Patterns and processes in shorebird survival rates: a global review

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Changes in demographic rates underpin changes in population size, and understanding demographic rates can greatly aid the design and development of strategies to maintain populations in the face of environmental changes. However, acquiring estimates of demographic parameters at relevant spatial scales is difficult. Measures of annual survival rates can be particularly challenging to obtain because large-scale, long-term tracking of individuals is difficult and the resulting data contain many inherent biases. In recent years, advances in both tracking and analytical techniques have meant that, for some taxonomic groups, sufficient numbers of survival estimates are available to allow variation within and among species to be explored. Here we review published estimates of annual adult survival rates in shorebird species across the globe, and construct models to explore the phylogenetic, geographic, seasonal and sex-based variation in survival rates. Models of 295 survival estimates from 56 species show that survival rates calculated from recoveries of dead individuals or from return rates of marked individuals are significantly lower than estimates from mark–recapture models. Survival rates also vary across flyways, largely as a consequence of differences in the genera that have been studied and the analytical methods used, with published estimates from the Americas and from smaller shorebirds (*Actitis*, *Calidris* and *Charadrius* spp.) tending to be underestimated. By incorporating the analytical method used to generate each estimate within a mixed model framework, we provide method-corrected species-specific and genus-specific adult annual survival estimates for 52 species of 15 genera.

Keywords: demography, global flyways, mark–recapture, recovery models, return rates, waders.

Global environmental change has driven widespread biodiversity loss through direct and indirect human impacts across the planet (Butchart *et al.* 2010). Understanding the demographic changes that lead to changes in abundance of populations is fundamental to designing strategies to reduce or reverse their impacts. However, for most species, we lack information on key demographic rates and how they vary over space and time. Comparing species' demographic rates across large spatial scales can help to identify regions, habitats or populations under threat before detectable abundance declines occur (Piersma *et al.* 2016). Although measures of productivity are often readily quantifiable, survival rates, particularly of long-lived, free-ranging animals, can be very challenging to estimate (Newton *et al.* 2016). However, over recent decades, advances in tracking and modelling techniques have greatly facilitated the estimation of survival rates, with avian research being particularly active on this front (e.g. MARK, White & Burnham 1999, E-Surge, Choquet *et al.* 2009).

The number of published estimates of avian survival rates has increased greatly in recent decades and, in some groups, sufficient estimates are available to allow exploration of the level and potential causes of variation in survival rates.

Migratory shorebirds (also known as waders) have been described as sentinels of global environmental change due to their global distribution, long migrations and complex habitat use (Piersma & Lindström 2004). This group includes some of the northernmost breeding terrestrial vertebrates on the planet, with most populations breeding in the arctic and subarctic zones but several also breeding in temperate and tropical areas (Delany *et al.* 2009). During the non-breeding season, migratory shorebirds occupy temperate and tropical coastal areas and, in some cases, also inland wetlands and other open habitats (Hayman *et al.* 1986, van de Kam *et al.* 2004). These ecosystems are currently among the most severely affected by environmental change, through processes such as global warming, sea level rise and land claim (Sutherland *et al.* 2012). Many shorebird populations are currently declining (Delany *et al.* 2009, Pearce-Higgins *et al.* 2017), some very rapidly (e.g. Black-tailed Godwit *Limosa limosa limosa;* Kentie *et al.* 2016) and to the point of being threatened with global extinction (e.g. Spoon-billed Sandpiper *Calidris pygmaea*; Zöckler *et al.* 2010). Although population declines have been reported across all the main shorebird flyways, their causes are not easy to identify (Hötker *et al.* 1998). Pinpointing factors that influence population change requires an understanding of the demographic rates operating in different populations, species and flyways throughout the world.

Comparative analyses of shorebird survival rates are scarce (but see Boyd 1962, Evans & Pienkowski 1984, Roodbergen *et al.* 2012) and have until recently been limited to relatively few species (mainly those in Europe and North America). Furthermore, the variation in survival estimates revealed in comparative analyses can reflect variation not only in true survival but also in sources of error from different estimation methods. Methods that allow estimation of true survival (i.e. the probability of an individual being alive over a given period) are likely to produce higher annual survival estimates than methods that estimate apparent (also known as local survival) or minimum survival based on return rates to specified locations. For example, return rates (the proportion of marked individuals that return to a given location) are likely to underestimate annual survival rates, as imperfections in the observation process are ignored (Lebreton *et al.* 1992, 1993) and no distinction is made between permanent emigration and mortality. Moreover, models that do not take into account variation in resighting or recapture probability, for example as a result of variation in detectability or observer effort (Pollock 1982, Kendall & Bjorkland 2001), can also result in underestimation. It is therefore important that the estimation method used to calculate survival rates is taken into account in comparative analyses (see Supporting Information material for full description of the methods most commonly used). Estimates of annual survival rates may also differ depending on the seasonal timing of capture and recapture or resighting. This could be due to seasonal variation in site-fidelity or detectability leading to different estimates of annual survival quantified between breeding seasons than between non-breeding seasons (Evans & Pienkowski 1984).

Variation in annual survival rates may also be the product of particular biological traits and ecological factors. The positive relationship between longevity and body size is well established (Boyd 1962, Székely *et al.* 2014) and survival rates may also vary in relation to nesting location, migratory status, sex and species' range. Ground-nesting shorebirds breeding at higher latitudes may benefit from lower predation risks (van der Wal & Palmer 2008, McKinnon *et al.* 2010) and, among birds generally, adult females often have lower survival rates than males (Liker & Székely 2005). Sex-biased survival may result from differences in body size, reproductive investment (e.g. mating system, parental care and cost of reproduction) or predation pressures (Liker & Székely 2005, Donald 2007, Székely *et al.* 2014), but sex-differences in dispersal behaviour (Tavecchia *et al.* 2002, Pakanen *et al.* 2015) and detection rates (Sandercock *et al.* 2005) can further complicate these estimates.

Most shorebird species make an annual round-trip migration between their breeding and wintering grounds, and environmental conditions at locations along these routes may influence annual survival rates. Decreases in annual survival rates and population sizes of several shorebird species using the East Asian-Australasian flyway have recently been reported and directly linked to the loss of coastal wetland habitats in the Yellow Sea

(Conklin *et al.* 2016, Piersma *et al.* 2016). Variation in shorebird survival rates across flyways may therefore reflect different environmental conditions and levels of habitat change.

The increasing number of published estimates of survival rates means that we are now able to examine how these estimates vary across species and between flyways. Here, we collate survival estimates of shorebird species from published studies and grey literature to examine the magnitude of variation in annual survival rates for this group and how much of that variation is associated with estimation method and how much with the biology of the species. Specifically, we explore the effect of estimation method on survival estimates and derive species- and genus-specific annual survival estimates corrected for estimation method. Then, while controlling for method, we investigate variation in shorebird annual survival as a function of body mass, genus, flyway, season of measurement and sex.

METHODS

Data extraction

Survival estimates

In September 2016, we searched Web of Science, SCOPUS and the Internet (Google search engine) using English language terms to identify relevant published and unpublished studies (e.g. reports and research theses). We used the following terms in the following combinations: (wader OR shorebird) AND (survival or demography) AND (adult). Studies of egg, chick and juvenile survival were not considered. Bibliographies of sources selected from these searches were subsequently searched for relevant additional information. We extracted the following parameters from these sources: (1) species survival estimate (**T** se), with separate estimates for adult male and adult female, where available; (2) type of data used (dead recoveries and/or live encounters); (3) estimation method used; (4) season of measurement (either non-breeding to non-breeding or breeding to breeding season); and (5) study location.

Analytical methods used for estimating survival rates

A range of statistical methods for analyses of recovery of dead individuals or encounters/recapture of live individuals have been developed and these techniques have advanced greatly in recent decades (reviewed in Sandercock 2003, 2006 and summarized in Appendix S1). As the use of different methods can generate different estimates, survival estimates were categorized by the data and estimation method used, as follows: (1) return rates (the proportion of marked individuals that are recaptured/resighted in subsequent years); (2) mark–recapture models (standard and modified Cormack-Jolly-Seber (CJS) models; apparent survival rates from live encounter data accounting for recapture/resighting rate); (3) dead recovery models (apparent survival rates from dead recovery data accounting for recovery rate) and old dead recovery models (apparent survival rates assuming that annual survival and recovery rates are constant through time using only the recovery data and not the number of birds ringed; Haldane 1955); and (4) more complex models that separate apparent survival into estimates of true survival and site fidelity, from live encounter (e.g. Barker and multi-state models) and live encounter and recovery data (e.g. Burnham model), both accounting for resighting/recovery rates (Table 1). Survival estimates from radiotelemetry tracking studies are only available for a very limited number of shorebird species and for short periods (daily or seasonal survival), hence these were not included in this study.

Body mass

We extracted body mass (in g) for each species from BTO Bird Facts (Robinson 2005) or, when absent in that source, from the Encyclopedia of Life website (EOL; http://eol.org/).

Flyway

Flyways describe the migration routes used by shorebird populations moving between breeding and wintering areas, delimiting populations at large scales (Boere & Stroud 2006). We grouped species into four major flyways: American (comprises the eastern Pacific, Mississippi and western Atlantic flyways), African-Eurasian (includes east Atlantic, Mediterranean/Black Sea and West Asia/East Africa flyways), Central Asian (comprises only this flyway) and East Asian-Australasian flyways (includes East Asia/Australasia and far east Russia/Alaska to the Pacific Islands flyways).

Data analysis

Estimates of survival in the year immediately after first capture (usually referred to as Φ^1) tend to be

Table 1. Annual adult survival estimates of shorebirds collated from the literature and predicted from a generalized linear model (GLM) in which survival rates were modelled as a function of species and estimation method.

Species	Location	Method	Range	Adult	Male	Female	Source
Actitis hypoleucos	Europe	Return rates	B	0.61–0.81			1,2
	Europe	Old dead recovery		0.52–0.79			2,3
		GLM		0.718 ± 0.033			This study
Actitis macularia	USA	Return rates		0.5–0.61	0.29–0.63	0.26–0.63	4,5
		GLM		0.497 ± 0.023	0.490 ± 0.026	0.415 ± 0.025	This study
Anarhynchus frontalis	New Zealand	Return rates	W	0.83			6,7
		GLM		0.836 ± 0.037			This study
Arenaria interpres	Europe	Return rates	B	0.78–0.85			8,9
	Europe	Return rates	W	0.72–0.86			10,11
	Europe	Old dead recovery		0.66			3
		GLM		0.809 ± 0.020			This study
Arenaria melanocephala	Alaska	Return rates	B	0.84	0.88	0.79	12
		GLM		0.842 ± 0.022	0.852 ± 0.020	0.810 ± 0.025	This study
Burhinus oedicnemus	Europe	Dead recovery		0.83			13
		GLM		0.832 ± 0.039			This study
Calidris alba	Europe	Return rates	B	0.83			9
	Europe	Old dead recovery		0.56			3
		GLM		0.836 ± 0.037			This study
Calidris alpina	Europe	Return rates	B	0.73–0.83			14,15
	USA	Mark–recapture	W	0.53–0.73			16
	Europe	Old dead recovery		0.62			3
		GLM		0.762 ± 0.017			This study
Calidris canutus	Europe	Old dead recovery	W	0.68–0.79			3,17
	Europe	Dead recovery	W	0.74–0.88			17,18
	USA, Argentina	Mark–recapture	SO	0.62–0.98			19,20
	Europe, Argentina, Chile	Mark–recapture	W	0.56–1			19,21
	Mauritania	Mark–recapture	W	0.77–0.83			22
	USA	Mark–recapture	SO	0.92			23
		GLM		0.801 ± 0.011			This study
Calidris ferruginea	Australia	Mark–recapture	W	0.73			24
	Europe	Old dead recovery		0.67			3
		GLM		0.709 ± 0.047			This study
Calidris himantopus	Canada	Return rates		0.53			25
		GLM		0.540 ± 0.051			This study
Calidris maritima	Europe	Return rates	B	0.8			11
	Europe	Return rates	W	0.66			26
	Europe	Mark–recapture	W	0.72–0.80			27,28
		GLM		0.736 ± 0.019			This study

(continued)

Table 1. (continued)

Species	Location	Method	Range	Adult	Male	Female	Source
Calidris mauri	Central America	Return rates	W	0.56	0.54	0.62	29,30
	Alaska	Return rates	B		0.58–0.65	0.4–0.49	14,29,31
	Central America	Mark–recapture	W	0.48	0.47–0.54	0.62	32,33
	Alaska	Mark–recapture	B	0.57	0.78	0.65	31,34
		GLM		0.558 ± 0.015	0.604 ± 0.015	0.529 ± 0.015	This study
Calidris minutilla	Canada	Return rates	B	0.54	0.65	0.38	35
		GLM		0.533 ± 0.031	0.551 ± 0.030	0.476 ± 0.030	This study
Calidris pusilla	Canada	Return rates	B	0.73	0.76	0.57	36,37
	USA	Return rates	SO	0.4			38
	Canada, Alaska	Mark–recapture	B		0.61–0.73	0.56–0.59	34,39
	Central America	Mark–recapture	W	0.65			40
		GLM		0.608 ± 0.018	0.681 ± 0.018	0.611 ± 0.020	This study
Calidris pygmaea	Russia	Return rates		0.66			41
		GLM		0.669 ± 0.048			This study
Calidris ruficollis		Return rates	B	0.8			42
	Australia	Mark–recapture	W	0.72			24
		GLM		0.754 ± 0.031			This study
Calidris temminckii	Europe	Return rates	B	0.63–0.76	0.79	0.71	43,44
	Europe	Mark–recapture	B	0.69			44 3
		GLM		0.720 ± 0.021	0.774 ± 0.024	0.717 ± 0.028	This study
Charadrius alexandrinus	Europe	Return rates	B	0.55			
	Europe	Old dead recovery		0.6			3
	Turkey	Mark–recapture	B	0.64	0.63	0.64	45
		GLM		0.593 ± 0.030	0.670 ± 0.033	0.6 ± 0.036	This study
Charadrius dubius	Europe	Old dead recovery		0.65			3
		GLM		0.616 ± 0.030			This study
Charadrius hiaticula	Europe	Return rates	B	0.59–0.8			46
	Europe	Old dead recovery		0.58			3
		GLM		0.721 ± 0.024			This study
Charadrius marginatus	South Africa	Mark–recapture	B	0.88			
	South Africa	Mark–recapture	B	0.9	0.87	0.93	47
		GLM		0.885 ± 0.017	0.91 ± 0.016	0.882 ± 0.020	This study
Charadrius melodus	USA, Canada	Return rates	B	0.74	0.75	0.56	48,49
	USA	Mark–recapture	B	0.66–0.74			50,51
	USA	Mark–recapture	B	0.74			52
	Canada	Mark–recapture	B	0.73			53
	USA	Complex	B	0.7			54
		GLM		0.705 ± 0.014	0.729 ± 0.019	0.664 ± 0.021	This study
Charadrius montanus	USA	Mark–recapture	B	0.68–0.87			55,56
		GLM		0.756 ± 0.032			This study

Table 1. (continued)

Species	Location	Method	Range	Adult	Male	Female	Source
Charadrius nivosus	USA	Return rates	B	0.74	0.58–0.79	0.51–0.73	57–59
	USA	Mark–recapture	B		0.64–0.69	0.57–0.69	60,61
	USA	Complex	B		0.73	0.69	62
		GLM		0.652 ± 0.014	0.691 ± 0.014	0.622 ± 0.015	This study
Charadrius obscurus	New Zealand	Mark–recapture	B	0.92			63
		GLM		0.912 ± 0.030			This study
Charadrius sanctaehelenae	Saint Helena	Mark–recapture	B	0.83			64
		GLM		0.778 ± 0.031			This study
Charadrius semipalmatus	Canada	Return rates	B		0.6	0.41	65
		Mark–recapture	B	0.71			66
	Canada	Mark–recapture	B	0.77			67
		GLM		0.639 ± 0.021	0.644 ± 0.024	0.571 ± 0.026	This study
Gallinago gallinago	Europe	Old dead recovery		0.48			3
	Europe	Mark–recapture	SO	0.76			68
	Europe	Mark–recapture	SO	0.75			68
		GLM		0.611 ± 0.026			This study
Haematopus bachmani	Canada	Return rates	B	0.96			69
		GLM		0.962 ± 0.019			This study
Haematopus finschi	New Zealand	Complex	B	0.89			70
		GLM		0.895 ± 0.031			This study
Haematopus ostralegus	Europe	Return rates	W	0.89–0.986	0.91	0.84	71–73
	Europe	Return rates	B	0.89			74
	Europe	Old dead recovery		0.84			3
	Europe	Dead recovery	W	0.87–0.91			18,75
	Europe	Mark–recapture	B	0.92			76
	Europe	Complex		0.85–0.87			77
		GLM		0.890 ± 0.009	0.892 ± 0.021	0.858 ± 0.026	This study
Haematopus palliatus	USA	Mark–recapture	B	0.81–0.95			78–80
	USA	Complex	B	0.94			79
	USA	Return rates	B	0.85			81
		GLM		0.892 891 ± 0.012			This study

(continued)

Table 1. (continued)

Species	Location	Method	Range	Adult	Male	Female	Source
Limosa lapponica	Europe	Return rates	B	0.88			[9]
	Europe	Old dead recovery		0.6			[3]
		GLM		0.862 ± 0.018			This study
Limosa limosa	Europe	Return rates	B	0.81–0.95			[82,83]
	Europe	Old dead recovery		0.7			[3]
	Europe	Dead recovery		0.77–0.8			[84,85]
	Europe	Mark–recapture	B	0.95			[86]
	Europe	Mark–recapture	W	0.87–0.94			[87,88]
	Europe	Mark–recapture	B	0.62–0.96			[89]
	Europe	Complex	B	0.7–0.93			[90,91]
		GLM		0.857 ± 0.009			This study
Lymnocryptes minimus	Europe	Old dead recovery		0.24			[3]
		GLM		NA			This study
Numenius americanus	USA	Mark–recapture	B	0.85			[92]
		GLM		0.836 ± 0.039			This study
Numenius arquata	Europe	Return rates	B	0.82–0.89			[93–96]
	Europe	Old dead recovery		0.74–0.75			[3,97]
	Europe	Mark–recapture	W	0.9			[98]
		GLM		0.864 ± 0.013			
Numenius phaeopus	Europe	Return rates		0.71–0.89	0.72–0.87	0.5–0.68	[99–101]
	Europe	Old dead recovery		0.69			[3]
		GLM		0.744 ± 0.021	0.761 ± 0.019	0.701 ± 0.022	This study
Numenius tahitiensis	Hawaii	Mark–recapture	W	0.85			[102]
		GLM		0.836 ± 0.039			This study
Philomachus pugnax	Europe	Old dead recovery		0.52	0.5	0.59	[3]
	Europe	Mark–recapture	SO		0.64–0.74	0.51–0.73	[103]
		GLM		0.631 ± 0.026	0.689 ± 0.023	0.621 ± 0.025	This study
Pluvialis apricaria	Europe	Return rates	B	0.72	0.73	0.7	[104]
	Europe	Mark–recapture	W	0.55–0.73			[105]
	Europe	Old dead recovery		0.54–0.61			[3]
	Europe	Dead recovery	W	0.65			[106]
	Europe	Complex	W	0.83			[105]
		GLM		0.692 ± 0.017	0.740 ± 0.026	0.677 ± 0.029	This study
Pluvialis fulva	Hawaii	Return rates	W	0.82			[107]
	Hawaii	Mark–recapture	W	0.67–0.8			[107]
		GLM		0.753 ± 0.026			This study
Recurvirostra avosetta	Europe	Old dead recovery		0.62			[3]
		GLM		NA			This study
Scolopax minor	USA	Dead recovery		0.49	0.52–0.58	0.23–0.39	[108,109]
		GLM		0.499 ± 0.030	0.535 ± 0.026	0.460 ± 0.026	This study

(continued)

Table 1. (continued)

Species	Location	Method	Range	Adult	Male	Female	Source
Scolopax rusticola	Europe	Old dead recovery		0.54–0.63			3,110,111
	Europe	Dead recovery	W	0.44			112
		GLM		0.443 ± 0.054			This study
Tringa glareola	Europe	Old dead recovery		0.54			3
	Europe	Mark–recapture	SO	0.71			68
		GLM		0.690 683 ± 0.035			This study
Tringa ochropus	Europe	Return rates	W	0.83			113
		GLM		0.845 ± 0.036			This study
Tringa semipalmatus	USA	Return rates	B	0.73			114
		GLM		0.738 ± 0.044			This study
Tringa totanus	Europe	Return rates	B	0.71–0.78			15
	Europe	Mark–recapture	B		0.75	0.72	115
	Europe	Mark–recapture	B	0.8			116
	Europe	Mark–recapture	W	0.73–0.93			117,118
	Europe	Mark–recapture	W	0.67–0.74			119
	Europe	Old dead recovery		0.69			3
		GLM		0.780 ± 0.012	0.778 ± 0.024	0.721 ± 0.028	This study
Vanellus gregarius	Central Asia	Mark–recapture		0.66			120
		GLM		0.636 ± 0.050			This study
Vanellus vanellus	Europe	Old dead recovery		0.66–0.70			3,121
	Europe	Dead recovery		0.75–0.83			91,122,123
	Europe	Complex		0.83			124
	Europe	Return rates	B	0.74			125
	Europe	Mark–recapture	B	0.76			126
		GLM		0.790 ± 0.019			This study

Predictions are provided with associated standard error. Range indicates whether survival was measured in breeding (B), wintering (W) or stopover (SO) locations. References are found in Appendix S2.

lower than survival estimates in subsequent years (usually referred to as Φ^{2+}), possibly reflecting capture and handling effects or the inclusion of transient birds that have lower subsequent resighting probabilities (Sandercock 2006). When both estimates were provided in the original study, only estimates of adult survival in years after capture (Φ^{2+}) were used in our analyses. Because not all variables of interest are provided in all original studies, we used different subsets of data in separate generalized linear mixed models (GLMMs) to explore (1) methodological and (2) biological and environmental factors that might contribute to variation in annual survival rates.

Methodological factors. To quantify the influence of analytical method on the survival estimates reported in each study, we used a GLMM in which survival rates were modelled with estimation method as a fixed effect and species as a random effect to account for variable numbers of estimates from each species. We used a logit link function and binomial error distribution using the *glmer* function from the *lme4* package (Bates *et al.* 2015) in R 3.2.2 (R Core Team, 2015). We first used the whole dataset and then excluded estimates derived from old recovery methods (Haldane 1955) because the latter can result in low (and unreliable) survival estimates (Roodbergen *et al.* 2012), and the estimates derived from these early recovery models did indeed significantly reduce the mean survival rates estimated by the recovery models. We made pairwise comparisons of estimation methods by computing the least-squares means and using a Tukey adjustment (*lsmeans* package; Lenth 2016).

To provide estimates of species-level survival rates from published sources that take account of the estimation method used, we used a generalized linear model (GLM) with logit link function and binomial error distribution to model survival as a function of species and estimation method.

Biological and environmental factors. To understand the variation in survival estimates among genera and flyways and in relation to body mass, we modelled survival estimates as a function of genus, flyway, body mass (on a $\log_e$ scale) and estimation method using a GLMM with logit link function and binomial error distribution, with species as random effect to account for variable numbers of estimates from each species. To test for significant differences between groups within 'flyway' and 'genus', we performed pairwise comparisons computing the least-squares means using a Tukey adjustment with the *lsmeans* package.

To test whether annual survival rates vary with season of measurement, we divided our data in subsets by selecting those species with survival estimates quantified on either the breeding or wintering grounds. We did not include estimates measured at stopover sites, as these were only available for four species (*Calidris canutus*, *Calidris pusilla*, *Gallinago gallinago* and *Tringa glareola*) or studies which mixed data from both wintering and breeding seasons. We modelled survival estimates using the same GLMM described above adding 'Season' as a fixed effect.

To test for sex-differences in annual survival rates, we selected data from studies where survival differences between sexes were explicitly tested. If survival rates varied significantly between males and females in the original study, separate survival estimates for females and males were extracted. However, if there were no significant differences between the sexes, only one estimate for adults was used. We modelled survival estimates as a function of sex (three categories: female, male, adult) and estimation method using a GLMM with logit link function and binomial error distribution, with species as random effect to account for variable numbers of estimates from each species. Other explanatory variables were not included in the model as there were insufficient data to fit all the variables in the model.

RESULTS

We extracted annual survival rates for 56 species from five families, totalling 126 studies and 295 survival estimates (Fig. 1, Table 1). Annual survival rates have been estimated at least once for approximately 50% of species in the Haematopodidae, over 30% of species in the Scolopacidae and Recurvirostridae, and < 30% of species among the Charadriidae and Burhinidae (Fig. 1a). The number of estimates available for each species also varies, with more than 11 estimates for species such as Eurasian Oystercatcher *Haematopus ostralegus*, Common Redshank *Tringa totanus* and Black-tailed Godwit *L. limosa*, but only one or two for most of the remaining species. Most studies were of species using the African-Eurasian and American flyways, whereas survival estimates for species on the

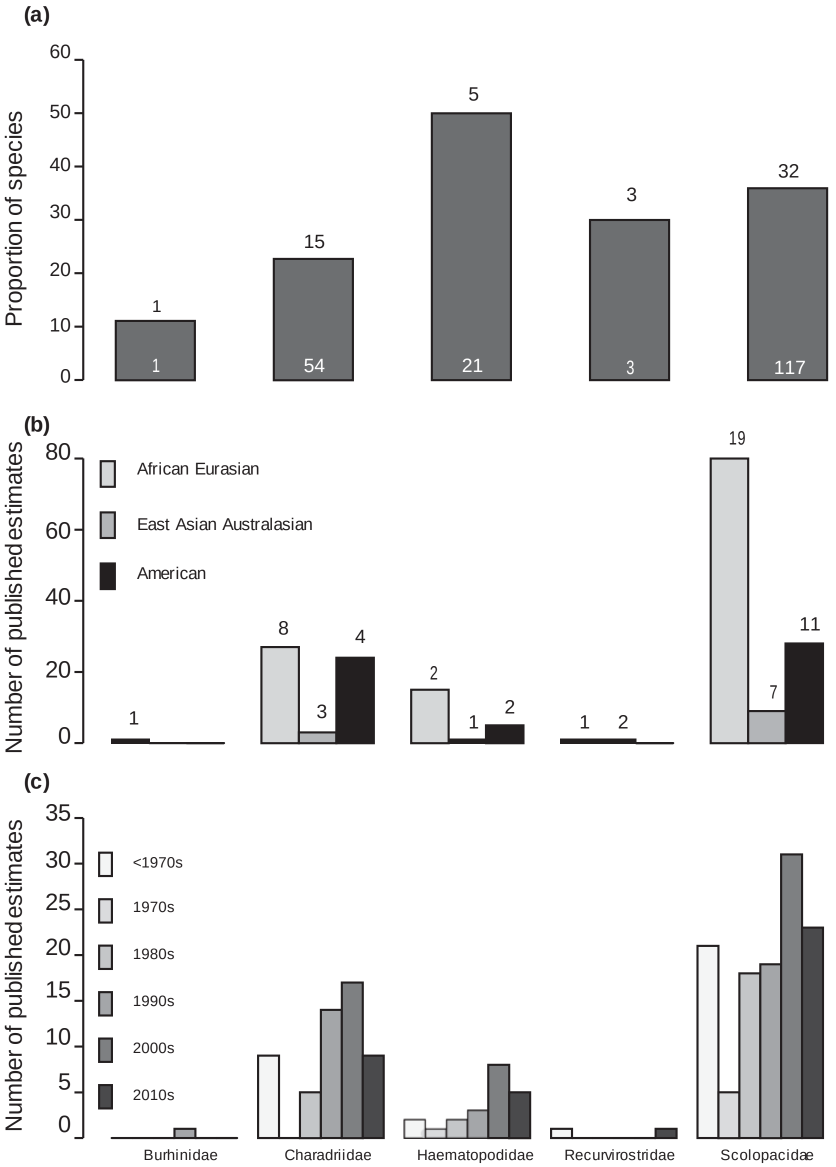

Figure 1. (a) Proportion of species from each shorebird family with published estimates of annual adult survival, (b) the number of published estimates for each family in different flyways and (c) the number of published estimates for each family in different time periods (decade of publication). Numbers above bars indicate the number of species and numbers within bars indicate the number of published estimates.

Central Asian and East Asian-Australasian flyways were absent or scarce, respectively (Fig. 1b). Although the number of published survival estimates has continued to grow for species in the Charadriidae, Scolopacidae and Haematopodidae, there are very few survival estimates for Burhinidae and Recurvirostridae, and these are from before the 1980s (Fig. 1c).

Live encounter data were most commonly used to generate annual survival through mark–recapture models or return rates (Table 2). Estimates from dead recovery models were available for most species on the African-Eurasian flyway, only one on the American flyway and none on the East Asian-Australasian flyway (Table 2). More complex models have been used less frequently and for a limited number of species, mostly on the African-Eurasian flyway (Table 2). For *Actitis*, *Anarhynchus*, *Arenaria*, *Burhinus*, *Lymnocryptes*, *Recurvirostra* and *Scolopax*, only survival estimates derived from return rates and/or dead recovery models were available and several of these were estimates computed using with Haldane's methods (Table 2).

Most studies were carried out during the breeding season, with individuals being both marked and recaptured, resighted or recovered during the breeding season. As a result, over 63% of the survival estimates originated from the breeding grounds, with 31% measured on the wintering grounds and 6% at stopover sites.

Factors affecting annual survival rates of adult shorebirds

On average, adult survival estimates were high for shorebird species, with most ranging between 0.7 and 0.9 (see entire range of survival estimates for shorebirds in Table 1). However, some survival estimates were very low (e.g. Spotted Sandpiper *Actitis macularia* from return rates; male = 0.29, female = 0.26; Table 1).

Methodological factors

Estimates of annual survival rates varied significantly depending on the estimation method from which they were generated (Table 3). Dead recovery models produced significantly lower estimates than other methods and return rates were lower than mark–recapture survival estimates (Table 3). However, when survival estimates derived from old recovery models (Haldane's) were excluded, the only remaining difference was that estimates from return rates were significantly lower than those from mark–recapture methods (Table 3). For *Lymnocryptes* spp. and *Recurvirostra* spp., the only estimates available were from Haldane's method (Table 1) and these species were therefore not included in subsequent analyses.

Biological and environmental factors

Body mass, genus and flyway. Annual adult survival increased with body mass (model slope on logit scale 0.51 ± 0.12 se, $P < 0.0001$; Fig. 2a). Our predicted survival rates on the American flyway were higher than observed survival rates, whereas model predictions and observed estimates were much closer for the other flyways (Fig. 2b, Table 4). Mean survival rate of species in the American flyway was significantly lower than for species in the African-Eurasian flyway (Tukey-adjusted comparisons, $P = 0.02$; Fig. 2b, see Table 4 for estimates). Survival rates of species on

Table 2. Summary of adult annual survival estimates available for each genus, across flyways (A = American, AE = African-Eurasian, EAA = East Asian-Australasian) and the method used.

	Return rate			Mark-recapture			Complex			Dead recovery		
	A	AE	EAA	A	AE	EAA	A	AE	EAA	A	AE	EAA
Actitis	6	2									2 (2)	
Charadrius	10	5		21	11	1	5				3 (3)	
Anarhynchus			1								1 (1)	
Lymnocryptes											1 (1)	
Calidris	17	11	2	22	12	3					7 (5)	
Gallinago					2			2			1 (1)	
Arenaria	3	4										
Tringa	1	5			13						2	
Philomachus					4						3 (3)	
Pluvialis		3	1		5	2		1			2 (2)	
Scolopax										5	5 (4)	
Vanellus		1			1			1			5 (2)	
Limosa		3			8	3		4			3 (2)	
Recurvirostra											1 (1)	
Burhinus											1	
Haematopus	2	5		4	1		2	2	1		5 (1)	
Numenius		10		1	3	1					3 (3)	

Numbers between brackets indicate estimates from Haldane's recovery models (a subset of dead recovery models). Genus in ascending order of mean body mass.

Table 3. Parameter estimates derived from a generalized linear mixed model with a logit link distribution and binomial error distribution, in which survival rates were modelled as a function of estimation method, with species as random effect using: (a) all 278 estimates and (b) excluding 33 estimates from Haldane's early recovery models.

	Method	Probability	se	LCL	UCL	Tukey-adjusted comparisons		
						Complex	Mark-recapture	Return rates
(a)	Dead recovery	0.658	0.022	0.613	0.700	< 0.0001	< 0.0001	< 0.0001
	Complex	0.739	0.021	0.695	0.779		0.150	0.987
	Mark–recapture	0.767	0.017	0.733	0.799			0.008
	Return rates	0.744	0.018	0.707	0.778			
(b)	Dead recovery	0.743	0.025	0.690	0.790	1.000	0.505	0.999
	Complex	0.744	0.022	0.700	0.784		0.183	1.000
	Mark–recapture	0.771	0.017	0.736	0.802			0.003
	Return rates	0.744	0.018	0.707	0.779			

Lower (LCL) and upper (UCL) confidence levels are 95%. Significant *P*-values of Tukey-adjusted comparisons across methods in bold.

the East Asian-Australasian flyway did not differ significantly from those of African-Eurasian ($P = 0.95$) and American ($P = 0.10$) flyways. However, most species for which estimates were available on the American and East Asian-Australasian flyways were smaller-bodied than those available for analysis on the African-Eurasian flyway (Table 2).

Annual adult survival also varied between genera, with the highest estimates from *Haematopus* and *Limosa* spp. and the lowest estimates from *Scolopax* and *Actitis* spp. (Fig. 2c, Tables 1 and 4). Our model predicted higher estimated annual survival than was observed for seven genera, with *Actitis*, *Calidris* and *Charadrius* spp. exhibiting the greatest deviation from observed values (Fig. 2c, Table 4). For the remaining genera, the model tended to predict slightly lower survival rates than were observed, with *Numenius* spp. showing the greatest deviation from observed estimates of annual survival. Only one estimate was available for *Anarhynchus* and *Burhinus*, thus results for these genera must be interpreted with caution.

Season of measurement and sex. We found eight genera with survival estimates measured on both breeding and wintering grounds (*Arenaria*, *Calidris*, *Haematopus*, *Limosa*, *Numenius*, *Pluvialis*, *Tringa* and *Vanellus*) but survival estimates did not differ significantly between seasons of measurement (predicted estimate on wintering grounds 0.810 ± 0.012 se, $n = 68$ and in breeding grounds 0.806 ± 0.012 se, $n = 89$; $P = 0.65$). For species where sex differences were tested in the original study, females had significantly lower average annual survival rates (predicted estimate 0.664 ± 0.039, Confidence interval (CI) 0.585–0.735)) than males (0.728 ± 0.034, CI 0.656–0.790) and adults where the sexes were pooled (0.724 ± 0.035, CI 0.650–0.787; $P < 0.0003$; Fig. 3).

DISCUSSION

Comparing shorebird survival rates globally provides insight into demographic processes operating at very large scales, establishes baseline survival estimates and identifies gaps in our current knowledge of the demography of this group. In addition, we have been able to derive corrected and more robust annual survival rates by accounting for analytical methods used in published estimates (Table 1).

Annual survival estimates of shorebird: where are the current gaps?

Shorebirds are a diverse group, comprising approximately 215 species unevenly distributed among 14 families (Colwell 2010), and although they are popular study organisms, long-term studies of population dynamics are still rare. Just over 25% of species have published annual survival estimates and these are unequally distributed among a small number of families. Only one or two estimates are available for each species, with the exceptions of Eurasian Oystercatcher, Redshank, Black-tailed Godwit and Piping Plover *Charadrius melodus*, for

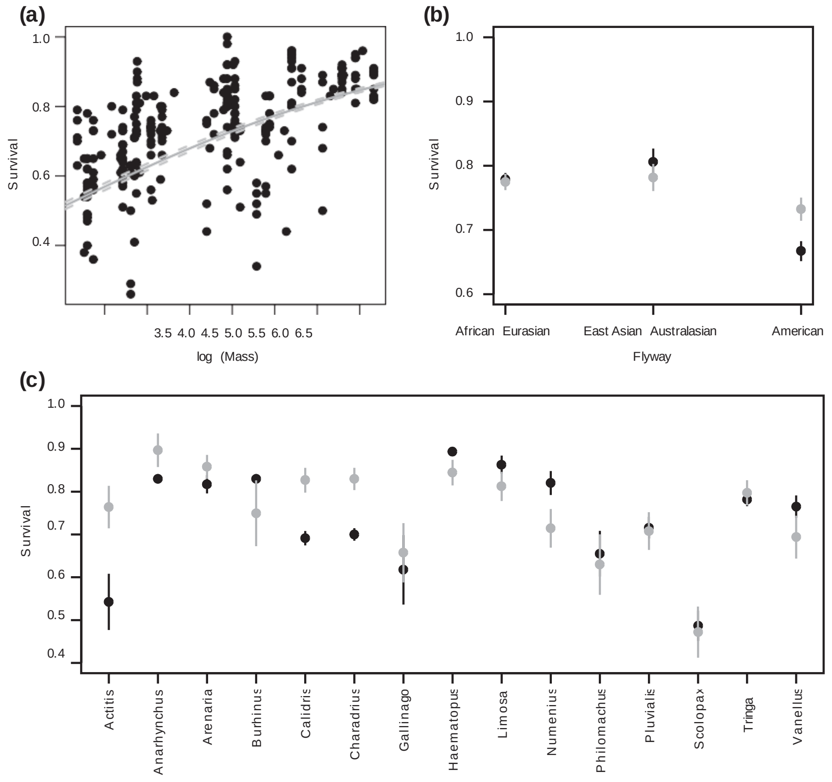

Figure 2. Variation in annual adult survival in relation to (a) body mass (log scale), (b) flyway and (c) genera. In all cases, black dots represent observed data (mean ± se) and grey dots (mean ± se) and continuous line represent mean back-transformed predictions from the generalized linear mixed model including all the predictors with dashed lines representing se.

which at least 10 estimates each are available. These are some of the very few species that have been the focus of long-term monitoring programmes (e.g. Eurasian Oystercatcher: van de Pol *et al.* 2010, Black-tailed Godwit: Gill *et al.* 2001, Alves *et al.* 2013a, Piping Plover: Calvert *et al.* 2006, LeDee *et al.* 2010, Catlin *et al.* 2015) but for the great majority of shorebird species, monitoring programmes capable of generating demographic estimates tend to be less well established and to last for shorter time periods. In addition, there are more survival estimates available for families with species that have broad distributions (e.g. sandpipers and oystercatchers) than families with species that tend to be more restricted in their distributions (e.g. Thick-knees, *Burhinidae*).

There is also geographical disparity in the availability of information on shorebird survival. In particular, studies from the African-Eurasian and North American flyways, where ringing data have been available since the early 1900s (Boyd 1962), are more common than studies from other flyways. For example, we could locate no published survival estimates from shorebirds on the Central-Asian flyway and only 15 from the East-Asian Australasian flyway, although the number of estimates from the latter flyway has increased in recent years (e.g. Conklin *et al.* 2014, Piersma *et al.* 2016) as rapid environmental changes and severe population declines in shorebirds have become increasingly apparent.

Methodological drivers of variation in shorebird annual survival estimates

Most of the published estimates of adult annual survival have been generated using live encounter data and associated analytical methods, resulting in estimates that represent minimum or apparent survival. The use of recovery data alone or combined with live encounter data has been limited to a few species occurring in the African-Eurasian flyway, particularly in Europe, where long-term and well established ringing programmes have resulted in large numbers of shorebirds being ringed and recaptured or recovered (Paradis *et al.* 1998,

Table 4. Mean survival rates, standard errors and parameter estimates derived from a generalized linear mixed model where survival rates were modelled as a function of body mass, flyway, genus and estimation method, with species as random effect.

	Observed survival	se	Estimated survival	se	Lower confidence level	Upper confidence leve
Flyway						
African Eurasian	0.779	0.010	0.775	0.013	0.749	0.799
East Asian-Australasian	0.806	0.020	0.782	0.021	0.737	0.820
American	0.667	0.015	0.732	0.018	0.695	0.766
Genus						
Actitis	0.543	0.066	0.764	0.050	0.654	0.847
Anarhynchus	0.830	NA	0.897	0.039	0.791	0.952
Arenaria	0.817	0.021	0.858	0.028	0.794	0.904
Burhinus	0.830	NA	0.749	0.077	0.573	0.870
Calidris	0.691	0.017	0.827	0.029	0.762	0.876
Charadrius	0.700	0.015	0.830	0.026	0.773	0.875
Gallinago	0.617	0.081	0.657	0.069	0.512	0.778
Haematopus	0.893	0.008	0.844	0.030	0.777	0.894
Limosa	0.863	0.021	0.812	0.034	0.736	0.870
Numenius	0.820	0.028	0.714	0.045	0.618	0.794
Philomachus	0.655	0.053	0.630	0.071	0.484	0.755
Pluvialis	0.716	0.025	0.708	0.044	0.615	0.786
Scolopax	0.487	0.035	0.472	0.060	0.358	0.588
Tringa	0.781	0.015	0.797	0.029	0.734	0.849
Vanellus	0.765	0.026	0.694	0.050	0.588	0.782

Piersma *et al.* 2005, Robinson *et al.* 2007). The degree to which models that generate estimates o true survival differ from estimates of apparent sur vival depends on the proportion of individuals tha emigrate (Sandercock 2003, 2006). However, we found no systematic differences between estimates generated through recovery or more complex models and those generated via mark–recapture models, which is likely to reflect the fact that most shorebirds are highly site-faithful, returning to the same breeding and non-breeding sites throughout their life (Burton & Evans 1997, Leyrer *et al.* 2006, Catry *et al.* 2012). Recovery and more complex models could fail to account for permanent emigration out of study areas if data collection were restricted to specific sites, resulting in estimates of apparent rather than true annual survival (Cohen *et al.* 2006, Roodbergen *et al.* 2008). Thus, although estimating true survival is most desirable, for shorebirds estimating apparent survival provides a good indication of this demographic parameter.

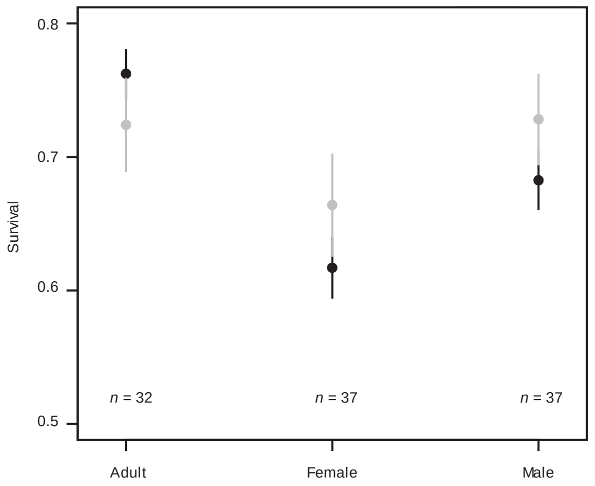

Figure 3. Variation on annual survival rates for studies testing for sex differences, with black dots representing observed data (mean ± se) and grey dots (mean ± se) model predictions. Estimates for which sex differences were not significant in the original study are included in the Adult category.

As expected, return rates generated lower estimates of survival, as these do not account for resighting/recapture probability. Although return rates can be biased estimates of true survival (Sandercock 2003), they can be potentially useful as an index of survival (always considered as minimum survival) when no other information is known and when the resources or capacity needed for more complex modelling are not available. Along with high site-fidelity, most shorebirds are very conspicuous during both the breeding season (particularly during display and chick-rearing) and non-breeding season (when many flock in large numbers and occur in open habitat), providing high resighting rates. Consequently, high return rates are very likely to reflect high rates of true survival; however, moderate return rates should be interpreted with caution as variation in site-fidelity or detection rates could be involved (Sandercock 2003).

Biological and environmental drivers of variation in annual survival

As expected, and in accordance with well-established allometric relationships (Boyd 1962), annual adult survival varied positively with ($\log_e$-transformed) body mass, even when controlling for phylogeny, migratory flyways and estimation methodology. Interestingly, the variation in survival within smaller species appeared to be much greater than within larger-bodied species. For example, estimated survival for Western Sandpiper *Calidris mauri* and Snowy Plover *Charadrius nivosus* (two small species of c. 27–41 g) differ by about 30%, whereas survival estimates for Eurasian Oystercatcher and Eurasian Curlew *Numenius arquata* (c. 540–784 g) differ by < 10% (Table 1). The variability in survival estimates of small waders may reflect greater variability in detectability (Johnston *et al.* 2014) but smaller species may also vary more in true survival rates, given that they may encounter a greater range of predators (small species will also be vulnerable to small predators that will not take larger species) and energetic constraints.

The observed variation in survival across the different genera can be partly confounded with body size. Genera with low survival estimates tend primarily to comprise small-bodied species (e.g. *Calidris* and *Charadrius*), whereas genera with high survival tend to comprise larger species (e.g. *Numenius* and *Haematopus*). In any case, the effect of genus in our analyses is in addition to the effect of body mass and remains significant when the effects of body mass are controlled for. These differences in survival among genera may potentially be related to variation in life-history traits associated with reproduction. In passerines, there is evidence for a trade-off between fecundity and adult survival, in which survival is negatively correlated with clutch size (Peach *et al.* 2001). In shorebirds, most species have a maximum clutch size of four eggs per nesting attempt (Maclean 1972) but other aspects of reproduction such as incubation duration (Bulla *et al.* 2016), re-nesting capacity, post-hatching parental care (Reynolds & Székely 1997) and mate fidelity (Lloyd 2008) may contribute to the variation in survival rates among species and genera.

Additional non-reproductive factors could also contribute to the observed variation in shorebird survival rates. For example, in ground-nesting species, levels of nest concealment can also influence adult survival, with species that nest in the open being able to detect predators earlier (Amat & Masero 2004, Miller *et al.* 2007). Variation in survival could also result from differences associated with migratory behaviour, depending on the environmental conditions experienced by individuals on the particular set of locations each uses along the flyway (Duriez *et al.* 2012, Alves *et al.* 2013a). It is important to note that survival rates reported for some *Scolopax* and *Actitis* species are very low and whereas these may reflect high levels of hunting pressure and habitat degradation for *Scolopax* spp. (Tavecchia *et al.* 2002, Duriez 2003, Oppelt 2006), the low survival rates reported for *Actitis* spp. are likely related to their breeding systems, as some studies report < 30% of unsuccessful breeders returning to the previous breeding location (Reed & Oring 1993).

Overall, our model suggests that published estimates of survival for small species, especially for *Actitis*, *Calidris* and *Charadrius,* may be underestimates. As indicated above, this may reflect lower detectability of smaller species; however, lower levels of site-fidelity in these species could also influence the published estimates. High return rates are common among large species, suggesting that detectability and site-fidelity are also high (Sandercock 2003), whereas published return rates in smaller species tend to be quite low (0.3–0.7, Table 1). Low return rates could reflect lower true survival, low site-fidelity, low detection rates or a combination of these.

Survival estimates were significantly lower in the American flyway than in the African-Eurasian and East Asian-Australasian flyways (EAAF). Although widespread population declines have occurred in the EAAF over the last two decades (Conklin *et al.* 2014), evidence for declines in survival has only recently been uncovered (Piersma *et al.* 2016) and our survival estimates for this flyway span a wide range of species and time periods. Published survival rates in the American flyway are lower than our model predictions and may reflect the fact that estimates from this flyway are mostly derived from small-bodied species (*Calidris* and *Charadrius* spp.) and are calculated using return rates (Table 2). Future work needs to be focused on the Central Asian flyway, as there is currently no information on the demographic parameters of shorebirds in this region.

Sandercock *et al.* (2002) argued that survival estimates generated on non-breeding grounds should be preferred, as fidelity to wintering sites may be determined by ecological factors, whereas fidelity to breeding sites may also be influenced by mate selection. Therefore, if site-fidelity is stronger during the winter period, then survival estimates should more reliably reflect mortality than permanent emigration. We found a tendency for annual survival to be slightly higher when estimated in wintering populations but the difference between estimations from both seasons was not significant, so any general seasonal effects of site-fidelity on survival estimates are not yet apparent. In addition, we found that most survival studies are carried out at breeding locations, reinforcing the fact that measuring survival during the non-breeding period can be challenging. In addition, any sex or age differences in distribution habitat use during the winter season (e.g. Alves *et al.* 2013b) may increase the probability of non-random samples of individuals contributing to survival estimates (Sandercock *et al.* 2002).

Sex-biased survival has implications for sex ratios and, ultimately, for breeding systems and population dynamics (Gunnarsson *et al.* 2012, Morrison *et al.* 2016). Our analyses provided further support for female shorebirds often having lower survival rates than males (Liker & Székely 2005), but adult survival (estimates attained when sex differences were not significant in the original paper) was higher than noted for either sex. However, the difference between overall adult and male survival was small in our model predictions. In a number of studies, the causes of lower estimates for female survival were identified, specifically sex differences in site-fidelity (Mullin *et al.* 2010), detection rates (Sandercock *et al.* 2005), dispersal behaviour (Pakanen *et al.* 2015) and parental care (Liker & Székely 2005). Differences in social status in wintering Eurasian Oystercatcher (Durell 2007) and migratory strategies in staging Ruff *Calidris pugnax* (Schmaltz *et al.* 2015) have also been suggested as possible drivers of sex differences in survival in shorebirds.

In conclusion, although the number of published survival estimates for shorebirds has increased in recent years, this effort has been concentrated on relatively few species. Estimates of survival for species in areas currently experiencing environmental degradation are particularly lacking and our capacity to assess flyway-level differences in survival rates is constrained by the limited number of estimates available from the Central Asian and East Asian-Australasian flyways, which support important and declining populations of many species (Studds *et al.* 2017). Although estimating true survival is ultimately desirable, reporting of all estimates of survival is valuable in facilitating analyses of within-species variation in survival rates and associated environmental drivers. Our corrected estimates of survival rates can potentially aid the rapid identification of locations in which species may be experiencing lower than expected survival rates (Tables 1 & 4) and may therefore be places where efforts should be focused to identify and address the causes. Given the global distribution of shorebirds, their sensitivity to environmental change and the capacity of declines in adult survival rates to drive rapid declines in population size in these long-lived species, empirical quantification of survival across species ranges can be a valuable tool for identifying drivers of change in species status across regions and stages of the annual cycle.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods used to estimate adult survival considered in this study.

Appendix S2. References list from Table 1.