

# ECOGRAPHY

## Research

### The large-scale drivers of population declines in a long-distance migratory shorebird

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Migratory species can travel tens of thousands of kilometers each year, spending different parts of their annual cycle in geographically distinct locations. Understanding the drivers of population change is vital for conserving migratory species, yet the challenge of collecting data over entire geographic ranges has hindered attempts to identify the processes leading to observed population changes. Here, we use remotely sensed environmental data and bird count data to investigate the factors driving variability in abundance in two subspecies of a long-distance migratory shorebird, the bar-tailed godwit *Limosa lapponica*. We compiled a spatially and temporally explicit dataset of three environmental variables to identify the conditions experienced by each subspecies in each stage of their annual cycle (breeding, non-breeding and staging). We used a Bayesian *N*-mixture model to analyze 18 years of monthly count data from 21 sites across Australia and New Zealand in relation to the remote sensing data. We found that the abundance of one subspecies *L. l. menzbieri* in their non-breeding range was related to climate conditions in breeding grounds, and detected sustained population declines between 1995 and 2012 in both subspecies (*L. l. menzbieri*,  $-6.7\%$  and *L. l. baueri*,  $-2.1\%$  year<sup>-1</sup>). To investigate the possible causes of the declines, we quantified changes in habitat extent at 22 migratory staging sites in the Yellow Sea, East Asia, over a 25-year period and found  $-1.7\%$  and  $-1.2\%$  year<sup>-1</sup> loss of habitat at staging sites used by *L. l. menzbieri* and *L. l. baueri*, respectively. Our results highlight the need to identify environmental and anthropogenic drivers of population change across all stages of migration to allow the formulation of effective conservation strategies across entire migratory ranges.



## Introduction

Widespread declines of migratory species are an emerging global phenomenon, yet the drivers of their population change are rarely well understood (Wilcove and Wikelski 2008, Bauer and Hoyer 2014). This is principally due to the vast geographic ranges of migratory species, which can cover thousands of kilometers across multiple countries, hindering attempts to identify the specific drivers of change (Webster et al. 2002, Piersma et al. 2015). Ecologists investigating the factors that influence population dynamics of migratory species have typically been limited to just one stage of their annual cycle, such as in wintering (hereafter non-breeding), staging or breeding areas. However, events during one stage of the annual cycle can carry-over to subsequent stages (Marra et al. 1998), leading to population changes that may be driven by processes occurring thousands of kilometers apart (Iwamura et al. 2013, Rushing et al. 2016, van Gils et al. 2016). For these reasons, understanding the range of factors that influence migratory bird populations throughout their full annual cycle remains a fundamental challenge in migration biology and is the principal knowledge gap hindering effective conservation of many migratory species (Bowlin et al. 2010, Hostetler et al. 2015).

Migratory shorebird populations in the East Asian-Australasian (EAA) Flyway, which complete annual migrations from breeding areas in the Arctic to non-breeding areas in Asia and Australasia, are rapidly declining (Amano et al. 2010, Clemens et al. 2016, Studds et al. 2017). A range of threatening processes are thought to contribute to the population declines, including habitat loss (Amano et al. 2010, Murray et al. 2014, Murray and Fuller 2015, Studds et al. 2017), habitat degradation (MacKinnon et al. 2012, Murray et al. 2015, Clemens et al. 2016) and human disturbance (Zockler et al. 2010, Dhanjal-Adams et al. 2016). These threats are considered most severe in migratory staging areas in the Yellow Sea region of East Asia (Melville et al. 2016), and their direct impact on survival during migration has emerged as a leading hypothesis on the mechanism causing shorebird declines in the EAA Flyway (Piersma et al. 2015, Studds et al. 2017).

Though threatening processes from human activities are known to impact shorebird populations, environmental conditions have also been shown to strongly influence populations of migratory shorebirds, primarily through direct effects on survival and reproduction, and indirect effects on prey, predators and competitors. For example, colder than average conditions at breeding grounds negatively influenced growth rate and survival of red knot *Calidris canutus canutus* (Boyd and Piersma 2001) and curlew sandpiper *Calidris ferruginea* (Schekkerman et al. 1998). Similarly, reduced precipitation has been suggested as a mechanism causing reduced survival of European black-tailed godwit *Limosa limosa limosa* at sites across their range, primarily by increasing population densities at foraging sites, although these effects were considered highly coupled with widespread habitat change (Gill et al.

2007). Recently, van Gils et al. (2016) found that earlier snowmelt in the arctic breeding range of red knot led to a timing mismatch with peak food abundance which inhibited the growth rate of chicks that ultimately led to reduced survival at their non-breeding grounds in Africa and an overall population decline (van Gils et al. 2016).

However, despite evidence that both anthropogenic threats and environmental conditions can lead to population change in migratory shorebirds, few studies have simultaneously investigated the influence of both of these factors on shorebird abundance across their entire migratory range. Indeed, understanding the factors influencing the abundance of migratory shorebirds requires spatially and temporally explicit analyses of data from sites that can occur across entire hemispheres. The rapid growth of satellite derived data, which permits the remote collection of data on factors known to influence the population dynamics of migratory species at relevant temporal and spatial scales, offers the potential to improve our understanding of these factors across the full annual cycle of migratory species. In this study, we utilize information from satellite tracking, ringing studies, high resolution satellite environmental datasets and a continent-wide shorebird monitoring program to investigate the factors that influence abundance across the entire range of a long-distance migratory shorebird, the bar-tailed godwit *Limosa lapponica*. We focus our analysis on two geographically separated subspecies (*L. l. menzbieri* and *L. l. baueri*) that have unique breeding and non-breeding areas and highly contrasting migration routes, allowing a comparative investigation of the range-wide factors that may explain population variability. First, we develop a spatially and temporally explicit dataset of three environmental variables that are known to influence survival, body condition or breeding performance of migratory shorebirds across their annual cycle. Second, we implement a population analysis of an 18-year time series from 21 sites across Australia and New Zealand using a Bayesian *N*-mixture model to identify the environmental drivers important for population abundance across the full geographic range of each subspecies. Last, because habitat loss is considered the primary cause of shorebird declines in the EAA Flyway, we quantify changes in extent of intertidal habitat at 22 internationally important migratory staging sites in the Yellow Sea region of East Asia using satellite images from the Landsat Archive.

## Material and methods

### Study species

Our analysis focuses on two subspecies of bar-tailed godwit that occur in the EAA Flyway. Recent satellite tagging studies have illustrated the vastly different migration routes of the two subspecies (Fig. 1), providing the most comprehensive migration route data for any species of shorebird in the flyway (Gill et al. 2005, Minton et al. 2006,

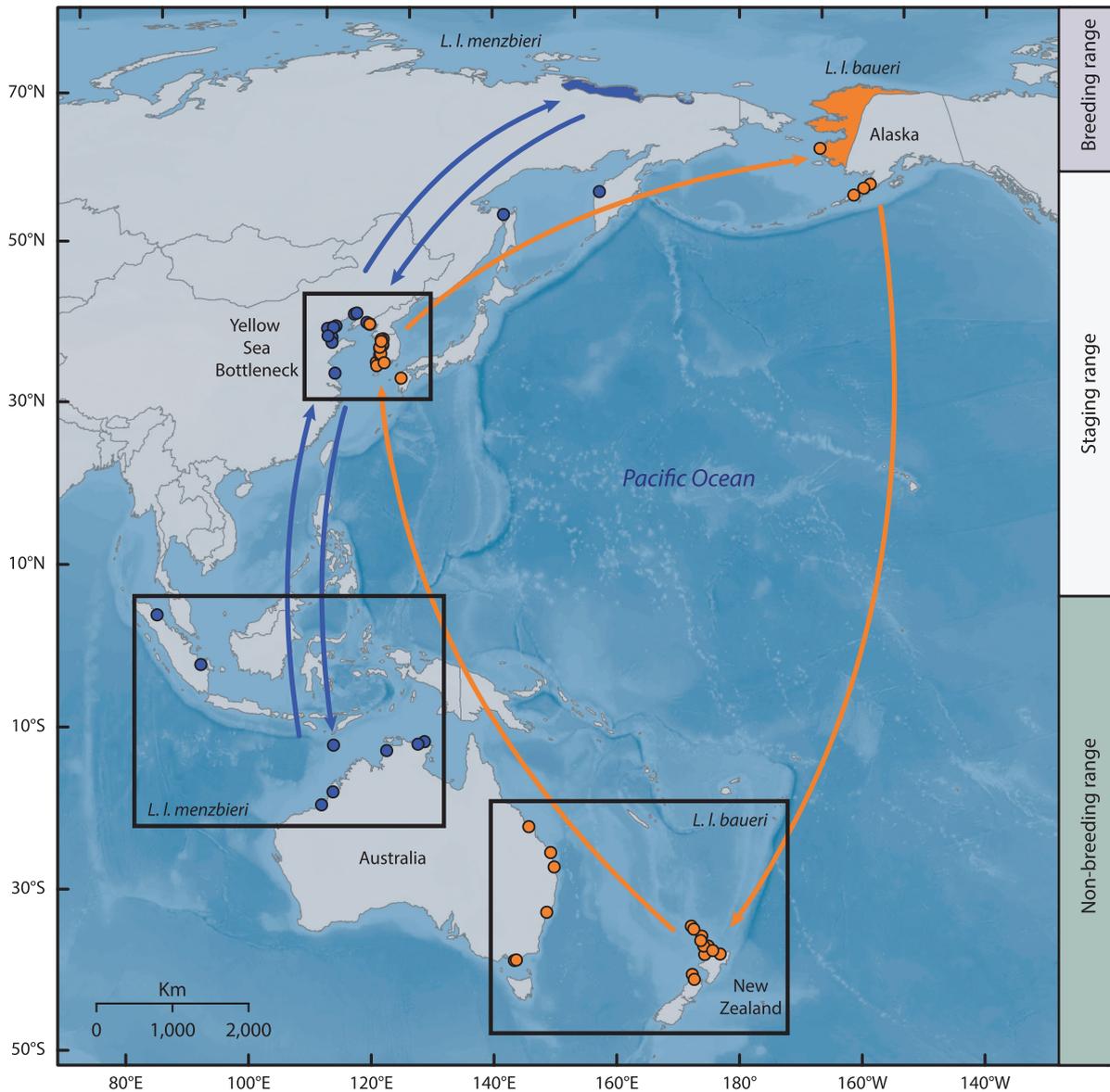


Figure 1. The contrasting migration routes of the two subspecies of bar-tailed godwit investigated in this study. The migration routes from breeding areas to non-breeding areas, via staging sites, are shown for *L. l. menzbieri* (blue arrows) and *L. l. baueri* (orange arrows). Points are internationally important sites, defined as supporting > 1% of the flyway population (Bamford et al. 2008). Data for the population trend analysis were available for 21 sites in Australia and New Zealand (Supplementary material Appendix 1 Fig. A1).

Wilson et al. 2007, Minton et al. 2011, Battley et al. 2012). The Alaskan-breeding subspecies *L. l. baueri* completes the longest recorded non-stop migratory flight of any shorebird (Gill et al. 2009), flying non-stop across the Pacific Ocean from Alaska to New Zealand and eastern Australia for the non-breeding season before migrating back to breeding grounds via staging sites in the eastern Yellow Sea region of East Asia (Wilson et al. 2007, Battley et al. 2012). In contrast, the Russian-breeding subspecies *L. l. menzbieri* migrates from breeding grounds in eastern Russia, through staging sites in the western Yellow Sea to non-breeding sites in remote north-western Australia, before returning to breeding grounds via the same route (Fig. 1; Wilson et al. 2007,

Battley et al. 2012). Although both subspecies stage in the Yellow Sea, there are differences in how they migrate through the region; *menzbieri* primarily stages on the western coast of the Yellow Sea, while *baueri* stages on the eastern coastline (Fig. 1; Wilson et al. 2007).

### Population data

To estimate total abundance and population trends of the two godwit species, we used 18 years of godwit count data from 21 non-breeding sites across Australia and New Zealand (1995–2012; Supplementary material Appendix 1 Fig. A1). Counts were conducted at high-tide roosts of five

*L. l. menzbieri* sites in north-west Australia and 16 *L. l. baueri* sites in east Australia and New Zealand by experienced observers from wader study groups (Clemens et al. 2012). We selected maximum counts conducted during January and February (peak non-breeding season) for use as replicates in the statistical analyses (*L. l. menzbieri*,  $n=64$  counts; *L. l. baueri*,  $n=328$  counts) because, at this time, godwits are unlikely to move between sites while in primary moult (Wilson et al. 2007). However, monthly counts were not available at all sites in all years, and the mean number of counts per site per year was 1.04 (range 0–2). Further details of the count dataset, including contributing organizations, quality assurance and a full list of observers, are provided in Clemens et al. (2012).

### Migratory network

Across the EAA Flyway, bar-tailed godwits occur at 58 sites in numbers exceeding 1% of their estimated total flyway population (Bamford et al. 2008). We developed a spatial dataset of these internationally important wetland sites to define the known flyway network of each subspecies (after Iwamura et al. 2013). Site boundaries were digitized and classified according to their role in the annual cycle, which included breeding sites in the arctic, non-breeding sites in New Zealand and Australia, and staging sites in the Yellow Sea, East Asia (Fig. 1; Wilson et al. 2007, Bamford et al. 2008, Battley et al. 2012). For further details of the site mapping protocol, see Iwamura et al. (2013).

### Environmental data

To investigate the influence of environmental conditions across the full annual cycle on godwit abundance, we compiled a spatially and temporally explicit dataset of environmental conditions encountered by godwits at each stage of their annual cycle (breeding, staging and non-breeding). We acquired global-scale gridded data for three environmental variables that have been shown to affect survival, condition or breeding performance of migratory shorebirds using global-scale gridded datasets (Supplementary material Appendix 1 Table A1). Changes in mean temperature have been shown to influence abundance through reduced growth rates of chicks, and reduced breeding success and survival (Schekkerman et al. 1998, Aharon-Rotman et al. 2015, Senner et al. 2015, van Gils et al. 2016), so we obtained monthly land surface temperature data from the NOAA Earth System Research Laboratory (LST; GHCN CAMS Gridded 2m Temperature). Second, precipitation has been shown to alter the availability of foraging habitat, increase population densities at foraging sites, influence the distribution and availability of benthic prey, and reduce breeding success at breeding sites (Farmer and Wiens 1999, Gill et al. 2007). We used Global Precipitation Climatology Project (GPCP) precipitation data from the NOAA Earth System Research Laboratory (Huffman et al. 2009). Third, chlorophyll-a, a proxy for primary productivity in coastal zones, was included in the analysis due to

a reported influence on the distribution and abundance of shorebirds globally (Butler et al. 2001). We used the SeaWiFS Global Monthly Mapped 9 km Chlorophyll-a concentration data (SeaWiFS Project 2003). The chlorophyll-a data only became available in 1998, so we assigned the mean of the corresponding stage of all other years to the first three years of chlorophyll data (Supplementary material Appendix 1 Fig. A2; Kéry and Schaub 2012). Further details of environmental data, including dataset names, data resolution, temporal availability, and sources are provided in Supplementary material Appendix 1 Table A1.

To develop the covariate dataset of environmental conditions encountered by migrating godwits, we first determined the annual migration schedule of each subspecies from published banding, observation and satellite tagging studies (Wilson et al. 2007, Conklin et al. 2010, Battley et al. 2012, Choi et al. 2016). The review indicated that godwits are present in their breeding range in June–July, non-breeding range in October–March, and staging sites in Apr–May (northern migration) and Aug–Sept (southern migration). Second, we calculated mean environmental conditions at each stage of the annual cycle for the period in which godwits were present; breeding season (June–July) and stopover data (April–May; August–September) were collected for the year prior to the count and non-breeding season data (October–March) were collected for the months that included the January and February counts. This process yielded a covariate dataset consisting of 9 covariates of environmental conditions (3 migration stages  $\cdot$  3 environmental variables) representing conditions encountered by godwits during each annual cycle (hereafter referred to as years) over the 18 year study period (1995–2012). We tested for covariation among the environmental covariates, which indicated that mean temperature and rainfall were highly correlated within breeding and non-breeding stages of the annual cycle (Pearson's  $|r| > 0.7$ ; Dormann et al. 2012). We retained breeding season land surface temperature over breeding season rainfall because changes in temperature have been shown to influence recruitment and survival of shorebirds in their breeding regions (Piersma et al. 2015, van Gils et al. 2016). Conversely, we opted to retain rainfall over land surface temperature in non-breeding areas because reduced rainfall has previously been shown to increase shorebird densities at non-breeding sites by reducing water availability in nearby areas (Gill et al. 2007, Clemens et al. 2016). Thus, the final seven environmental covariates for the statistical analysis were land surface temperature in staging and breeding regions ( $tem_{st}$ ,  $tem_{br}$ ), rainfall at staging and non-breeding regions ( $rai_{st}$ ,  $rai_{nb}$ ) and coastal chlorophyll-a at staging, breeding and non-breeding regions ( $chl_{st}$ ,  $chl_{br}$ ,  $chl_{nb}$ ). For each covariate, we subtracted the mean and divided by the standard deviation prior to the statistical analysis (Kéry and Schaub 2012).

### Statistical analysis

We used a Bayesian  $N$ -mixture model to analyze the abundance and population trends of the bar-tailed godwit

subspecies in relation to the spatially and temporally explicit environmental covariate dataset. The  $N$ -mixture model is a hierarchical extension of a generalized linear mixed model (GLMM) that provides estimates of abundance that account for detection error (Royle 2004, Kéry and Schaub 2012, Kéry and Royle 2015).  $N$ -mixture models are particularly useful for obtaining ecologically realistic estimates of abundance where repeated counts have been conducted and where the inclusion of covariates relevant to abundance is possible (Kéry 2008, Joseph et al. 2009). Two relevant assumptions of  $N$ -mixture models are (i) that the population is closed between replicate counts in year  $k$  and (ii) that there are no identification errors (such as false inclusion or double counting) in the count data (Kéry and Schaub 2012). Bar-tailed godwits exhibit very high site fidelity at non-breeding sites within seasons (Conklin et al. 2010) and all counts were conducted by experienced observers (Clemens et al. 2012).

Initially, we used an indicator variable selection method to investigate which environmental covariates were potentially important predictors of abundance (Hooten

and Hobbs 2015). Indicator variable selection is useful for identifying influential predictors for models that, like those used here, propagate estimation uncertainty (Mutshinda et al. 2013, Hooten and Hobbs 2015). To perform indicator variable selection, we introduced an indicator variable with Bernoulli prior (0.5) to the model for abundance (specified below). In each Markov chain iteration, the indicator variable adopts a value of 1 if the  $x$ th covariate at site  $i$  in year  $k$  is an influential predictor of abundance and 0 if not, allowing infrequently selected variables to be assessed as unimportant (i.e. with posterior inclusion probabilities  $\leq 0.25$ ) and more frequently selected variables as uncertain or potentially important predictors of abundance ( $> 0.25$ ; Mutshinda et al. 2013). Three covariates were identified as potentially important and were retained in the final model for abundance (Fig. 2).

We assumed that abundance ( $N_{ik}$ ) at site  $i$  in year  $k$  followed a *Poisson* distribution with mean  $\lambda_{ik}$ :

$$N_{ik} = \text{Poisson}(\lambda_{ik})$$

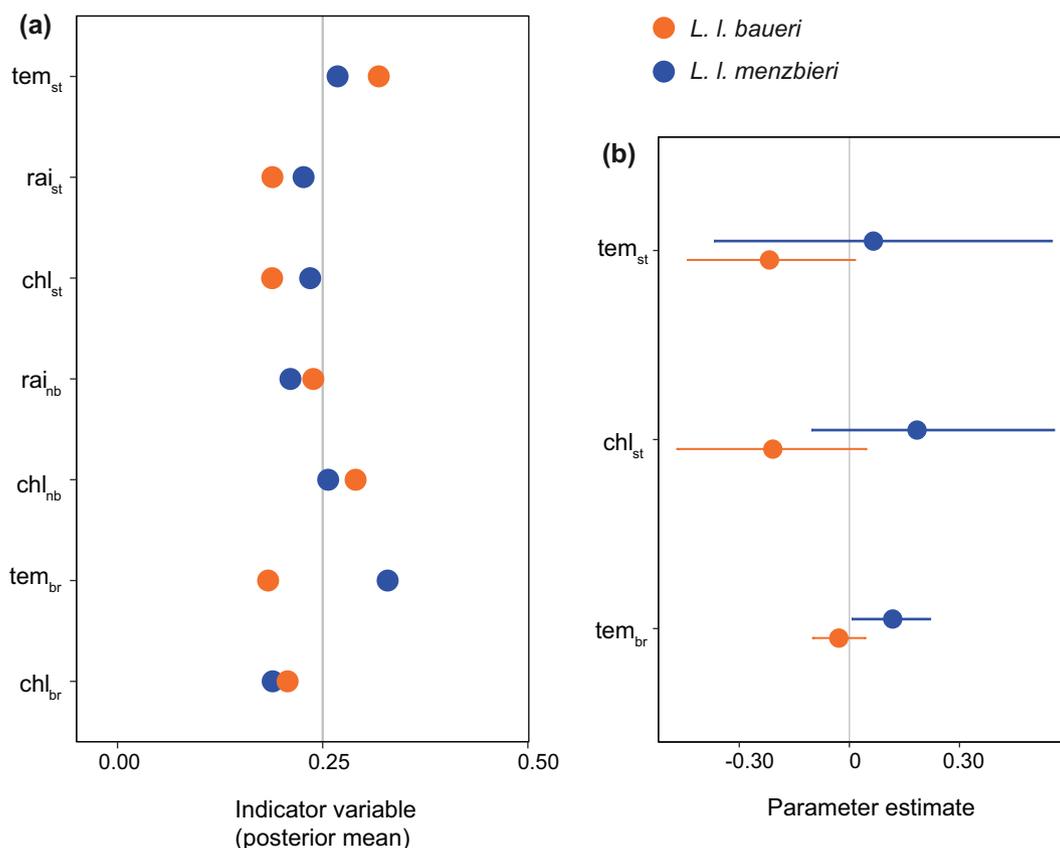


Figure 2. Variable importance (a) and parameter estimates (b) of covariates used in Bayesian  $N$ -mixture models of estimated abundance of bar-tailed godwit in the East Asian-Australasian Flyway. (a) Indicator variable selection. Covariates with posterior inclusion probabilities  $\leq 0.25$  were considered unimportant and removed from the final model for abundance. Covariates  $> 0.25$  were considered potentially important and included in the final model for abundance. (b) Parameter estimates of the three covariates included in the final model for abundance. Points show the posterior means and lines indicate the 95% credible intervals. Coding of covariates are rain (rai), land surface temperature (tem), chlorophyll-a (chl) at staging ( $_{st}$ ), breeding ( $_{br}$ ) and non-breeding ( $_{nb}$ ) sites.

Then, our model for expected abundance ( $\lambda_{ik}$ ) for each subspecies ( $s$ ) was:

$$\log(\lambda_{iks}) = \omega_i + \alpha_s + \beta_s(k - k^*) + \sum_{c=1}^c \beta_{cs} X_{ik} + \varepsilon_{ik}$$

The model includes a random effect for each count site ( $\omega_i$ ), a sub-species specific intercept ( $\alpha_s$ ), a sub-species specific slope estimate of population trend ( $\beta_s$ ) centered on mean year  $k^*$ , species-specific slopes ( $\beta_{cs}$ ) for each of  $c$  environmental covariates ( $X_{ik}$ , see Environmental data), and an additional term to account for unmodeled variation in counts at each site in each year ( $\varepsilon_{ik}$ ). Diffuse priors with a mean drawn from a normal distribution of mean 0 and variance 0.001, and with a variance drawn from a gamma distribution with a shape and scale of 0.001 were specified for  $\alpha_s$ ,  $\beta_s$ ,  $\beta_{cs}$  and  $\varepsilon_{ik}$ .

Detection probability ( $p$ ) was modeled as:

$$\text{logit}(p_{ijk}) = \gamma_k + \delta_{ijk}$$

where the  $\gamma_k$  is the mean detection probability in year  $k$  and  $\delta_{ijk}$  is a random effect that allows detection probability to vary by site  $i$ , count  $j$  and year  $k$ . We specified a uniform distribution for  $\delta_{ijk}$  with range 0–1. Although it is possible to incorporate covariates for detection probability in  $N$ -mixture models (Joseph et al. 2009), no covariates were included our model because information such as tide height and weather conditions that could be used reliably across all sites and years was not available (Clemens et al. 2012).

We used JAGS via the ‘R2jags’ package in R (Plummer 2003, Su and Yajima 2013) to fit the  $N$ -mixture model simultaneously to each subspecies (model code is provided in Supplementary material Appendix 2). We ran three Markov chains for 800 000 iterations and, after discarding the first 200 000 iterations, drew samples at a thinning rate of 1 in 20 from the posterior ( $n = 90\,000$  samples). Gelman-Rubin statistics ( $\hat{R} < 1.1$ ) and trace-plots indicated convergence of all parameters in the model (Gelman and Hill 2007). We diagnosed model fit through a posterior predictive check, which compares the chi-squared goodness of fit in the observed data to the goodness of fit in data simulated from the posterior distribution. The proportion of MCMC samples where goodness of fit in the observed data exceeds that of the replicate data should have a Bayesian p-value near 0.50 when model fit is good. Even when model structure is correct, the variance may still be too large (Kéry and Royle 2015). We therefore tested for over-dispersion in the data with the  $\hat{c}$  ratio, which should be close to 1.00 when model fit is good. A posterior predictive check indicated good model fit ( $p = 0.507$ ) and there was no evidence of over-dispersion ( $\hat{c} < 1.004$ ).

### Habitat loss data

To provide context for the population analysis, we obtained a remotely-sensed dataset of intertidal wetland loss for the entire Yellow Sea staging region for the period 1980–2009. The dataset, developed from Landsat TM and ETM+ imagery,

allowed the estimation of the extent of intertidal habitat remaining at staging sites for each subspecies in relation to historical extents (Murray et al. 2012, 2014). We extracted tidal flat extent data for the staging sites used by the two subspecies of godwit ( $n = 22$  staging sites) and determined the percentage of habitat lost at each site over a ~30 year period (Table 1; Murray and Fuller 2015). Although the habitat loss data could not be included in the statistical analysis due to a lack of yearly data and its confounding effect with the linear time trend (van Gils et al. 2016), habitat loss is thought to be the leading driver of shorebird population declines in the EAA Flyway (Piersma et al. 2015, Clemens et al. 2016, Conklin et al. 2016, Studds et al. 2017) and therefore warrants consideration in our study.

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.3879g>> (Murray et al. 2017).

## Results

### Environmental drivers of abundance

The indicator variable selection analysis suggested that rainfall and coastal chlorophyll-*a* in staging areas ( $\text{rai}_{st}$ ,  $\text{chl}_{st}$ ), rainfall at non-breeding sites ( $\text{rai}_{nb}$ ) and coastal chlorophyll-*a* at breeding sites ( $\text{chl}_{br}$ ) were unimportant in influencing non-breeding abundance of godwits (Fig. 2a). With posterior inclusion probabilities of  $> 0.25$ , land surface temperature at staging sites ( $\text{tem}_{st}$ ) and coastal chlorophyll-*a* at north-west Australian non-breeding sites ( $\text{chl}_{nb}$ ) were identified as potentially important for both subspecies. Temperature at breeding sites ( $\text{tem}_{br}$ ) was also identified as a potentially influential predictor for *L. l. menzbieri*. The posterior distributions of the parameter estimates from the  $N$ -mixture model indicated that abundance *L. l. menzbieri* increased after warmer breeding seasons, but there was no evidence that abundance was related to the other environmental variables (Fig. 2b). No relationship between the three environmental variables and the abundance of *L. l. baueri* was detected (Fig. 2b).

### Population trends

Our analysis revealed that between 1995 and 2012, both subspecies of bar-tailed godwit exhibited sustained population declines across their entire non-breeding range (Table 1; Fig. 3a, b). The Russian breeding subspecies (*L. l. menzbieri*) declined at a greater rate ( $-6.7\%$  year $^{-1}$ , 95% credible intervals, CRI:  $-9.7$  to  $-3.9$ ) than the Alaskan breeding subspecies (*L. l. baueri*;  $-2.1\%$  year $^{-1}$ , 95% CRI:  $-3.3$  to  $-1.0$ ). In 1995, total abundance across all sites in Australia and New Zealand was estimated to be 229 480 (95% CRI: 160 599–347 041) individuals of *L. l. menzbieri* and 180 171 (95% CRI: 161 165–204 522) individuals of *L. l. baueri*. By 2012, populations had declined 56.6%

Table 1. Extent and rate of change of tidal flats at sites used by *L. l. baueri* and *L. l. menzbieri* during staging in the Yellow Sea, East Asia in relation to non-breeding population trend estimates.

Subspecies	No of staging sites with remote sensing data	Initial		Remaining		Change metrics			Population Trend estimate (95% CRI)
		Tidal flat area, $A_1$ (ha)	Year of satellite imagery, $t_1$ (mean yr)	Remaining tidal flat area, $A_2$ (ha)	Year of satellite imagery, $t_2$ (mean yr)	Period elapsed between images, $t_2 - t_1$ (yrs)	Net change (%)	Continuous rate of change, $r$ (% yr <sup>-1</sup> ) <sup>a</sup>	
<i>L. l. baueri</i>	12	5651	1984.9	4153	2009.4	24.5	-26.5	-1.18	-0.021 (-0.033, -0.01)
<i>L. l. menzbieri</i>	13	11466	1980.6	8151	2008.0	27.4	-28.9	-1.66	-0.067 (-0.097, -0.039)

<sup>a</sup>Continuous rate of change of tidal flats calculated as  $r = (100 / (t_2 - t_1)) \times \ln(A_2 / A_1)$ .

and 22.7% for *L. l. menzbieri* and *L. l. baueri* respectively, with estimated total abundances of 100 160 (95% CRI: 88 436–121 263) and 139 357 (95% CRI: 126 331–154 919). Mean detection probabilities estimated from the model for each subspecies were 0.46 (*L. l. menzbieri*; 95% CRI: 0.32–0.61) and 0.48 (*L. l. baueri*; 95% CRI: 0.4–0.55; Supplementary material Appendix 1 Fig. A3).

### Habitat losses at staging sites

The analysis of Landsat Archive imagery indicated a net loss of 3315 ha of tidal flat habitat across all staging sites used by *L. l. menzbieri* and 1498 ha of tidal flat habitat at *L. l. baueri* sites (Table 1). Tidal flats declined faster (–1.66% year<sup>-1</sup>) at sites used by the more rapidly declining *L. l. menzbieri* than at sites (–1.18% year<sup>-1</sup>) used by *L. l. baueri* (Table 1). However, although rates of habitat loss were higher at sites used by *L. l. menzbieri*, the area of intertidal habitat remaining at *L. l. menzbieri* sites (8151 ha) was nearly twice the extent as *L. l. baueri* sites (4153 ha; Table 1).

### Discussion

Understanding the impact of environmental change on migratory species is critical to conserve declining populations, yet determining the underlying drivers of population change has been limited by the difficulty of obtaining relevant data across entire migration pathways. By integrating data from across the full annual cycle of two subspecies of bar-tailed godwit, we have conducted a comprehensive analysis of the factors that may influence abundance across the entire range of a migratory shorebird. Our results support hypotheses that the extensive loss of tidal flat habitat at migratory staging sites plays a central role in the long-term declines of migratory shorebird populations in the EAA Flyway. In addition to providing further support to the habitat loss hypothesis for EAA Flyway population declines, our study also provides intriguing evidence that non-breeding shorebird abundance in the EAA Flyway may also be related to large-scale climatic drivers.

Our approach of analyzing environmental conditions at breeding, non-breeding and migratory staging areas while simultaneously quantifying habitat loss allows several new insights into the state of the EAA Flyway. First, our analysis of Landsat Archive imagery revealed widespread and rapid losses of tidal flat habitat at the staging sites used by both of the subspecies considered in our analysis. In particular, we found that tidal flats used by the more rapidly declining *L. l. menzbieri* subspecies have disappeared at a faster rate than sites used by the more moderately declining *L. l. baueri*. Theoretical models demonstrate that these patterns of decline should be expected, and typically result in higher densities of birds in remaining habitat, lower prey intake rates, higher mortality and a greater rate of population decline in the population experiencing a greater rate of habitat loss (Sutherland and Dolman 1994). However, the

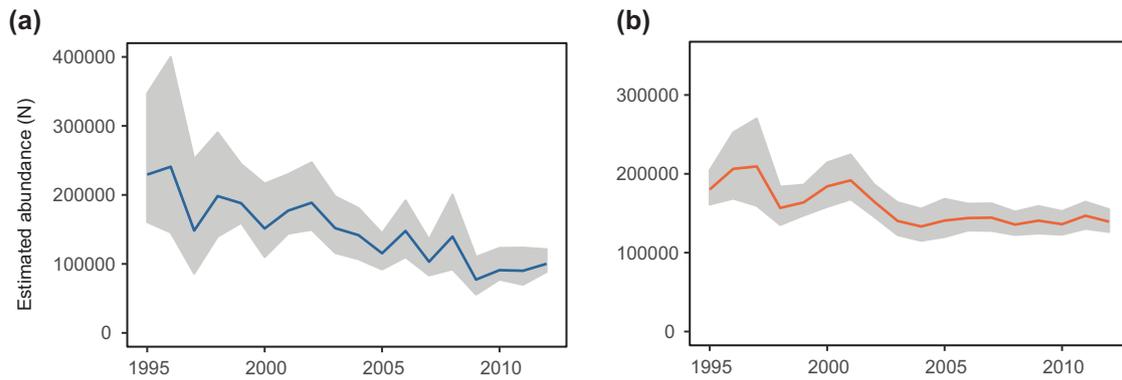


Figure 3. Total abundance estimates for the two subspecies of bar-tailed godwit, *L. l. menzbieri* (a) and *L. l. baueri* (b), investigated in this study. Solid colored lines indicate the posterior mean abundance estimate and shading areas indicate the 95% credible intervals. We detected significant declines in both species during the study period (1995–2012; *L. l. menzbieri*,  $-6.7\%$  year $^{-1}$ ; *L. l. baueri*;  $-2.1\%$  year $^{-1}$ ).

extent of habitat remaining at *L. l. menzbieri* sites was nearly twice that of *L. l. baueri* sites which, because both populations are of similar size, may suggest that habitat at *L. l. menzbieri* staging sites is of lower quality (Sutherland 1996) or has undergone greater degradation (Norris 2005, Sheehy et al. 2011). Degradation of tidal flat habitats around the Yellow Sea is unlikely to be uniform, and this result could suggest that the quality of remaining tidal flat habitat at western Yellow Sea sites occurring in China is poorer than at eastern Yellow Sea sites that occur in North and South Korea.

However, the differential rates of population decline in the two subspecies seem better explained by the highly contrasting migration routes of the two sub-species (Fig. 1). Specifically, the Russian breeding *L. l. menzbieri* traverses the Yellow Sea region of East Asia twice in each annual cycle (on both north and south migration), whereas *L. l. baueri* migrates through the region only once (on northern migration), migrating directly across the Pacific Ocean on southern migration. Recently reported survival estimates from a mark-recapture study (Piersma et al. 2015) indicated that survival of shorebirds are considerably lower while traversing the Yellow Sea than in breeding and non-breeding seasons. Therefore, by doubling the exposure to a region that is known to directly influence survival, impacts to the *L. l. menzbieri* population should be greater than the *L. l. baueri* population, leading to a greater rate of population decline. This echoes the findings of a recent flyway-wide analysis of shorebird population trends, which found that species with a greater reliance on Yellow Sea for stopover have declined at greater rates than the species which have lower reliance on this region to complete their annual cycle (Studds et al. 2017). Thus, shorebird populations that are more exposed to threats in the Yellow Sea, both spatially and temporally, are expected to be at the greatest risk of decline, and therefore actions that reduce the impacts of threats in the Yellow Sea on shorebird populations should be a conservation priority.

Our population analysis indicated a positive relationship between breeding temperature and the non-breeding abundance of the *L. l. menzbieri* population. Such large-scale population responses to temperature have been detected

in shorebird species in other migration flyways, both by increasing breeding productivity which drove positive population growth rates (Schekkerman et al. 1998) and by increasing mortality as a result of timing mismatches with food resources (van Gils et al. 2016). That *L. l. baueri* did not show a similar response to breeding temperature could be due to a range of reasons, including that individuals of each subspecies complete a vastly different migration and are likely to encounter a wide range of environmental conditions and threats across their full annual cycle, making the relationship between climate drivers and populations difficult to detect (Piersma et al. 2015, van Gils et al. 2016). Nevertheless, this result suggests that shorebirds in the EAA flyway may also be susceptible to extreme and changing climatic conditions, compounding the impacts of threats in their staging areas.

Unfortunately, high-resolution data are not frequently available for all of the factors that could influence the demographic parameters and vital rates of migratory shorebirds, particularly for migratory birds with ranges that span large areas of the globe. For example, some studies have suggested that, given the long-distance non-stop migratory flights completed by godwits, wind conditions during migration could influence survival and, by extension, whole populations (Gill et al. 2009, Conklin and Battley 2011, Klaassen et al. 2011). Although godwits have recently been shown capable of selecting departure timing, migration routes and altitudes to avoid adverse conditions during migration (Gill et al. 2014), further work to reliably incorporate wind conditions, extreme climatic events and finer-scale climatic data into population analyses would be useful, but will require highly detailed information on flight altitudes, breeding distributions and migration timing. Furthermore, our study shows that research which aims to further disentangle the influence of variable population drivers such as temperature fluctuations with long-term drivers such as habitat loss, habitat degradation and climate change are needed within the EAA Flyway (van Gils et al. 2016).

With confirmed declines of many shorebird species that migrate across the EAA Flyway, our study provides valuable

new information on the environmental and anthropogenic factors that drive change in migratory shorebird populations. It is also among the first studies to investigate drivers of abundance across the entire migratory range of a species, and the first to examine the consequences of disparate migration strategies of two subspecies. Additionally, our investigation adds to the growing number of studies that have confirmed widespread declines of shorebird species in the EAA Flyway. Clearly, swift action to improve the population trajectories of migratory shorebirds in the EAA Flyway is needed, and immediate action to halt the loss of tidal flat habitat should be promoted at Yellow Sea staging sites.

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Supplementary material (Appendix ECOG-02957 at <[www.ecography.org/appendix/ecog-02957](http://www.ecography.org/appendix/ecog-02957)>). Appendix 1–2.