where endangered is defined as a 50–80% decline in abundance and vulnerable is a 30–50% decline calculated over 10 years).

Differences between the state-space and linear-regression models were partially explained by autocorrelated residuals. Also, for every species, the linear-regression model had a lower AIC<sub>c</sub> than the state-space model. Nevertheless, the properties of information-theoretic model-selection indexes applied to state-space models are not well understood (Dennis et al. 2006), and process noise, ubiquitous in ecological systems, inflates the proportion of false detections in the regression models (Wilson et al. 2011). By substantially lowering the probability threshold used in the regression models, a comparable false detection rate with the state-space approach was achieved while a higher power to detect trends was retained. For the Moreton Bay data, the results when we lowered the probability threshold for GLS/LR were comparable to the results for the state-space model. Which model is preferable depends on both whether it is necessary to detect small declines in abundance and false detections of declines are acceptable and the relative costs of different types of errors (Field et al. 2004). Nevertheless, selection of a model for a given application is not related only to error rates, but also to the underlying assumptions and whether they are correct. In a data set that is known to have high levels of noise, an analytical approach that ignores environmental variability may lead to false detection of trends, so the state-space approach might be preferable. Conversely, when data are limited, a relatively complex stochastic model may overfit data, so linear regression might be preferred. The fact that both linear-regression and state-space models produced similar results gives us confidence that abundances of migrant species in this assemblage are declining.

Collecting monthly data as opposed to a single estimate of abundance in summer or winter resulted in approximately 50% more power to detect declines in abundance of 20–80% over 15 years. Whether this is a good return for the extra effort involved depends on the aims of the monitoring scheme and the time period over which

inferences about population trends are needed. In addition to the increase in power, a number of other analyses are made possible by monthly estimates, including identifying changes in arrival or departure times and investigating spatial and temporal patterns of site use.

If conditions in Moreton Bay were deteriorating for shorebirds in general, we would expect migrant and resident species to be affected equally. Nevertheless, we found a greater proportion of the abundances of migrants was declining, despite no higher power to detect trends than for resident species. This suggests that the cause of declines lies outside Moreton Bay, perhaps elsewhere in the flyway. A recent study of the Great Knot shows a correlation between loss of habitat at migratory stopover sites and a reduction in abundance of birds at nonbreeding sites in northwestern Australia (Rogers et al. 2006). All the species we identified as declining are highly dependent on stopover sites in the Yellow Sea region (Bamford et al. 2008; van de Kam et al. 2010), where land-reclamation projects have reduced the extent of intertidal feeding habitats in some regions by up to 50% in the last 20 years (Barter 2002; Moores 2006). Use of the Yellow Sea region has also been correlated with declines in the numbers of wading birds at nonbreeding sites in Japan (Amano et al. 2010). Another potential explanation is that migrants are affected more by reductions in local habitat quality than are residents, perhaps because of increased difficulty in gaining enough energy for migration (Bairlein & Gwinner 1994; Baker et al. 2004).

No trend data have been published for two-thirds of the 57 shorebird populations in Australia (Wetlands International 2006). Recently, Nebel et al. (2008) published data on population trends of shorebirds in inland eastern Australia that were based on aerial counts. They observed significant declines of “small shorebirds” and 4 resident species. Nevertheless, these declines are more likely related to lack of water flow due to water extraction by humans. Other preliminary analyses from southern Australia show significant local declines in several shorebird species (Gosbell & Clemens 2006; Rogers & Gosbell 2006). Bar-tailed Godwit is declining at sites in Victoria and Tasmania, but the trends in annual estimates of abundance are not significant.

The declines in abundance we detected in some species in Moreton Bay are likely to prove reliable indices of their overall population trends. Species with strong declines in Moreton Bay, such as Red Knot (*Calidris canutus*) and Bar-tailed Godwit, are concentrated at fewer sites in the nonbreeding season than many other species (Bamford et al. 2008). An estimated 3.6% of the East Asian–Australasian Flyway population of Bar-tailed Godwit occurs at Moreton Bay. Moreton Bay is also the southernmost site with internationally important numbers of Whimbrel (1.5% of population). Declines in species’ abundances near the limits of their nonbreeding distribution (Reid & Park 2003) are often the first signs of

more widespread trends (Gosbell & Clemens 2006). If the declines in Moreton Bay are consistent with trends from other sites across the flyway as a whole, then abundances of a large number of species are in significant decline.

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