



Generating population estimates for migratory shorebird species in the world's largest flyway

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Population estimates are widely used to underpin conservation decisions. However, determining accurate population estimates for migratory species is especially challenging, as they are often widespread and it is rarely possible to survey them throughout their full distribution. In the East Asian–Australasian Flyway (EAAF), this problem is compounded by its size (85 million square kilometres) and the number of migratory species it supports (nearly 500). Here, we provide analytical approaches for addressing this problem, presenting a revision of the EAAF population estimates for 37 migratory shorebird species protected under Australian national environmental legislation. Population estimates were generated by (1) summarizing existing count data in the non-breeding range, (2) spatially extrapolating across uncounted areas, and (3) modelling abundance on the basis of estimates of breeding range and density. Expert review was used to adjust modelled estimates, particularly in under-counted areas. There were many gaps in shorebird monitoring data, necessitating substantial use of extrapolation and expert review, the extent of which varied among species. Spatial extrapolation to under-counted areas often produced estimates that were much higher than the observed data, and expert review was used to cross-check and adjust these where necessary. Estimates of population size obtained through analyses of breeding ranges and density indicated that 18 species were poorly represented by counts in the non-breeding season. It was difficult to determine independently the robustness of these estimates, but these breeding ground estimates were considered the best available data for 10 species that mostly use poorly surveyed freshwater or pelagic habitats in the non-breeding season. We discuss the rationale and limitations of these approaches to population estimation, and how they could be modified for other applications. Data available for population estimates will vary in quality and extent among species, regions and migration stage, and approaches need to be flexible enough to provide useful information for conservation policy and planning.

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The conservation of migratory species requires identification of key habitats that support geographically defined populations throughout their annual cycle (Runge *et al.* 2015). This often depends on estimating the population size of species, because such estimates underpin the development of numerical threshold criteria. These include the Ramsar Convention criteria for determining internationally important wetlands, and similar threshold-based criteria for triggering conservation management action. Accurate population size estimates are crucial to ensure such processes correctly identify qualifying sites.

Regular revisions of population estimates are needed to keep information current and relevant (Andres *et al.* 2012). The East Asian–Australasian Flyway (EAAF) is the largest of the nine global flyways, supporting over 50 million birds of 492 migratory species (Conklin *et al.* 2014, BirdLife International ND). Many of these species are declining rapidly (Wilson *et al.* 2011, Clemens *et al.* 2016, Studds *et al.* 2017). Existing population estimates (Bamford *et al.* 2008, Wetlands International 2012) do not reflect these rapid declines, and threshold-based conservation decisions might therefore be erroneous.

Several methods have been used to generate population estimates for migratory species. Minimum or maximum abundances can be calculated directly from count data and adjusted by using extrapolation or expert opinion. For example, shorebird population estimates in North America used expert opinion to apply confidence limits to species estimates rather than numerically extrapolating to uncounted areas (Andres *et al.* 2012). Data on the population size of Arctic-breeding shorebirds in the Americas included some of the most rigorous sampling of Arctic-breeding shorebirds ever undertaken (Bart & Johnston 2012), although data from non-breeding areas were poor by comparison. In the UK, land-bird population estimates used a mixed approach of trend and spatial extrapolations (Musgrove *et al.* 2013), whereas waterbird population estimates for Great Britain used predominantly spatial extrapolation to uncounted areas (Musgrove *et al.* 2011). These differences in methods exemplify the flexibility

needed to generate population estimates tailored to the available data.

The challenges confronting an analyst wishing to produce population estimates for migratory species can be broadly grouped into: (1) variability in distributions over space and time; (2) decreasing or increasing populations; (3) low count coverage and effort; (4) imperfect and variable detectability; (5) alternative possible taxonomic treatments; and (6) identification errors (Andres *et al.* 2012, Musgrove *et al.* 2013).

For migratory shorebirds in the EAAF, there are relatively fewer data from the breeding and staging areas than in other flyways, with the most systematic monitoring being an annual count during the middle of the non-breeding season between November and March. Monitoring effort varies greatly across the non-breeding grounds, with some sites having continuous long-term data and others counted only sporadically (Clemens *et al.* 2012), although there has been a large increase in count effort and coverage in Australia over the last decade (Hansen *et al.* 2016). Counts are increasingly comprehensive in other places in the flyway, including Japan, South Korea, parts of mainland China and Taiwan, with regular counts during the migration and the non-breeding period as part of the annual Asian Waterbird Census coordinated by Wetlands International (Mundkur *et al.* 2017). Despite this, many regional shorebird counts detect only a small proportion of the birds actually present (Wilson *et al.* 2011), and there are still vast areas, particularly in inland Australia and many parts of Asia, that are rarely or never counted. This biased survey coverage has received only limited attention in past EAAF population estimates because of the difficulty of accounting for unsurveyed areas when tallying count data (Watkins 1993, Bamford *et al.* 2008).

We developed flyway population size estimates for the 37 migratory shorebird species listed under Australia's national environmental legislation (the *Environment Protection and Biodiversity Conservation Act* 1999), because those estimates are required to support wetland conservation designations in Australia. In this paper, we describe the analytical approaches we used for producing flyway population estimates for migratory shorebirds

using citizen-derived long-term monitoring data and discuss how they could be improved or modified with additional data.

METHODS

Source data

The main data sources were the Australian National Shorebird Monitoring programme (formerly Shorebirds 2020), the Queensland Wader Study Group, the Ornithological Society of New Zealand and the Asian Waterbird Census (Mundkur *et al.* 2017). We used additional count data obtained from the literature and through communication with other shorebird researchers and survey coordinators (Hansen *et al.* 2016). For the northern hemisphere breeding species, only data from November to March were used for statistical analyses, because this is the period when movement between non-breeding sites is considered at its minimum. Counts from April to July were used for the Double-banded Plover *Charadrius bicinctus*, an austral migrant (Hansen *et al.* 2016). Clemens *et al.* (2012) and Mundkur *et al.* (2017) provide further details of count methods and coverage.

Overview of analytical approach

Three main analytical steps were implemented to generate estimates for each species: (1) summarizing the available count data; (2) estimating shorebird numbers in uncounted areas through extrapolation; and (3) creating independent population estimates using information on densities of birds present in the breeding ranges (Fig. 1). The distribution of most subspecies in the EAAF remains poorly resolved, particularly during the non-breeding season, so we estimated flyway populations at the species level.

Summarizing EAAF count data

We calculated a mean count for each shorebird area (collection of roost sites thought to form a single stable non-breeding population, e.g. an estuary) in Australia and New Zealand using data over the 5-year period between 2011/12 and 2015/16. For sites with highly variable or poor survey coverage, data from the period 2007–2016 were used. Variable count coverage of individual roost sites or impacts of weather or other factors on the quality

of a count meant that some mean counts were probably unrepresentative of the number of birds usually using a shorebird area. Experts with local knowledge of the shorebird area were asked to evaluate whether maximum or mean counts provided the more accurate estimate of shorebird numbers, and they were also asked to evaluate predicted mean and maximum counts (upper 95% confidence interval) derived from generalized additive models where count was the dependent variable, year was the independent variable and a penalized cubic regression spline with penalty modified to shrink towards zero was used to capture non-linear changes in counts over time (Hansen *et al.* 2016). Experts typically recommended using the mean observed count over a 5-year period, with predicted mean values usually being recommended in cases with substantial missing count data in those 5 years.

Data from non-breeding grounds elsewhere in the EAAF were sourced from the Asian Waterbird Census as point location data. Counts from these locations were summarized on a national basis by computing the maximum count at any site during the annual January count where available, but over the austral summer period (November–March) where not available, in the years 2005/06–2014/15 (the most current data available at the time) and summing site maxima in each country.

Estimating shorebird numbers in uncounted areas through extrapolation

Although there are relatively high-quality count data for coastal Australia and New Zealand, and some other areas in the flyway, shorebird count data in many other regions are often sparse, and there is a significant amount of shorebird habitat that is outside counted areas. To adjust for this, we (1) modelled the abundance of migratory shorebirds using the poorly monitored inland areas of Australia and (2) estimated the proportion of potential coastal shorebird habitat that is not counted during EAAF systematic surveys.

For step (1) we included 14 species that frequently occur in inland Australia. The distributions of shorebirds across Australia's arid interior vary greatly in space and time due to the temporary presence of water, and there are only patchy count data available. To generate estimates from these areas, monthly non-breeding season predictions of

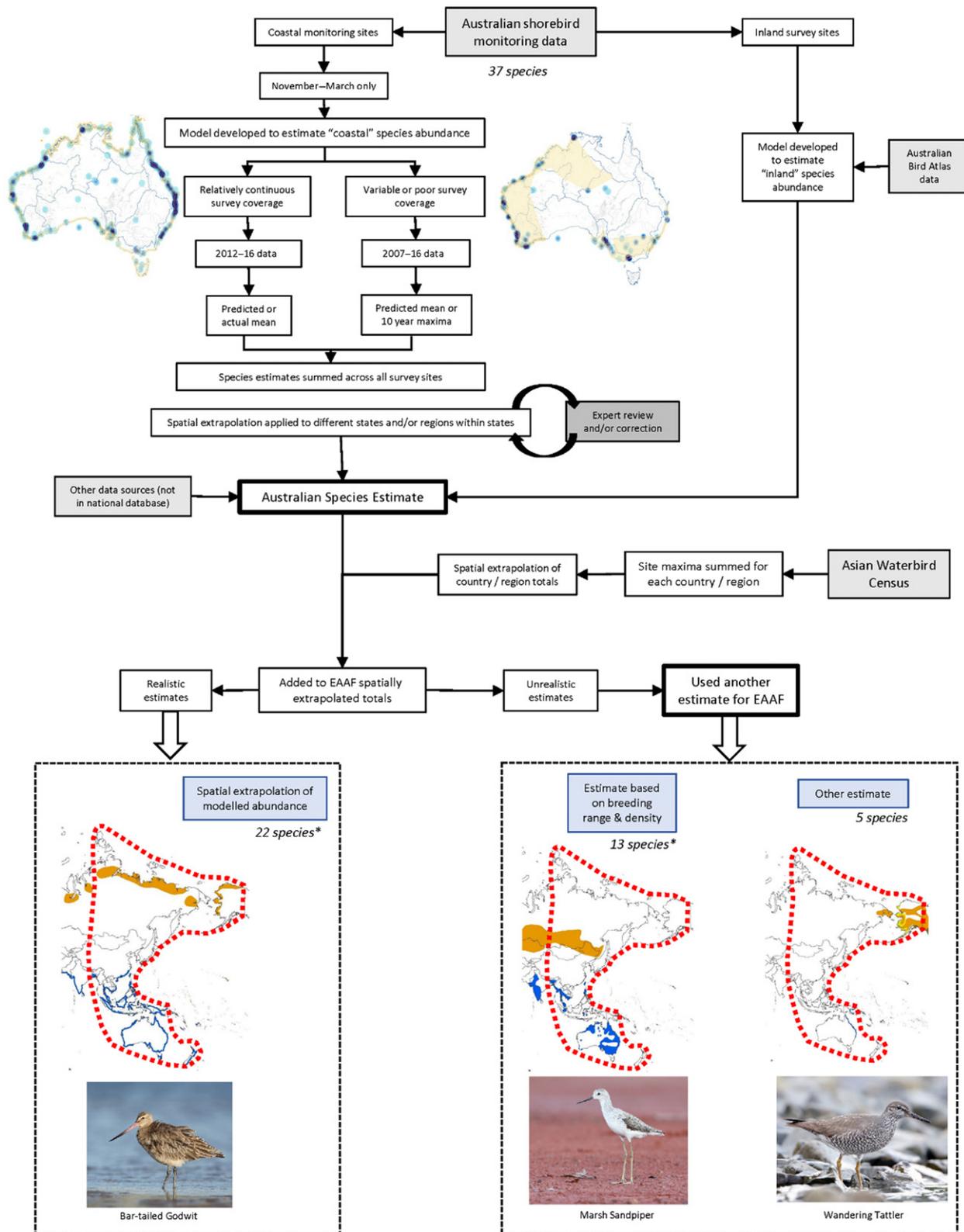


Figure 1. Graphic showing the analytical steps taken to generate population estimates for 37 migratory species in the East Asian–Australasian Flyway (EAAF). The centre flow diagram illustrates the modelling, expert review and decision steps used for Australian shorebird data. The two insets show the final population estimate basis chosen for individual species. The dashed red line on distribution maps is the EAAF extent. The number of species is given in italics next to the final estimate. The asterisk refers to three species for which both estimates were selected (see Table 1). Range maps were sourced from BirdLife International and NatureServe (2015). Small Australian maps were reproduced with permission from Clemens *et al.* (2020). [Colour figure can be viewed at wileyonlinelibrary.com]

abundance were taken from Clemens (2016). Predictions were made at 0.1° resolution, summed across the interior of Australia and averaged over the 5 years between 2011/12 and 2015/16. Predictions were generated using two-stage boosted regression trees where the predicted probability of occurrence was multiplied by the predicted abundance. The predictor variables reflected wetland condition, and included interpolated river flow volume, soil moisture estimates, length of mapped wetland edge, rainfall, temperature and estimated groundwater depth (Clemens 2016).

For step (2) we estimated the extent of coastal shorebird habitat that had not been monitored and used this to extrapolate population estimates of coastal counts. The extrapolated estimates were only applied to species that wholly or principally use intertidal habitats to reduce the need for extrapolation in species where it would make minimal difference to the estimates. At the time of this study, no comprehensive mapping of intertidal habitat existed for the EAAF, beyond products available for the Yellow Sea (Murray *et al.* 2012) and Australia (Dhanjal-Adams *et al.* 2016). In the case of Australia, we overlaid polygon representations of shorebird survey areas (<https://birddata.birdlife.org.au/>) onto an existing map of intertidal habitats classified directly from remote sensing data (Dhanjal-Adams *et al.* 2016) to produce an estimate of the proportion of intertidal habitat counted in Australia.

Outside Australia, we mapped areas in which intertidal habitat could potentially occur based on combining bathymetry and tidal amplitude data. To map potential intertidal habitat, we identified all pixels (1×1 km) in a global bathymetry map (ETOPO1 Global Relief Model; <https://www.ngdc.noaa.gov/mgg/global/global.html>) that are shallow enough to be exposed by the tide (based on overlaying a global model of tidal amplitude from Lovelock *et al.* 2015). We removed any pixels with an elevation > 0 m above sea level, assuming these are not intertidal, and also removed all areas that are covered in winter sea ice. We then clipped the dataset of potential intertidal

habitat to all areas with a 5-km buffer of the coastline, using a high-resolution coastline dataset (<https://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html>). This constrained our estimate of potential intertidal habitat to a reasonable proximity to the coastline.

Comprehensive polygonal maps of shorebird count areas outside Australia do not exist, so we began by selecting all 577 Asian Waterbird Census count locations that had geographical coordinates within 20 km seaward and 2 km landward of the coastline. We then defined a buffer of 10-km radius around the coordinates of each site in which we could calculate the extent of intertidal habitat. This buffer radius represents a reasonable estimate of the distance travelled by roosting birds from feeding areas (Rogers 2003), and the extent of habitat typically covered when counting shorebirds in a site. Finally, we calculated the proportion of all potential intertidal area in each country that occurred within shorebird count area polygons to yield an estimate of the proportion of habitat that had been counted in each country.

We took advantage of the comprehensive intertidal habitat mapping available for Australia to calibrate the method based on potential intertidal habitat, dividing Australia into eight regions. We constructed a linear model of the relationship between the proportion of counted habitat in a region as estimated from potential habitat mapping (independent variable) and the proportion of counted habitat as estimated from directly remote-sensed habitat mapping (dependent variable). The relationship was strongly positive, albeit with some degree of scatter ($y = 0.8088x + 0.2882$; $R^2 = 0.331$; $n = 8$), and the fact that the intercept of this relationship was well above zero suggests that in situations where few sites are counted in a region, these often tend to be those sites with the greatest concentration of suitable habitat (Fig. 2). However, the sample size for this analysis was low, and only a modest amount of variation was explained, highlighting an area where further work to reduce uncertainty would be useful.

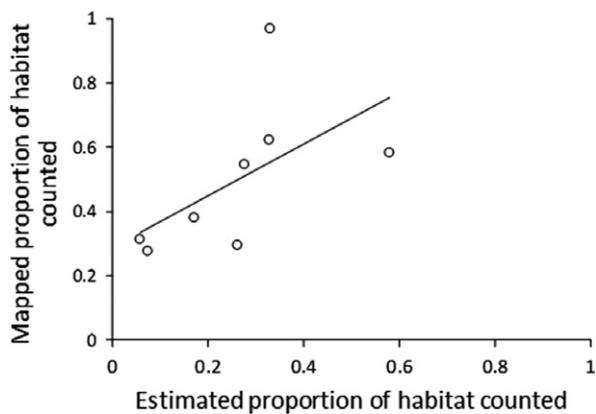


Figure 2. Relationship between two alternative ways of deriving the proportion of coastal shorebird habitat that has been counted. This plot shows ‘mapped’ counted habitat, created by overlaying maps of shorebird areas onto remotely sensed habitat maps, and ‘estimated’ counted habitat, created by overlapping buffered centroids of count sites onto estimates of intertidal areas using bathymetry/tidal amplitude models.

The estimates derived from steps (1) and (2) above were summed by species to produce population estimates based on extrapolated data.

Population estimates based on breeding distribution and density

Species population sizes might be expected to correlate positively with the size of their breeding range (Gaston *et al.* 2000). We modelled the relationship between breeding range area and our population estimate for species judged to have been counted adequately on the non-breeding grounds. We then used this relationship to estimate the population size of species for which the size of the breeding range is known, but for which data from non-breeding ground counts are inadequate.

Breeding distribution shapefiles were obtained from BirdLife International and NatureServe (2015), and modified as necessary through literature review and expert consultation (Supporting Information Fig. S1). Each species was classified *a priori* into one of the following three breeding density categories:

- 1 High density: species known to nest in high densities in the core of their breeding range or expected to nest in high densities by comparison with closely related species; this category also included species in which an unusually large proportion of the calculated breeding range was expected to be occupied.

- 2 Moderate density (default).
- 3 Low density: species known to nest in relatively low densities in the core of their breeding range or expected to nest in low densities by comparison with closely related species; this category also included species in which the calculated breeding range was suspected to be inflated because the range map included habitats that are unsuitable for nesting.

A generalized linear model was constructed in R (R Core Team 2020), using number of birds counted on the non-breeding grounds (Supporting Information Table S1, estimates included extrapolations) as the dependent variable, breeding range size as a continuous variable and breeding density as a fixed factor. No constant was included in the original model (Hansen *et al.* 2016) because it was assumed that if breeding range was zero, the population would also be zero. The modelling was repeated including a constant to check for inflation of the R^2 value.

The coefficients generated from these regressions were used to estimate EAAF populations of species for which count data from the non-breeding grounds were considered inadequate (Supporting Information Table S2), and were also helpful in assessing concurrence between estimates generated from other methods.

Expert validation and EAAF estimate selection

We circulated extrapolation estimates of the proportion of habitat that had been counted to local experts, who adjusted them where necessary, noting in particular that mapping habitat extent alone does not provide information about variation in habitat suitability. Expert-adjusted proportions were used to produce an extrapolation factor for any given species and/or area – the default was no expert modification (Hansen *et al.* 2016).

We used the extrapolation factors resulting from the expert review of the proportion of habitat counted to adjust Australian state totals. To these adjusted state totals we added the inland estimates (where available for any given species), which we circulated again to the same experts for further review. We summed these reviewed and adjusted state totals to provide a national estimate for each species in Australia.

In New Zealand, coastal extrapolation factors were applied to survey location totals. Double-banded Plover estimates were the only exception to this, and a previous population estimate for this species in New Zealand was used instead (Southey 2009).

For coastal areas outside Australia and New Zealand, we applied coastal extrapolation factors to summed maximum counts on a country or regional basis. This produced an extrapolated figure for that country or region for all coastal species, which was added to the Australian and New Zealand totals and produced a flyway estimate based on extrapolated count data.

Spatially extrapolated counts were generally selected for species considered primarily coastal in distribution in Australia (Fig. 1). Breeding range and density estimates were used for species considered non-coastal obligate species (more commonly associated with inland waterbodies and/or grasslands), and for species where insufficient count data rendered spatial extrapolations unrepresentative. There were several cases where neither approach seemed optimal, and, in these cases, we used another estimate and documented its derivation (Fig. 1).

RESULTS

The volume of count data has increased greatly in the last decade, and five species, before analytical treatment, produced higher estimates than previously reported (WPE5: Wetlands International 2012). These species were Great Knot *Calidris tenuirostris* (360 000 cf. 290 000 in WPE5), Greater Sand Plover *Charadrius leschenaultii* (150 000 cf. 79 000), Grey-tailed Tattler *Tringa brevipes* (62 000 cf. 44 000), Oriental Plover *Charadrius veredus* (190 000 cf. 145 000–155 000) and Sanderling *Calidris alba* (23 000 cf. 22 000; Table 1).

Outcomes of spatial extrapolation

The predicted abundance of five shorebird species within inland Australia (Sharp-tailed Sandpiper *Calidris acuminata*, Red-necked Stint *Calidris ruficollis*, Curlew Sandpiper *Calidris ferruginea*, Common Greenshank *Tringa nebularia* and Marsh Sandpiper *Tringa stagnatilis*) were based on species distribution models that showed excellent model performance indicated by mean cross-validation AUC values ranging from 0.93 to 0.96 (Clemens

2016). When predictions were tested against an independent dataset, absences were correctly identified more than 98% of the time, although presences were only correctly identified between 40% and 87% of the time (Clemens 2016). Moreover, the model substantially underpredicted abundance in many inland wetlands, with occasional very high counts being difficult to model accurately. Although these model outputs are probably underestimates in many cases, because no other data are available, they were retained for 12 predominantly non-coastal species (Hansen *et al.* 2016), and added to extrapolated coastal estimates.

Expert review of extrapolated estimates

We made adjustments to extrapolated estimates in Australia, resulting in a 7% reduction to the total spatially extrapolated EAAF population estimates (Hansen *et al.* 2016). No expert adjustments were made to extrapolation factors for other EAAF countries, because suitable reviewers could not be identified. In all cases where expert adjustments were made, they either resulted in a decrease to the extrapolation factor, no change or a split into regions representing different coastal habitat suitability (i.e. with different extrapolation factors applied to each, for example eastern Queensland coast and the Queensland Gulf of Carpentaria coast).

Breeding range and density

There was a strong positive relationship between breeding range size and estimated EAAF population size for the 18 species for which we had the best count data from the non-breeding grounds (Fig. 3; Table 2). The inclusion of a constant had negligible effects on the model coefficients and prediction intervals, although population size predictions did change slightly for some species from Hansen *et al.* 2016 (Supporting Information Table S2). The *y*-intercept did not differ significantly from zero, and the distribution of residuals suggested that the assumption of a linear relationship between breeding range and population size was justified (Supporting Information Fig. S2). Confidence limits were larger for larger populations (Supporting Information Table S2). For example, Red-necked Phalarope *Phalaropus lobatus*, a largely pelagic and poorly monitored species in the non-breeding period, had a predicted

Table 1. Population estimates produced using different analytical approaches for 37 migratory shorebirds. Final population estimate basis: light grey = SE, dark grey = BRD, B = both SE and BRD as upper and lower limits, T = trend correction to previous (see main text)

Common name	Latin name	Total count	SE	BRD	Final population estimate (2016)	Bamford <i>et al.</i> (2008)	WPE5 estimate
Asian Dowitcher ^C	<i>Limnodromus semipalmatus</i>	4837	14 172	12 673	14 000	24 000	23 000
Bar-tailed Godwit ^C	<i>Limosa lapponica</i>	274 647	319 182	237 552	325 000	325 000	279 000
Black-tailed Godwit ^{C,IW}	<i>Limosa limosa</i>	90 981	159 652	157 800	160 000	160 000	139 000
Broad-billed Sandpiper ^C	<i>Limicola falcinellus</i>	15 755	30 139	24 340	30 000	25 000	25 000
Common Greenshank ^{C,IW}	<i>Tringa nebularia</i>	34 367	62 953	105 216	110 000	60 000	100 000
Common Redshank ^C	<i>Tringa totanus</i>	32 436	75 884	146 406	75 000–150 000 ^B	75 000	45 000–1 200 000
Common Sandpiper ^{C,IW}	<i>Actitis hypoleucos</i>	22 846	55 238	193 024	190 000	25 000–100 000	50 000
Curllew Sandpiper ^{C,IW}	<i>Calidris ferruginea</i>	85 086	92 294	68 494	90 000	180 000	135 000
Double-banded Plover ^{C,IW}	<i>Charadrius bicinctus</i>	13 057	18 786	19 559	19 000	50 000	50 000
Far Eastern Curlew ^C	<i>Numenius madagascariensis</i>	24 914	33 840	34 862	35 000	38 000	32 000
Great Knot ^C	<i>Calidris tenuirostris</i>	359 719	419 186	536 565	425 000	375 000	290 000
Greater Sand Plover ^C	<i>Charadrius leschenaultia</i>	150 373	199 258	295 048	200 000–300 000 ^B	110 000	79 000
Grey Plover ^C	<i>Pluvialis squatarola</i>	42 812	77 616	100 324	80 000	125 000	104 000
Grey-tailed Tattler ^C	<i>Tringa brevipes</i>	61 612	71 016	74 220	70 000	50 000	44 000
Latham's Snipe ^{IW,G}	<i>Gallinago hardwickii</i>	1124	1260 ^a	35 127	35 000 ^T	36 000	25 000–1 000 000
Lesser Sand Plover ^C	<i>Charadrius mongolus</i>	146 168	284 105	182 910	180 000–275 000 ^B	140 000	188 500–218 500
Little Curlew ^{IW,G}	<i>Numenius minutus</i>	36 648	76 913	109 105	110 000	180 000	180 000
Little Ringed Plover ^{C,IW}	<i>Charadrius dubius</i>	21 707	48 761	154 970	150 000	25 000	50 000–125 000
Long-toed Stint ^{C,IW}	<i>Calidris subminuta</i>	582	587 ^a	230 939	230 000	25 000	25 000
Marsh Sandpiper ^{C,IW}	<i>Tringa stagnatilis</i>	50 014	102 439	130 457	130 000	100 000–1 000 000	100 000–1 000 000
Oriental Plover ^{C,IW,G}	<i>Charadrius veredus</i>	190 388	232 124	160 468	230 000	70 000	145 000–155 000
Oriental Pratincole ^{IW,G}	<i>Glareola maldivarum</i>	588 972	587 051	1 274 398	2 880 000 ^b	2 880 000	2 880 000
Pacific Golden Plover ^C	<i>Pluvialis fulva</i>	66 402	122 379	176 009	120 000	100 000–1 000 000	135 000–150 000
Pectoral Sandpiper ^{C,IW}	<i>Calidris melanotos</i>	89	78 ^a	231 533	1 220 000–1 930 000 ^b	No estimate	1 220 000–1 930 000
Pin-tailed Snipe ^{IW,G}	<i>Gallinago stenura</i>	6	10 ^a	168 125	170 000	25 000–1 000 000	25 000–1 000 000
Red Knot ^C	<i>Calidris canutus</i>	97 005	112 920	147 501	110 000	220 000	99 000–122 000
Red-necked Phalarope ^C	<i>Phalaropus lobatus</i>	50	98 ^a	249 671	250 000	100 000–1 000 000	100 000–1 000 000
Red-necked Stint ^{C,IW}	<i>Calidris ruficollis</i>	282 882	477 990	285 343	475 000	325 000	315 000
Ruddy Turnstone ^C	<i>Arenaria interpres</i>	24 191	29 367	30 670	30 000	35 000	28 500
Ruff ^{C,IW}	<i>Calidris (Philomachus) pugnax</i>	3	5 ^a	271 526	25 000–100 000 ^b	No estimate	25 000–100 000

(continued)

Table 1. (continued)

Common name	Latin name	Total count	SE	BRD	Final population estimate (2016)	Bamford <i>et al.</i> (2008)	WPE5 estimate
Sanderling ^C	<i>Calidris alba</i>	22 554	29 835	33 605	30 000	22 000	22 000
Sharp-tailed Sandpiper ^{C,IW}	<i>Calidris acuminata</i>	71 642	85 829	120 684	85 000	160 000	160 000
Swinhoe's Snipe ^{IW,G}	<i>Gallinago megala</i>	22	68 ^a	41 511	40 000	25 000– 1 000 000	25 000– 1 000 000
Terek Sandpiper ^C	<i>Xenus cinereus</i>	30 761	49 949	54 265	50 000	60 000	50 000– 55 000
Wandering Tattler ^C	<i>Tringa incana</i>	322	400 ^a	58 456	10 000– 25 000 ^b	No estimate	10 000– 25 000
Whimbrel ^C	<i>Numenius phaeopus</i>	38 208	66 701	48 364	65 000	100 000	55 000
Wood Sandpiper ^{IW}	<i>Tringa glareola</i>	9717	15 249	127 339	130 000	100 000– 1 000 000	100 000

Dominant habitat use in Australia is represented by superscripts C = coastal, IW = inland wetlands or G = grasslands.

Abbreviations: BRD, breeding range and density estimate; SE, spatially extrapolated estimate.

^aExtrapolations unrepresentative as count data insufficient to derive estimates for these species. ^bWPE5 (Wetlands International 2016).

Final estimates were rounded up or down following the rounding rules of Bamford *et al.* (2008): population size rounding: < 10 000 nearest 500; 10 000–25 000 nearest 1000; 25 000–100 000 nearest 5000; 100 000–250 000 nearest 10 000; > 250 000 nearest 25 000.

Breeding range and density estimates are as reported in original analyses (Hansen *et al.* 2016). Refined analyses, predictions and prediction intervals are provided in Table S2.

population estimate of 250 000 with prediction intervals ranging from 133 000 to 450 000 (Supporting Information Table S2). For seven species, the population size estimated from breeding range and density far exceeded counts on the non-breeding grounds (Fig. 3; Table 1).

Totals based on non-breeding season count data, even after spatial extrapolation, were clearly too low for a number of species, and in 10 cases the breeding season estimates produced more realistic numbers (Table 1).

Special cases

Several species were treated individually. Breeding range and density estimates could not be applied to Ruff *Calidris pugnax*, Pectoral Sandpiper *Calidris melanotos* or Wandering Tattler *Tringa incana* because their breeding areas are occupied by birds that predominantly migrate to different flyways (Supporting Information Fig. S1). For example, small numbers of Pectoral Sandpipers occur in the EAAF and are presumed to nest in Siberia, but these Siberian breeding grounds are also used by very high numbers of Pectoral Sandpipers that migrate to non-breeding grounds in the Americas

(Alerstam *et al.* 2007, Kempenaers & Valcu 2017). We had no way to estimate the proportion of Pectoral Sandpipers that migrate within the EAAF and there is no evidence of geographical differentiation between flyway populations on the breeding grounds. It was therefore considered most appropriate to regard these species as representing a (small) proportion of a population that predominantly occurs elsewhere, and the existing estimates of these populations were retained.

Latham's Snipe *Gallinago hardwickii* was subject to a trend correction based on Amano *et al.* (2012), who found an annualized rate of decrease of –0.001 over 10 years. This was applied to the 1986 breeding grounds population estimate of 36 000 (Bamford *et al.* 2008), resulting in a new estimate of 34 945. A similar approach was intended for Oriental Pratincole *Glareola maldivarum*, but there was no available trend information so no correction was made to the past estimate of 2.88 million obtained in 2004 from northwest Australia (Sitters *et al.* 2004). For the two sand plover species, it was difficult to choose (on the basis of biology) between spatial extrapolation and breeding range estimates, and estimates are therefore given as a range. Similarly, we presented a range of

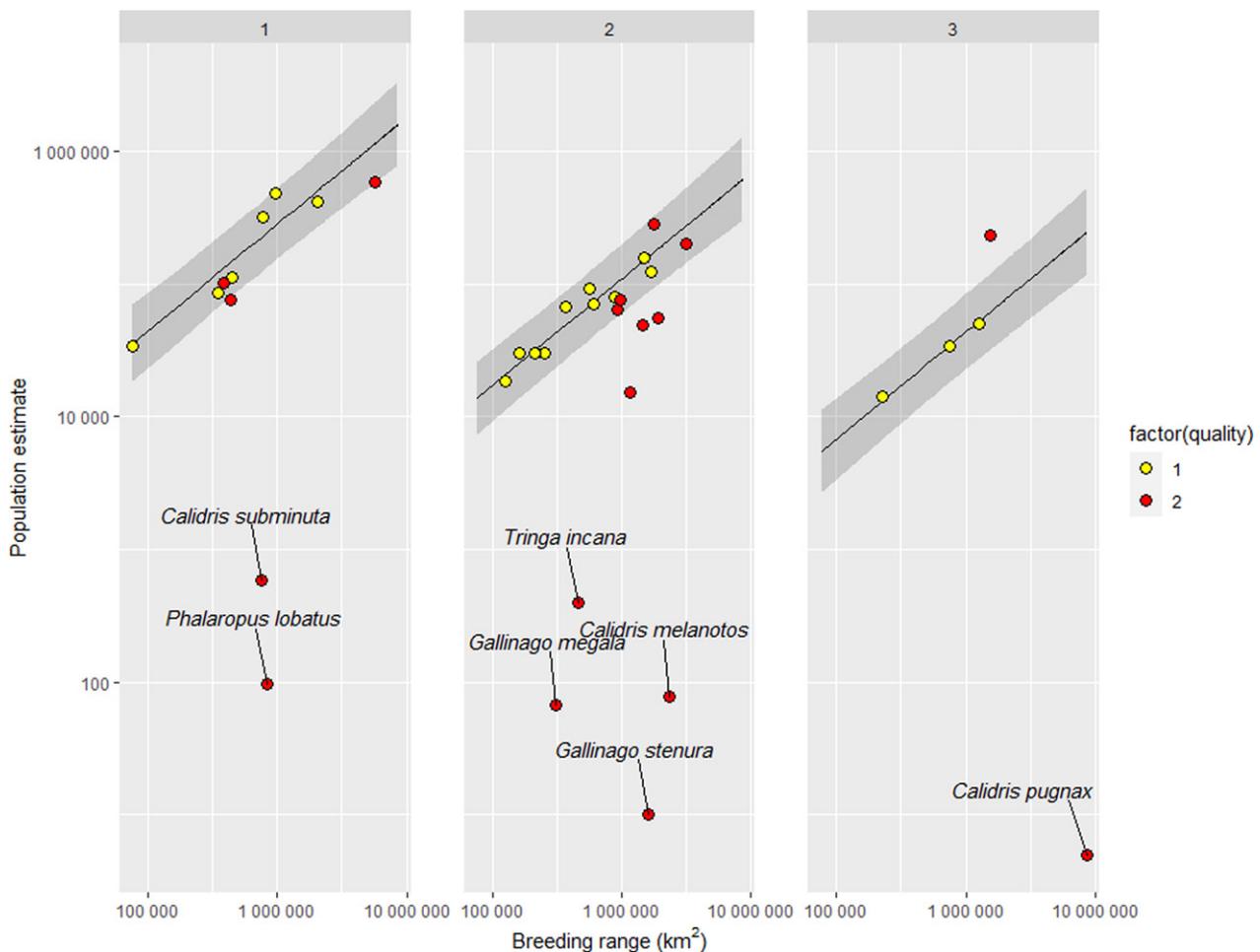


Figure 3. Estimated populations (log scale) on the non-breeding grounds (calculated through counts and spatial extrapolations) plotted against breeding range for species that nest at high density (Panel 1), moderate density (Panel 2) and low density (Panel 3). Linear models (Table 2) and their prediction intervals are shown; they were derived from species in which non-breeding estimates were considered adequate (yellow dots) and used to estimate populations of species for which non-breeding estimates (red dots) were considered inadequate. [Colour figure can be viewed at wileyonlinelibrary.com]

values for Common Redshank *Tringa totanus* as it was not possible to assess whether the estimate derived from extrapolation of flyway count total or the estimate based on the (poorly known) breeding range was more accurate.

DISCUSSION

The combined use of available flyway count data with both qualitative and quantitative estimates of unsurveyed areas has resulted in estimates for 24 EAAF shorebird species that differ substantially from the previous EAAF estimates, which were based on count data from 1986–2000 (Bamford *et al.* 2008). Despite clear evidence that many of

these shorebird species are decreasing at the flyway scale (Clemens *et al.* 2016, Studds *et al.* 2017), some population estimates were higher than previous figures (Bamford *et al.* 2008, Wetlands International 2012). This change, in part, reflects the increase in survey effort and, hence, the amount of count data available in the EAAF, and suggests that previous approaches did not sufficiently extrapolate across uncounted habitat.

Comparison with previous estimates

The greatest increases in EAAF population estimates compared with previous numbers were Long-toed Stint *Calidris subminuta* (920%) and

Table 2. Output of linear model estimating non-breeding population on the basis of breeding range (a continuous variable) and breeding density (fixed factor).

Coefficients	Estimate	se	t value	P value
Intercept	0.520	0.879	0.591	0.563
Breeding range (default density)	0.802	0.067	11.917	<0.001
D1 (high breeding density)	0.960	0.136	7.049	<0.001
D3 (low breeding density)	-0.917	0.174	-5.261	<0.001

Residual standard error: 0.263 on 15 degrees of freedom. Multiple $r^2 = 0.9429$, Adjusted $r^2 = 0.9314$, F -statistic 82.51 on 3 and 15 degrees of freedom, $P < 0.001$.

Common Sandpiper *Actitis hypoleucos* (380%; Table 1), resulting from the use of breeding density estimates for these species. In addition, estimates were markedly higher for Greater Sand Plover (253%), Red-necked Phalarope (250% from the lower end of the WPE5 range), Grey-tailed Tattler (159%), Oriental Plover (159%) and Red-necked Stint (151%). Some of these species have low count coverage on the non-breeding grounds, and therefore the estimates were based on breeding range and density. For example, Long-toed Stint is a very difficult species to monitor on the non-breeding grounds because it makes extensive use of inland freshwater marshes (Higgins & Davies 1996) and rice fields. Species with more modest increases on previous estimates (up to 50% higher than WPE5) were mostly derived from spatial extrapolation, with only three exceptions that instead used breeding range and density (Marsh Sandpiper, Wood Sandpiper *Tringa glareola* and Common Greenshank). For most species that were well counted on the non-breeding grounds, increases in count coverage and effort in recent years combined with a small amount of spatial extrapolation were combined to create the new population estimates.

Cases where our population estimates were markedly lower than WPE5 included Sharp-tailed Sandpiper (53%) and Double-banded Plover (38%). These figures reflect declining trends documented elsewhere (Southey 2009, Clemens *et al.* 2016), despite increases in the amount of count data available for analyses.

Spatial extrapolation and expert review

The spatial extrapolations we have used provide a novel approach in population estimation to make a

first-pass assessment of the proportion of 'missing' birds for species that predominantly use coastal habitats. The Democratic People's Republic of Korea (DPRK) and the eastern Indonesian region (including Timor l'Este and Papua New Guinea) had the highest extrapolation factors (range 3.30–3.47). The latter is reflected by the low percentage of potential shorebird habitat covered by Asian Waterbird Census sites (1% in Papua New Guinea and 2% in eastern Indonesia). Anecdotal evidence suggests that there are large numbers of shorebirds in various locations in the Indonesian region, and addressing the lack of data from Indonesia and Papua New Guinea would be useful. Recent surveys of the Yellow Sea coastline in the DPRK have led to a significant increase in information and knowledge about shorebird populations in the country (Riegen *et al.* 2017). These data are also expected to dramatically decrease the spatial extrapolation factor for the DPRK by providing, for the first time, comparable monitoring data for the country (although the timing of surveys is outside our analytical period of November to March).

Expert review resulted in downward adjustment to extrapolation factors at local and sub-regional scales within Australia, which made a difference of 7% to the total EAAF population estimate. It is possible that some adjustments were too conservative and species estimates should be higher. Regardless, expert elicitation served two purposes: first, it drew on years of expertise of local counters, and their familiarity with their local area and representation of individual species within those areas; and secondly, shorebird monitoring is conducted almost entirely by volunteers (citizen scientists), and it is important that their voices are heard in this process (Hansen *et al.* 2019). Overall, the expert review has helped strengthen estimates through refinement based on local knowledge of species distributions, detectability and behaviour.

Breeding range and density

In species for which the population size could be estimated adequately on the basis of counts from the non-breeding grounds, there was a strong positive relationship between breeding range and population size, indicating that the rationale behind the modelling approach was justified. It also suggests that there was reasonable inter-specific consistency in our approach to estimating breeding range and the non-breeding population of coastal

species, although the broad prediction intervals indicate that the models could be improved. There were no direct measures of breeding density across most of the range and our categorization of breeding densities as low, medium or high is very likely to be an oversimplification of the range of variation. Despite this, inclusion of a coarse estimate of breeding density was an improvement on calibrating the models on breeding range size alone. Given the sparsity of data, it was necessary to use all historical distribution records, and we were unable to explore the possibility that the breeding range of some decreasing species might have contracted (as has been demonstrated for Spoon-billed Sandpiper *Calidris pygmaea* by Zöckler *et al.* 2010).

In species that spend the non-breeding season predominantly at sea (e.g. Red-necked Phalarope), in terrestrial habitats (e.g. Little Curlew *Numenius minutus*) or in non-tidal wetlands (10 species, such as Wood Sandpiper), the number of birds counted during the non-breeding season was lower than the population size predicted on the basis of breeding range. In extreme examples (e.g. Long-toed Stint, Pin-tailed Snipe *Gallinago stenura* and Swinhoe's Snipe *Gallinago megala*), the number of birds counted during the non-breeding season was less than 1% of the likely population size. Although our approach to estimating population size from breeding range was undoubtedly coarse, we consider the resultant estimates for the 10 species that used breeding range and density as the final estimate to be far closer to reality than estimates based solely on non-breeding counts.

Limitations and future analyses

The breeding range and density analysis were reliant on the quality of breeding range mapping. BirdLife International has compiled one of the most comprehensive sets of range maps for the world's birds, but some of these are out of date (e.g. Latham's Snipe), and others are imprecise in the EAAF (e.g. Common Redshank). Hence, they required substantial refinement for use in this study. The three-category code we used for classifying breeding density exerted a strong effect on predictions, and future population estimate revisions could refine these methods. This may be achieved by incorporating breeding density data more directly, and using remote sensing analysis to determine finer-scale distribution (and patchiness) of key habitats. Regardless of this drawback, we believe some

correction for density variation is preferable to no correction at all when using this approach.

Expert review made an important contribution to error checking, site-specific estimate validation and identifying where count data were missing from central databases, refining extrapolation factors and, ultimately, refining species estimates for regions where large areas of intertidal habitat were not counted. However, this process could have been more quantitative by, for example, generating uncertainty bounds placed around expert estimates. This would require some expert scoring to calculate errors arising from differences in expert judgement (Moody & Grand 2012, Fraixedas *et al.* 2019).

The modelling approach used here to extrapolate across uncounted areas cannot be expected to accurately map all available intertidal habitat, as the resolution of the available data at the time was not sufficient for detailed analyses. Similarly, our habitat mapping did not incorporate variation in habitat quality, which was instead addressed using expert review. Targeted surveys in data-poor areas are the logical next steps from spatial extrapolation. A refined spatial extrapolation analysis would help to target the largest geographical gaps.

Future revisions will require the estimation of subspecies population sizes and attempts to partition species/subspecies by flyway (as is adopted in the Waterbird Population Estimates Portal and used by the Ramsar Convention and the EAAF Site Network for identification of internationally important sites). Tracking of birds within their different flyways is a powerful tool for disentangling relative distributions within and between flyways, as demonstrated by the recent tracking of Oriental Pratincoles from a single non-breeding population in northwest Australia to breeding grounds on both the Indian subcontinent and the southeast Asian mainland (Australasian Wader Studies Group unpubl. data). Finally, we note that all improvements to these approaches and refinements to population estimates will be most effective by expanding the collection of regular count data from under-represented geographical areas, and by improving data sharing among monitoring groups in different countries.

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CONFLICTS OF INTEREST

The authors do not have any conflicts of interest to declare.

ETHICAL NOTE

None.

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AUTHORS' CONTRIBUTIONS

Birgita D. Hansen: Project leadership; coordination; integration of results; production of final estimates; co-development of project methodology; writing – original draft; writing – review and editing. **Danny I. Rogers:** Data – cleaning and analysis; integration of results; co-development of project methodology; production of final estimates; writing – original draft; writing – review and editing. **Doug Watkins:** Data–cleaning and analysis; integration of results; provision of significant datasets; production of final estimates; writing – original draft; writing – review and editing. **Dan R. Weller:** Data – cleaning and analysis; integration of results; provision of significant datasets; production of final estimates; writing – original draft; writing – review and editing. **Robert S. Clemens:** Data – cleaning and analysis; integration of results; co-development of project methodology; production of final estimates; writing – original draft; writing – review and editing. **Mike**

Newman: provision of significant datasets; production of final estimates; writing – original draft; writing – review and editing. **Eric J. Woehler:** provision of significant datasets production of final estimates; writing – original draft; writing – review and editing. **Taej Mundkur:** provision of significant datasets production of final estimates; writing – original draft; writing – review and editing. **Richard A. Fuller:** Data – cleaning and analysis; integration of results; co-development of project methodology production of final estimates; writing – original draft; writing – review and editing.

Data Availability Statement

ALA (2013), BirdLife Australia (2019), BirdLife International & NatureServe (2015), International Waterbird Census (2020), Sullivan & eBird Basic Dataset (2017).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Visual representation of how breeding range distribution maps (from BirdLife International) of individual species were modified and updated for use in the breeding range and density analyses.

Figure S2. Residual plots from linear modelling estimating non-breeding population on the basis of breeding range and breeding density.

Table S1. Data and explanation of *a priori* assumptions used in analysis of the relationship between breeding range and population size.

Table S2. Predictions from revised breeding range and density modelling conducted in this study, with lower and upper limits of prediction intervals.