

University of Groningen

Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability

Conklin, Jesse R.; Lok, Tamar; Melville, David S.; Riegen, Adrian C.; Schuckard, Rob; Piersma, Theunis; Battley, Phil F.

Published in:
Emu

DOI:
[10.1071/MU15058](https://doi.org/10.1071/MU15058)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Conklin, J. R., Lok, T., Melville, D. S., Riegen, A. C., Schuckard, R., Piersma, T., & Battley, P. F. (2016). Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability. *Emu*, 116(2), 147-157. <https://doi.org/10.1071/MU15058>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/297715460>

Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability

Article in *Emu* · March 2016

DOI: 10.1071/MU15058

CITATIONS

23

READS

555

7 authors, including:



Jesse R Conklin

University of Groningen

34 PUBLICATIONS 745 CITATIONS

[SEE PROFILE](#)



Tamar Lok

NIOZ Royal Netherlands Institute for Sea Research

29 PUBLICATIONS 792 CITATIONS

[SEE PROFILE](#)



David S. Melville

81 PUBLICATIONS 1,194 CITATIONS

[SEE PROFILE](#)



Rob Schuckard

26 PUBLICATIONS 280 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Genetics of the migration timing in bar-tailed godwits [View project](#)



Tundra plovers [View project](#)

Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability

Jesse R. Conklin^{A,H}, Tamar Lok^{A,B}, David S. Melville^C, Adrian C. Riegen^D, Rob Schuckard^E, Theunis Piersma^{A,F} and Phil F. Battley^G

^AConservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands.

^BCentre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Campus CNRS, 1919 Route de Mende, 34293 Montpellier, Cedex 5, France.

^C1261 Dovedale Road, RD2 Wakefield, Nelson 7096, New Zealand.

^D231 Forest Hill Road, Waiatarua, Waitakere 0612, New Zealand.

^EPO Box 98, Rai Valley 7145, New Zealand.

^FDepartment of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands.

^GEcology Group, Institute of Agriculture and Environment, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand.

^HCorresponding author. Email: conklin.jesse@gmail.com

Abstract. Like many migratory shorebird populations using the East Asian–Australasian Flyway, Bar-tailed Godwits *Limosa lapponica baueri* in New Zealand have significantly declined since the mid-1990s, but census data indicate a relatively stable population since 2004. The demographic drivers of both the decline and stabilisation remain unknown. We estimated annual survival from mark–recapture data of adult godwits in New Zealand during 2005–2014. Annual adult survival declined over the study period from 0.89–0.96 in 2005–2010 to 0.83–0.84 in 2011–2012. The simultaneous decline in annual survival found in a separate study of Bar-tailed Godwits *L. l. menzbieri* in north-west Australia suggests a common effect of their high dependence on threatened migratory staging sites in the Yellow Sea; the more extreme decline in *L. l. menzbieri* may reflect ecological differences between the populations, such as timing and extent of use of these sites. At current apparent recruitment rates, persistent adult survival of ~0.84 would lead to a population decline of 5–6% per year in *L. l. baueri*. Our study implies that the demographic precursors to a population decline developed during a period of apparent population stability; this suggests that monitoring a single index of population stability is insufficient for predicting future trends.

Additional keywords: East Asian–Australasian Flyway, *Limosa lapponica baueri*, mark–recapture, shorebirds.

Received 30 May 2015, accepted 13 November 2015, published online 10 March 2016

Introduction

The East Asian–Australasian Flyway (EAAF) features many of the world's most spectacular shorebird migrations (Gill *et al.* 2009; Handel and Gill 2010; Minton *et al.* 2011; Battley *et al.* 2012; Tomkovich *et al.* 2013). Unfortunately, the future of these migrations is in question, as widespread declines of migratory shorebird populations in the EAAF have occurred in the last two decades (Barter 2002; Amano *et al.* 2012; Garnett *et al.* 2011; Wetlands International 2013; Conklin *et al.* 2014). Although loss of intertidal wetlands in staging areas of the Yellow Sea has emerged as the most likely cause of shorebird declines on the flyway (Barter 2003; MacKinnon *et al.* 2012; Murray *et al.* 2014; Murray *et al.* 2015), establishing explicit links between environmental factors and key demographic parameters (e.g. fecundity, recruitment, or adult survival) is required for designing realistic

strategies to reverse these population declines (Hua *et al.* 2015). As may be expected in relatively long-lived species, recent work indicates that decreasing adult survival may be driving declines in at least four EAAF shorebird populations (Rogers and Gosbell 2006; Piersma *et al.* 2016). However, more work is needed to determine whether this can be generalised across more populations and species.

The Alaska-breeding population of Bar-tailed Godwits (*Limosa lapponica baueri*) makes a round-trip annual migration of ~30 000 km (Gill *et al.* 2009; Battley *et al.* 2012), spending the non-breeding season (September–March) in New Zealand and eastern Australia (~65% and 35% of a population estimated at 133 000 individuals; Bamford *et al.* 2008; Conklin *et al.* 2014). A significant decrease in godwit numbers in New Zealand during 1994–2003 (Fig. 1) from ~101 000 to 83 000 (Sagar *et al.* 1999;

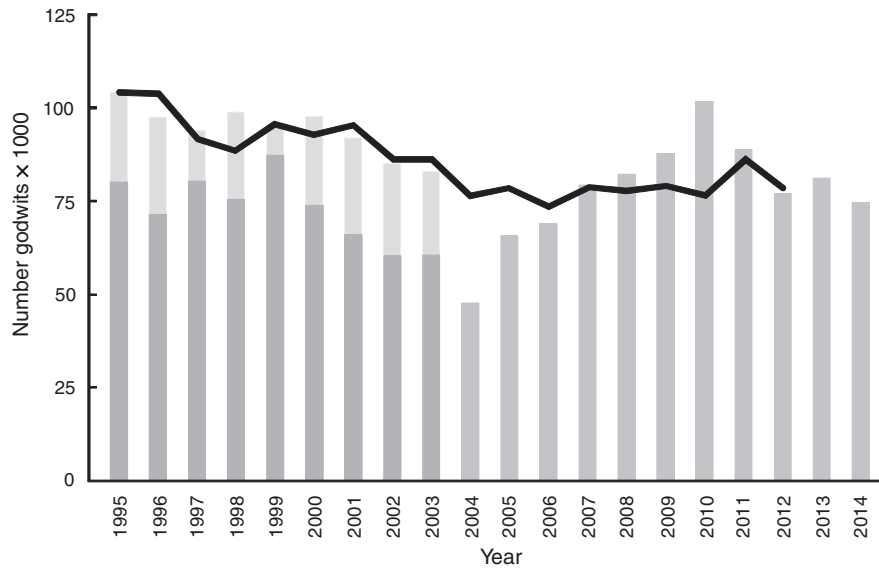


Fig. 1. Population trend in the Bar-tailed Godwit subspecies *Limosa lapponica baueri* during 1995–2014. Dark grey bars indicate raw November census totals in New Zealand (OSNZ, unpubl. data); light grey bars indicate New Zealand population estimates for 1995–2003, adjusted for sites uncounted in the census (Southey 2009). Solid line indicates preliminary modelled New Zealand population trend 1995–2012, accounting for uncertainty and variation in spatial coverage of census data (C.E. Studds and R.A. Fuller, pers. comm.).

Southey 2009) led to a reassessment of the population's official conservation status in New Zealand: in 2013, it was recategorised as 'At Risk, Declining', with the additional qualifier 'Threatened Overseas' (Robertson *et al.* 2013). In 2015, the Bar-tailed Godwit was reclassified from Least Concern to Near Threatened status on the IUCN Red List (BirdLife International 2015), and two subspecies using the EAAF (*L. l. baueri* and *menzbieri*) meet requirements for Red List status at the regional scales of the flyway (Conklin *et al.* 2014) and Australia (Garnett *et al.* 2011), based on observed and predicted population declines. Additionally, four subspecies of Bar-tailed Godwits (including those using the EAAF) were proposed in 2014 as additions to the Cooperative Action List of the Convention on Migratory Species (Leyrer *et al.* 2014). Preliminary modelling of the population trend confirms the previously observed decline of godwits in New Zealand, but also suggests a stabilisation of the population since it reached a low point of ~75 000 in 2004 (Fig. 1; C.E. Studds and R.A. Fuller, pers. comm.). The demographic drivers and consequences of this decline and subsequent stabilisation have yet to be examined.

Piersma *et al.* (2016) detected dramatic declines since 2009 in adult survival in three long-distance migratory shorebird populations using Roebuck Bay, Western Australia (Bar-tailed Godwit *L. l. menzbieri*, Red Knot *Calidris canutus piersmai*, and Great Knot *C. tenuirostris*). Seasonal survival analyses showed that survival declines were restricted to the period of breeding and migration, implicating passage through the Yellow Sea as the likely survival bottleneck common to all three populations. Providing an intriguing comparison, the unique migration of New Zealand Bar-tailed Godwits differs from these populations in two important respects: (1) their trans-Pacific southward migration from Alaska features the longest non-stop migratory flight yet recorded (>11 500 km; Gill *et al.* 2009); and (2) this migratory

'detour' means that adult birds pass through the Yellow Sea only once per year (on northward migration), rather than twice. In this study, we use mark–recapture analysis to estimate adult annual survival of New Zealand Bar-tailed Godwits during 2005–2013. We discuss these results with regard to population monitoring data during 1995–2014 and comparable adult survival estimates in the west Australian population *L. l. menzbieri*.

Methods

Individual marking and resighting

Since 2004, Bar-tailed Godwits were captured by cannon-net or mist-net at coastal sites spanning the North and South Islands of New Zealand (latitude 34°32'S–46°39'S) and individually marked with either a unique combination of flag and four colour bands or an engraved flag with a 3-digit alphabetical code. Godwits were aged by plumage or state of primary feather moult. For details regarding sites, marking, and ageing, see Battley *et al.* (2011).

During 2005–2014, individually marked godwits were observed and recorded at non-breeding sites across New Zealand; data were compiled from concerted efforts by the authors and colleagues to resight marked godwits as part of a study of individual movements (Battley *et al.* 2011), and from both regular and opportunistic resights submitted by amateur shorebird observers. Resighting effort was particularly high at one site (the Manawatu River estuary) as part of an intensive long-term study of individual moult and behaviour (Conklin *et al.* 2013).

Data selection

For this study, we included only sites with relatively high marking and resighting effort during 2005–2013 (>300 unique annual

Table 1. Overview of the number of individuals seen at least twice per non-breeding season (dataset 2), per site and type of marking, where non-breeding season year i covers the period October of year $i-1$ to March of year i
CB = colour bands, EF = engraved flags

Site	Mark type	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	No. unique birds	Total bird years
Auckland	CB	75	142	130	133	98	82	39	25	28	55	225	807
Auckland	EF	0	4	10	40	216	237	187	61	126	198	430	1079
Christchurch	CB	45	48	42	40	49	64	74	60	53	38	112	513
Foxtton	CB	0	31	40	57	55	52	49	41	67	80	136	472
Foxtton	EF	0	0	0	0	8	10	8	7	6	5	12	44
Golden Bay	CB	6	33	61	66	44	53	6	23	12	18	104	322
Tasman Bay	CB	12	66	72	109	61	73	63	37	32	13	162	538
Total		138	324	355	445	531	571	426	254	324	407	1181	3775

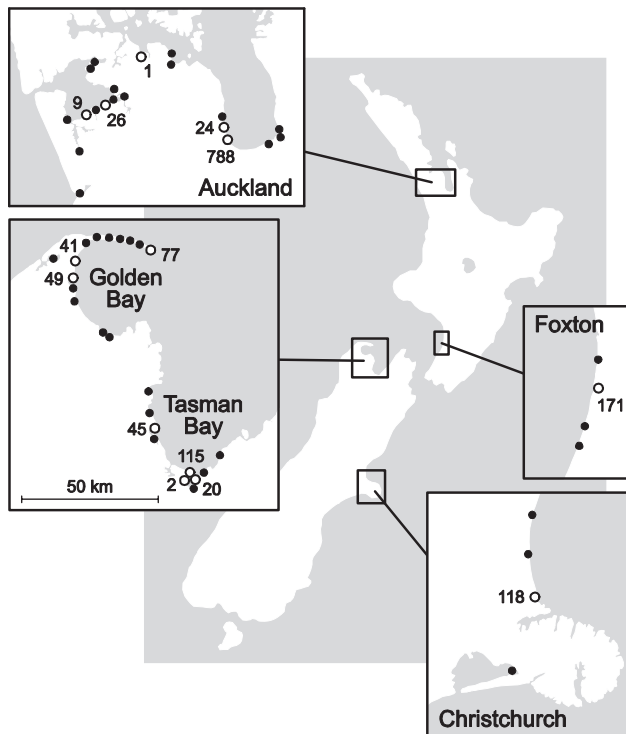


Fig. 2. Five New Zealand regions ('sites') included in the survival analysis. Open circles indicate trapping locations; numbers indicate total godwits marked during February 2004–February 2013. Filled circles indicate other resighting locations included in each site.

resightings, i.e. bird years; Table 1). We defined 'sites' as geographic areas connected by regular movements of individual birds; thus, several capture and resighting locations in close proximity were grouped into a single site. The final sites in our analysis (Fig. 2) were: Auckland (comprising the Firth of Thames, Manukau Harbour, and sites in between), Foxtton (Manawatu River estuary and nearby beaches and estuaries), Christchurch (Avon-Heathcote estuary and nearby areas), Golden Bay (including Farewell Spit), and Tasman Bay (including Nelson, Motueka, and Waimea Inlet).

An individual's encounter history started with the first observation (not including initial capture) as an adult of presumably migratory age (3+ years). This approach excluded birds that were never resighted after capture, and thus prevented the necessity of separately modelling survival rates (1) during the first year after capture, to account for transients (birds passing through only once, that were not non-breeding residents) and for potential capture-induced mortalities, and (2) for younger birds that do not yet migrate and can be expected to have different rates and patterns of survival. To enable modelling of resighting probability as a function of site, we included only observations made at an individual's site of marking (see Fig. 2).

Mark–recapture modelling

We used Cormack–Jolly–Seber (CJS) mark–recapture models to derive estimates of apparent (or local) survival (Φ) from resighting data, while accounting for imperfect detection (Lebreton *et al.* 1992). These models are based on individual encounter histories, which in our case start with the first observation of an individual Bar-tailed Godwit when adult (≥ 3 years old). In the next non-breeding season, an individual may or may not be seen. The probability that an individual was alive and seen is Φp . When an individual is not seen, there are two options: the bird was still alive but not seen (with probability $\Phi(1 - p)$) or the bird died (with probability $1 - \Phi$). As resightings are only performed on distinct non-breeding sites in New Zealand, emigration away from these sites will be confounded with mortality (Lebreton *et al.* 1992). However, Bar-tailed Godwits are known to show strong fidelity to non-breeding sites in New Zealand (Battley *et al.* 2011); accordingly, only 61 of 1486 individuals (3–12 per year during 2005–2013) were seen elsewhere after the last non-breeding resight at their banding site. In addition, although there are recorded movements of godwits between New Zealand and Australia (Wilson *et al.* 2007; Minton *et al.* 2010), there is no unambiguous case of a resident permanently emigrating from New Zealand to Australia (OSNZ, unpubl. data). As such, in our study system, estimates of apparent survival will approach true survival. Correcting for the number of birds alive and seen at their banding site each year (Table 1), permanent emigration rates are in the order of 0.01–0.03 per year. We pooled resightings from October–March to serve as resighting periods. Taking the

midpoints of the resighting periods, annual survival probabilities were estimated from ~1 January in year i to 1 January in year $i + 1$.

Evaluating model assumptions

The following assumptions should be met to ensure unbiased estimates from CJS models: (1) all individuals alive and present at time i have the same probability to be resighted, (2) all individuals alive at time i have the same probability to survive to time $i + 1$, (3) marks are not lost or misread, and (4) the periods of resighting are negligible relative to the interval over which survival is estimated (i.e. the interval between resighting periods).

Our study violates the fourth assumption of instantaneous resighting periods as we pooled resightings over 6 months to estimate survival over 12 months. However, simulation studies have shown that pooling of resightings over a longer period (with up to 50% of the annual mortality occurring during that period) did not bias and in fact even increased the precision of survival estimates (Hargrove and Borland 1994; O'Brien *et al.* 2005).

To assess whether assumptions 1 and 2 were met, we used the tests implemented in program U-CARE (Choquet *et al.* 2009a). These tests assess whether the data fit a fully time-dependent CJS model, which in our case is $\Phi_{(s \times m \times t)} p_{(s \times m \times t)}$, where s = site, m = mark type (colour bands vs engraved flags; the latter were only used in Auckland ($n=470$) and Foxton ($n=13$)), and t = time. We found no evidence for the presence of transients (Test3.SR: $\chi^2_{43} = 52.28$, $P=0.16$) but strong evidence for trap dependence at all sites (Test2.CT: $\chi^2_{36} = 240.63$, $P < 0.001$), likely driven by individual differences in the probability of being resighted. The overall \hat{c} (level of overdispersion) estimated from U-CARE (averaged over all 4 tests) was 2.69, which would justify a 'simple' correction for lack of fit, not making any structural adjustments to the standard CJS model (Burnham and Anderson 2002). However, the substantial heterogeneity in resighting probabilities, as indicated by Test2.CT, may bias survival estimates (Abadi *et al.* 2013). We therefore included models in our candidate model set that accounted for individual variation in resighting probability, using a finite mixture model with two classes of individuals that differ in their probability of being resighted. In addition to apparent survival and resighting probabilities, these models estimate the proportion of individuals with high and low resighting probabilities.

Whether assumption 3 ('marks are not lost or misread') is violated is more difficult to test, but we performed some explorative analyses to get an indication. For Bar-tailed Godwits marked with a combination of colour bands and a flag, partial mark loss will likely be detected before the loss of all marks. We excluded the two birds with known partial mark loss from the analysis. This is not possible for engraved flags, as the loss of the engraved flag cannot (easily) be detected: the bird will only have a metal band left that cannot be distinguished (unless in hand) from birds originally banded with a metal band only. To get an idea of the extent to which engraved flags are lost, or become unreadable (in other studies, problems with fading inscriptions on engraved flags have been reported; C.J. Hassell, pers. comm.), we compared the survival of the birds with an engraved flag with that of birds with a combination of colour bands and a flag. If mark loss or fading is a significant problem, the survival of engraved flag birds

should generally be lower, especially for birds that were marked already for a longer time (senescence of marks), than that of colour-banded birds.

In addition (the second part of assumption 3), surveyors may make mistakes while reading marks, resulting in false records of birds that are in fact dead. To assess the role of misreading, we compared survival rates for two datasets (derived from the same raw resighting data). In the first dataset (hereafter referred to as 'dataset 1'), a single resighting during the non-breeding season was sufficient for the bird to be considered as seen during that non-breeding season. In the second dataset (hereafter, 'dataset 2'), at least two resightings during a non-breeding season were required for an individual to be considered as seen. If misreadings never or rarely occur, survival estimates should be similar for the two datasets and resighting probabilities should be lower for dataset 2 (as birds correctly seen only once during a non-breeding season are in this dataset considered to be 'not seen' during that season). If misreadings occur regularly, survival rates are expected to be biased high in dataset 1 (and hence lower and less biased in dataset 2).

Model selection procedure

Due to limited data, and because we expect that annual survival rates are primarily affected by factors away from the non-breeding grounds, we modelled survival as a function of time, but not of site. We expected the different sites to have different resighting probabilities that may vary in different ways over the years (due to variation in observation effort). Moreover, we expected that the mark type (i.e. colour bands vs engraved flags) could affect the probability of resighting. As such, the most parameterised candidate model was $\Phi_{(s \times t \times m \times h)}$, where h reflects capture heterogeneity modelled as two classes of individuals that differ consistently in their probability of resighting. In addition to annual variation in survival, we considered reduced models in which survival changed linearly over time (T) or was constant (c). Furthermore, we assessed whether resighting probabilities could be more parsimoniously modelled with year as an additive effect (i.e. removing the interaction with site) without an effect of mark type or without accounting for capture heterogeneity. This method resulted in a set of 15 candidate models, plus the full model for which goodness-of-fit was assessed (but for which many parameters were not estimable due to limited data).

Model selection was performed on the basis of QAIC_c (Akaike Information Criterion, adjusted for small sample size and overdispersion) where a model was considered as better supported than other models when its QAIC_c was at least two points lower (Burnham and Anderson 2002). Models were constructed in R v. 2.13.0 (R Core Team 2013) using package RMark (Laake 2013) and run using the optimisation algorithm of program MARK (White and Burnham 1999). For optimising the 2-mixture model, we used program E-Surge using multiple random starting values, as these models are prone to local minima (Choquet *et al.* 2009b).

Predicting population growth rates and trajectories

To estimate the recruitment rate required to offset the estimated rates of mortality (i.e. to maintain a stable population), we applied the following non-breeding season census age-structured population matrix model:

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_{\geq 4} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & p_3 R & p_{\geq 4} R \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & S_{\geq 4} \end{bmatrix}_t \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_{\geq 4} \end{bmatrix}_t$$

where N_i is the population size of age class i , S_i is the survival rate of individuals in age class i , and R is the per capita recruitment rate (i.e. the number of offspring per breeding pair, or more precisely,

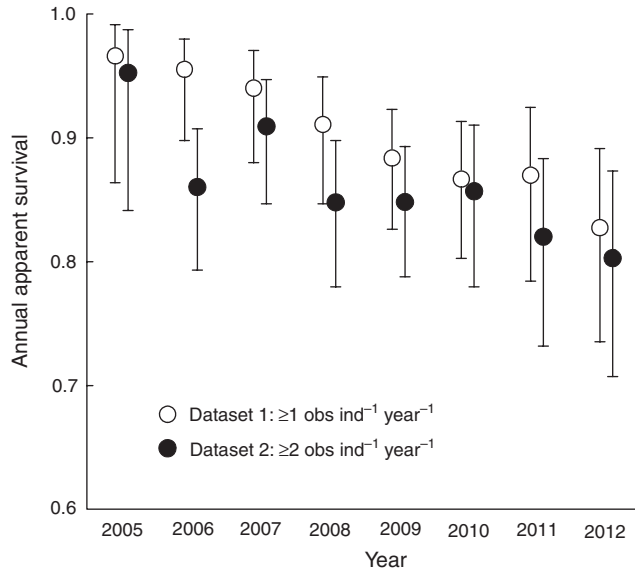


Fig. 3. Annual apparent survival estimates for the model $\Phi_t p_{(s \times t + b)}$ for dataset 1 (open circles) and dataset 2 (filled circles). Error bars represent 95% confidence intervals corrected for overdispersion ($\hat{c} = 2.69$ and $\hat{c} = 1.92$). Note that survival during 2013 could not be estimated, as it is confounded with the resighting probability in 2014.

the number of female offspring per adult female that survive to the midpoint of their first non-breeding season in New Zealand). We assumed $S_1 = S_2 = 0.99$ based on estimates of survival of immature *menzbieri* Bar-tailed Godwits after the midpoint of their first non-breeding season (Piersma *et al.* 2016). Furthermore, we assumed that 50% of the godwits start breeding at age 3 ($p_3 = 0.5$), whereas all godwits breed when ≥ 4 years old ($p_{\geq 4} = 1.0$). For S_3 and $S_{\geq 4}$ we used the estimates of adult annual survival from the best-supported model.

Results

As survival estimates were considerably lower for dataset 2 than for dataset 1 (Fig. 3), we conclude that the frequency of misreadings was sufficient to produce biased-high survival estimates in dataset 1. We therefore proceeded with our analyses using dataset 2. The level of transience for dataset 2 was somewhat higher than for dataset 1, whereas the level of trap dependence was lower (TEST3.SR: $\chi^2 = 67.77$, d.f. = 43, $P = 0.009$ and TEST2.CT: $\chi^2 = 112.72$, d.f. = 34, $P < 0.001$). The overall level of overdispersion (averaged over the four tests; see *Methods*) for dataset 2 was estimated at $\hat{c} = 1.92$, which was used to calculate QAIC_c values and adjust confidence intervals.

We found no evidence of substantial band loss or fading of inscriptions of engraved flags, as models with an interaction between age since marking (either as continuous or categorical variable) and mark type (colour bands vs engraved flags) were consistently less supported than models with additive effects of mark type and age (see Table S1 in Supplementary material, available online only).

Resighting probabilities differed among years, sites, and individuals (Table 2, Fig. 4), and were higher for birds with engraved flags than for birds with colour bands and a flag ($\beta = 1.10$, 95% CI: 0.67–1.52 estimated by model 1; Table 2). Translated to the probability scale, when colour-banded birds had

Table 2. Model selection results for dataset 2, corrected for overdispersion ($\hat{c} = 1.92$)

t = time as categorical variable, T = time as continuous variable, s = site, m = mark type (colour bands or engraved flag), c = constant, h = heterogeneity in resighting probability (2-mixture model)

Model			K	ΔDeviance	ΔQAIC _c	Akaike weight
1	Φ_T	$P_{(t \times s + m + h)}$	49	9.31	0.00 ^A	0.91
2	Φ_c	$P_{(t \times s + m + h)}$	48	23.31	5.23	0.07
3	Φ_t	$P_{(t \times s + m + h)}$	55	0.00 ^B	7.54	0.02
4	Φ_T	$P_{(t \times s + m)}$	47	147.54	67.84	0.00
5	Φ_c	$P_{(t \times s + m)}$	46	166.23	75.51	0.00
6	Φ_t	$P_{(t \times s + m)}$	53	138.53	75.51	0.00
7	Φ_T	$P_{(t \times s)}$	46	178.56	81.93	0.00
8	Φ_c	$P_{(t \times s)}$	45	195.27	88.57	0.00
9	Φ_t	$P_{(t \times s)}$	52	169.00	89.31	0.00
10	Φ_T	$P_{(t + s + m)}$	15	398.97	133.50	0.00
11	Φ_T	$P_{(t + s)}$	14	410.28	137.37	0.00
12	Φ_c	$P_{(t + s + m)}$	14	416.26	140.49	0.00
13	Φ_t	$P_{(t + s + m)}$	21	390.32	141.13	0.00
14	Φ_c	$P_{(t + s)}$	13	427.71	144.43	0.00
15	Φ_t	$P_{(t + s)}$	20	401.33	144.84	0.00
16	$\Phi_{(t \times s \times m)}$	$P_{(t \times s \times m)}$	109	66.78	155.80	0.00

^AQAIC_c = 3162.12.

^BDeviance = 1137.60.

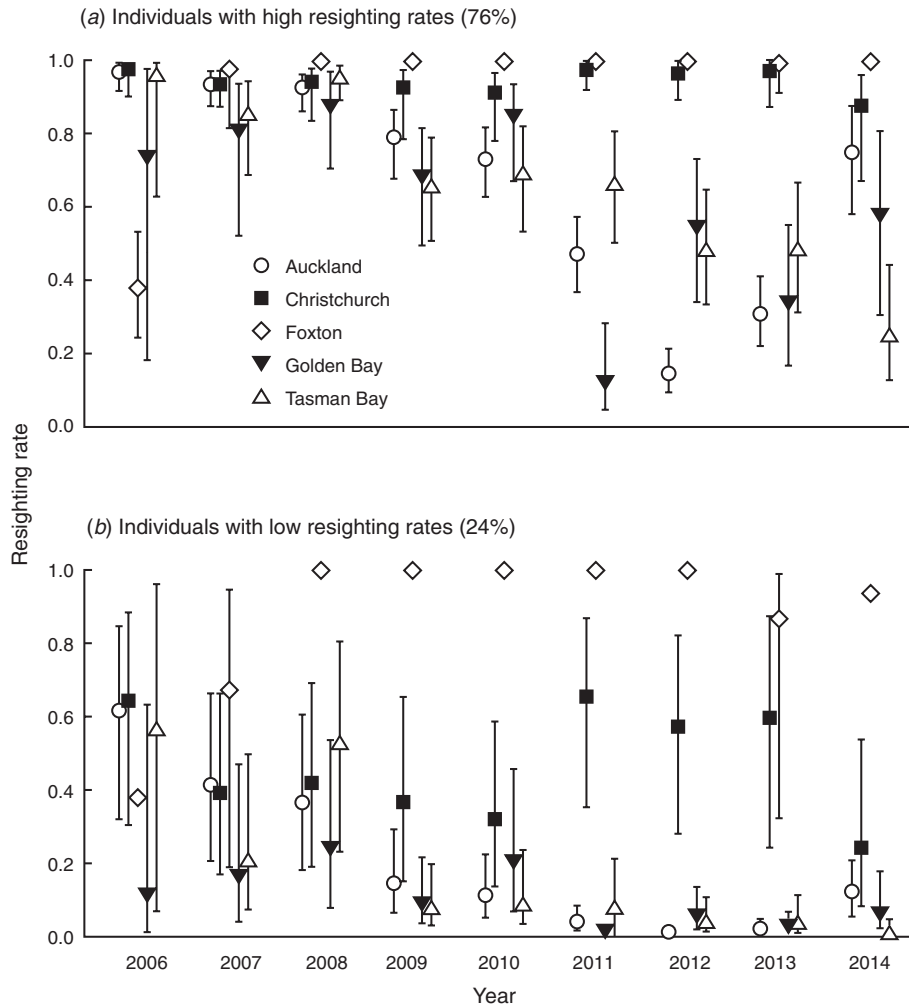


Fig. 4. Resighting probabilities for birds with colour bands and a flag, estimated by the model $\Phi_T p_{(t \times s + m + h)}$ (Model 1 in Table 2), distinguishing birds with (a) high and (b) low resighting probabilities (upper 76% and lower 24% of individuals at each site, respectively). Error bars represent 95% confidence intervals corrected for overdispersion ($\hat{c} = 1.45$). Note that the goodness-of-fit improved as we accounted for individual variation in resightability.

a resighting probability of 0.50 (which approximates their mean resighting probability in Auckland in 2009–2014, when most of resightings of birds with engraved leg flags were performed; see Table 1), birds with an engraved flag had a resighting probability of 0.75. Survival estimates were substantially higher in models that accounted for individual heterogeneity in resighting probabilities compared with models that did not, with relative increases in survival of 3.2–3.7% (model 3 vs 6 in Table 2), whereas temporal patterns of survival were similar (filled circles in Fig. 3 vs Fig. 5).

The year-to-year variation in survival was best described by a linear decline in survival (model 1; Table 2, Fig. 5). Ignoring the high and imprecise estimate of survival in 2005, which is based on relatively few individuals (see Table 1), this temporal trend was driven by relatively stable and high survival of 0.89–0.94 during 2006–2010, followed by a drop to 0.83–0.84 during 2011–2012 (Fig. 5).

With an estimated average annual survival of 0.91 during 2005–2010, a recruitment rate (R) of 0.10 is required to approximate the observed stable population trajectory during this period (Fig. 1). If adult annual survival then drops and persists at 0.84 (as in 2011–2012), maintaining a stable population would require an 80% increase of the recruitment rate to 0.18. If R remained at 0.10, persistent adult survival of 0.84 would lead to a population decline of 5–6% per year; this rate predicts a population loss (relative to the current population) of 25% in 5 years and 44% in 10 years. With elasticity values being very low (<0.08) for all demographic parameters except adult survival (0.67), moderate changes in immature survival, the proportion of 3rd year birds that breeds, and recruitment rate have little effect on population growth rate.

Discussion

We found strong support for a decrease in adult annual survival in New Zealand Bar-tailed Godwits during our study, which

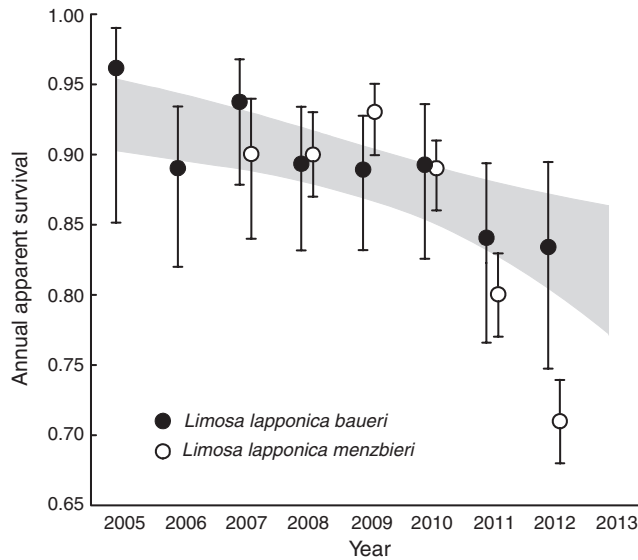


Fig. 5. Estimates of annual apparent survival from the best-supported model that still included annual variation in survival ($\Phi_T p_{(t \times s+m+h)}$, filled circles) and the most parsimonious model that described survival as a linear trend ($\Phi_T p_{(t \times s+m+h)}$, grey area). The open circles show the estimated annual survival for the subspecies *L. l. menzbieri* that spends the non-breeding season in north-west Australia (Piersma *et al.* 2016). Error bars and grey area represent 95% confidence intervals corrected for overdispersion ($\hat{c} = 1.45$). Note that for the model $\Phi_T p_{(t \times s+m+h)}$, survival could not be estimated separately for 2013, as it is confounded with the resighting probability in 2014, but that the model $\Phi_T p_{(t \times s+m+h)}$ included 2013 in its estimation of survival as a linear trend.

featured a conspicuous drop in 2011–2012 after a six-year period of higher and relatively stable survival. This is strikingly similar to patterns found in north-west Australian populations of Bar-tailed Godwit, Red Knot, and Great Knot, all of which showed dramatic declines in adult annual survival from 0.84–0.93 in 2006–2010 to 0.67–0.80 in 2011–2012 (Piersma *et al.* 2016; see also Fig. 5). The similarity of survival declines in at least four EAAF shorebird populations suggests the pattern may be common to many other species with similar migration strategies or use of staging sites, and may imply the recent crossing of some critical threshold (e.g. carrying capacity) on the flyway.

Methodological considerations

We believe that comparing survival estimates between a dataset in which only a single resighting of an individual during a non-breeding season is sufficient to consider this individual to be alive and seen, against a dataset in which at least two resightings are required (which will to a large extent exclude erroneous observations) has good potential to assess the importance of mark-reading mistakes. In our case, the survival estimates became lower when singleton observations were excluded, indicating that erroneous observations of individuals that were in fact already dead indeed occurred to an extent that they produced biased-high survival estimates.

In addition, we show that accounting for heterogeneity in resighting probabilities substantially increased the survival estimates. Because Bar-tailed Godwits are also highly site-faith-

ful in New Zealand (Battley *et al.* 2011), we therefore believe that survival estimates, calculated after removing singleton observations and accounting for individual heterogeneity in resighting probabilities (Fig. 5), closely approximate true adult survival in this population. This is important when one aims to make predictions about the level of breeding output required to maintain a stable population. If survival is consistently over- or underestimated, such an exercise is rather useless.

In our study, the resighting probability for birds with engraved flags was higher than for those with colour bands. We also found no apparent difference in the senescence (loss) of the two mark types, although we could only assess the persistence of engraved flags up to five years after marking, due to infrequent deployment of engraved flags before 2009. We don't believe that this necessarily means that engraved flags are a superior solution for similar studies, as the relative ease of resighting for the two methods will depend upon several site-specific factors, such as how close birds can be approached and whether they frequently roost in water or vegetation (in our case, colour bands are applied to the tarsus, and engraved flags to the tibia). As mark type was explicitly accounted for in our models, this does not explain the additional variation we found in individual resighting probabilities, which we believe results simply from individuals being faithful to sites (or parts of sites) that are visited more or less frequently by observers.

Potential causes of survival declines

What are the main influences on adult survival in *L. l. baueri*? New Zealand is a remarkably hospitable non-breeding area, featuring relatively low rates of disturbance and intertidal habitat loss, a complete lack of avian predators specialising on shorebirds, and a mild, temperate Antipodean summer; accordingly, apparent mortality of adult godwits in New Zealand is extremely low (J.R. Conklin and P.F. Battley, unpubl. data). Adult mortality on Arctic breeding grounds is also generally low in shorebirds, although rare freezing events have been linked to adult mortality (Boyd and Piersma 2001; Meltofte *et al.* 2007). Therefore, we expect most mortality to be associated with migration, when godwits in this population must prepare for and perform three of the longest non-stop flights yet recorded (Piersma and Gill 1998; Battley and Piersma 2005; Gill *et al.* 2009; Battley *et al.* 2012). Their annual migration exposes godwits to density-independent mortality risk from stochastic weather events during transoceanic flights (Gill *et al.* 2009; Gill *et al.* 2014), which alone may explain much annual variation in adult survival. However, this is unlikely to cause directional trends, unless the frequency of storms or degree of wind assistance also changes gradually (e.g. due to climate-related alteration of prevailing wind patterns).

The greatest risk to *L. l. baueri* appears to stem from their dependence on very few high-quality staging sites to fuel their epic flights (Conklin *et al.* 2014). On southward migration, the entire population concentrates at a few estuaries in south-western Alaska (Gill and Handel 1990; Gill and McCaffery 1999; Battley *et al.* 2012); however, these remote and productive intertidal areas remain essentially untouched by human activity. More precarious is the godwits' reliance on a few areas of abundant intertidal resources in the Yellow Sea during northward migration where they are threatened by disturbance, degradation, and complete

loss of fuelling sites (MacKinnon *et al.* 2012; Murray *et al.* 2015; Melville *et al.* 2016) which may decrease adult survival. Because loss of wetlands in the Yellow Sea is pervasive and incremental, it is rare that events at particular sites can be linked with shorebird population changes (e.g. Baker *et al.* 2004); however, this was the case with the dramatic loss of tens of thousands of Great Knots coincident with the Saemangeum reclamation in South Korea in 2006 (Moores *et al.* 2016). This event may also have affected Bar-tailed Godwits, but to a lesser extent: peak numbers in the vicinity of Saemangeum (which include a minority of *L. l. menzbieri*) were >18 000 in 2006, ~12 000 in 2007, and 16 500 in 2008 (Moores *et al.* 2016). Although these counts may also reflect movements in and out of the area, this drop and partial recovery roughly mirrors patterns in both adult survival (Fig. 5) and census data (Fig. 1) during the same years.

In the Yellow Sea, by far the most important site for Bar-tailed Godwits is China's Yalu Jiang National Nature Reserve, Liaoning Province, where more than 49 000 *L. l. baueri* and 18 000 *L. l. menzbieri* individuals staged during March–May 2010–2012 (Choi *et al.* 2015); changes here could potentially have the greatest effect on annual survival. In fact, the construction of a new seawall at the east end of the reserve, underway by 2009 (fig. S11 in Melville *et al.* 2016), has likely influenced tidal flow and sediment deposition near the most important foraging area for godwits. This was followed by local population collapses in two of the godwits' major benthic prey species, ghost shrimps (*Nihonotrypaea japonica*) in 2011 and bivalves (*Potamocorbula laevis*) in 2012 (Choi *et al.* 2014). Due to a lack of optimal-sized and high-quality prey, total intake rates by godwits at Yalu Jiang dropped ~50% from 2011 to 2012 (Choi 2015). These findings suggest that godwits may find it increasingly difficult to prepare adequately for the 5000–8000 km flight from Asia, resulting in unusually high mortality *en route* or upon arrival in Alaska; this may be particularly true if individual migration schedules are endogenous and strictly adhered to (Conklin *et al.* 2010; Conklin *et al.* 2013; but see Conklin and Battley 2011; Gill *et al.* 2014), rather than condition-dependent. To date, bivalve communities at Yalu Jiang have not recovered (H.B. Peng and D.S. Melville, pers. obs.); therefore, a continuing effect on survival may persist beyond our current data.

Our study began with several years of high adult survival, so it is reasonable to question what caused the previous population decline during 1994–2003. This steady ten-year decline was unlikely to be primarily driven by so many consecutive years of poor breeding conditions, although numbers of non-migrant (predominantly immature) godwits in New Zealand were also conspicuously low during 2002–2004 (Fig. 6). More importantly, loss of staging areas in the Yellow Sea was particularly severe during this period. For example, along the west coast of South Korea alone there were at least 14 major intertidal reclamation projects (affecting a total area of ~1100 km²) ongoing during 1995–2005 (Fig. 2 in Choi 2014), some of which are still ongoing in 2015. These areas include at least five sites where internationally important numbers of Bar-tailed Godwits (predominantly *L. l. baueri*) occurred during 1998–1999 (specifically: Dongjin and Mangyung River estuaries, Haenam Hwangsan, Namyang Bay, and Yeongjong Island, with summed high counts of >22 000 individuals; Conklin *et al.* 2014). Loss or degradation (e.g. due to pollution, aquaculture, etc.) of intertidal staging sites

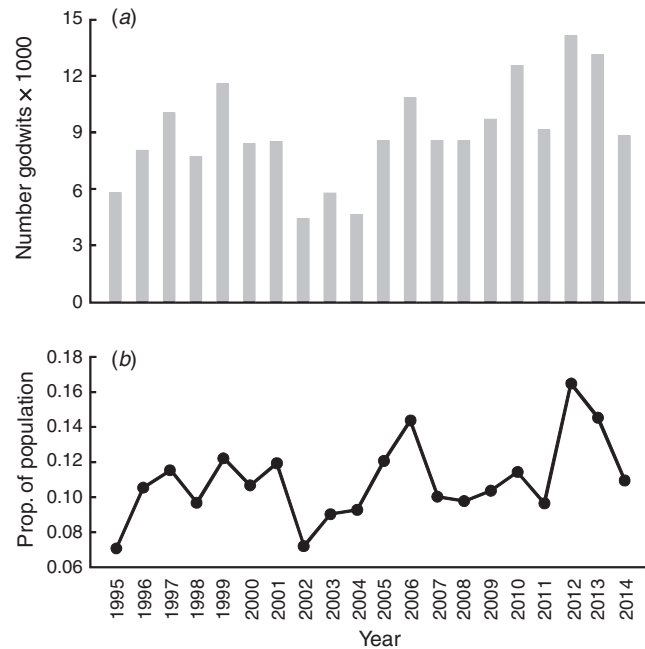


Fig. 6. Number of non-migrant Bar-tailed Godwits spending the breeding season in New Zealand during 1995–2014, shown as (a) nationwide June–July census totals (OSNZ, unpubl. data), and (b) proportion of the subsequent non-breeding census in November of the same year (Fig. 1).

was similarly widespread in China during this period (Murray *et al.* 2014; Melville *et al.* 2016), including a major port development adjacent to the Yalu Jiang National Nature Reserve. Therefore, the most likely driver of the earlier decline was rapid loss of migratory staging habitat associated with a drop in adult survival, after which survival rebounded to a higher rate as the population stabilised under new circumstances. Such a scenario is expected if a temporary perturbation (such as sudden habitat loss) permanently reduces the carrying capacity of a system; after the population stabilises at a lower but sustainable level, the demographic drivers of the population decline (in this case, reduced adult survival) will no longer be evident (Rakhimberdiev *et al.* 2015).

Why did survival decline more in *L. l. menzbieri* than in *L. l. baueri*?

While adult survival of *L. l. baueri* and *menzbieri* godwits was similarly high (0.88–0.94) during 2006–2010, the drop in survival during 2011–2012 was much more drastic in the latter (to 0.71) than the former (to 0.83; Fig. 5). The two populations differ in many respects that could potentially affect their survival probabilities, including: (1) non-breeding area (temperate New Zealand vs tropical north-west Australia), (2) location of staging sites in the Yellow Sea during northbound migration (overlapping, but primarily east side vs west side; Wilson *et al.* 2007; Battley *et al.* 2012), (3) timing of staging in the Yellow Sea (overlapping, but generally earlier vs later), (4) overall migration distance (round-trip ~30 000 vs 20 000 km), (5) breeding and post-breeding staging areas (Alaska vs eastern Siberia), (6) southbound migration strategy (non-stop transoceanic vs two-stage continental), and (7) degree of use of the Yellow Sea

(northbound only vs northbound and southbound migration). However, the simultaneous drops in survival during 2011–2012 in the two populations suggests that a shared factor affected them to differing degrees; therefore, we should most profitably look at what they had in common during this period.

In *L. l. menzbieri*, analysis of seasonal survival probability revealed that declines in adult survival were restricted to the breeding and migration periods (i.e. time spent away from Australia; Piersma *et al.* 2016). In *L. l. baueri* and *menzbieri*, shared adult mortality in the breeding season would require simultaneous (presumably environmental) changes affecting Arctic regions separated by >1000 km and the Chukchi and Bering Seas. This scenario seems unlikely, as annual conditions are far from uniform across the Arctic; for example, mean July temperatures in 2011 were 1–2°C above normal in the west Siberian breeding range of *L. l. menzbieri*, but 0–2°C below normal across much of the Alaska breeding range of *L. l. baueri* (Tomkovich and Soloviev 2013). Likewise, poor conditions during flights (e.g. devastating cyclones) are unlikely to similarly affect populations with completely different routes and largely different timing of migration. Therefore, we conclude that the most likely driver of simultaneous survival declines in these populations is their shared dependence on deteriorating intertidal areas of the Yellow Sea for migratory refuelling.

Multiple spatial and temporal differences in their use of Yellow Sea staging areas could lead to more rapidly declining survival in *L. l. menzbieri* than in *baueri*. Although both populations make extended stops of ~4–6 weeks in the region during northbound migration, *L. l. baueri* arrives in the Yellow Sea on average two weeks earlier, stays for several days longer, and generally uses more easterly staging areas (Battley *et al.* 2012; Choi *et al.* 2015). While recent loss of intertidal wetlands has been substantial in all parts of the Yellow Sea, it has been more severe on the west coast (China), particularly in Bohai Bay, than on the Korean Peninsula (Murray *et al.* 2014). Additionally, if intertidal resources in the Yellow Sea are generally depleted throughout the northward staging period (March–early June), we might expect greater negative impacts on the condition of birds attempting to fuel later in the season. Either of these factors could explain the more dramatically declining survival in *L. l. menzbieri*.

A more striking difference between the populations is that New Zealand godwits, due to their non-stop trans-Pacific southbound migration, depend on the Yellow Sea only once per year, on northbound migration. Despite an arguably more strenuous southbound flight, *L. l. baueri* has the ‘luxury’ of staging on the relatively pristine coast of south-west Alaska, featuring negligible anthropogenic effects and much less direct competition for fuelling resources. In contrast, *L. l. menzbieri* passes through the Yellow Sea region on both migrations, and therefore may suffer two critical bottlenecks each year. Accordingly, in the EAAF, migratory shorebird populations with a greater dependence on the Yellow Sea for staging are more likely to be declining (Amano *et al.* 2012; Wilson *et al.* 2011; Iwamura *et al.* 2013).

Demographic consequences of declining adult survival

For long-lived organisms that mature and reproduce slowly, changes in adult survival have a much greater impact on population growth rates than do changes in annual reproduction rates

(Sæther and Bakke 2000); on the EAAF, Bar-tailed Godwits show delayed maturity (McCaffery and Gill 2001) and can live more than 25 years (Hassell 2013). Average adult annual survival of ~0.91 (as we observed during 2005–2010) was apparently sufficient to maintain a stable or increasing population: during this period, the New Zealand godwit population increased from ~73 000–76 000 in 2004–2006 to ~85 000 in 2011 (Fig. 1). Our population matrix modelling exercise indicated that a recruitment rate (into the non-breeding population) of 0.10 was required to maintain a stable population during 2005–2010, but that a significant increase in reproductive output would be required to maintain a stable population with the lower adult survival rates observed in 2011 and 2012.

Meanwhile, counts of non-migratory godwits (those spending the breeding season in New Zealand, which are presumed to be predominantly young birds of <3 years of age) increased from under 6000 in 2004 to ~14 000 in 2012, which was the highest number and proportion of non-migrants observed since 1995 (Fig. 6). Increasing numbers of young godwits could reflect a period of above average breeding conditions, or might represent a density-dependent response to the previous population decline during 1994–2003. For example, lower numbers of competing adults on post-breeding staging grounds in Alaska could increase a juvenile’s probability of surviving its first southbound migration; however, there is currently no evidence that godwits are resource-limited in Alaska or New Zealand. An alternative, but not mutually exclusive, explanation for growing non-migrant numbers is that godwits are increasingly delaying maturity or skipping migration as adults; there are currently insufficient data to evaluate these possibilities.

It is perhaps premature to evaluate the magnitude of the recent decline in adult survival (2011–2012) on absolute numbers of godwits in New Zealand, particularly if a temporary surge of reproduction is to some extent masking the expected decline. Although not yet formally analysed, recent count data indeed suggest a downward trend: despite a higher coverage of sites than previous years, the November census totals in 2013–2014 declined to ~75 000 godwits (OSNZ, unpubl. data), representing a loss of ~10 000 individuals since 2011 (Fig. 1). Our projection of 5–6% decline per year should only be observed if adult survival persists at the low rates observed in 2011–2012; if intertidal staging sites in the Yellow Sea are indeed the limiting factor for this population, this scenario would require continued degradation or disappearance of such sites. Otherwise, we might expect a density-dependent correction in which survival rates rebound as the population stabilises at a new, lower level (Rakhimberdiev *et al.* 2015), as presumably occurred after the previous decline during 1994–2003.

Our study illustrates the limitations of relying on only a single index (i.e. census numbers) to evaluate population viability. Despite an apparently stable population during 2004–2012, important demographic changes occurred in the New Zealand Bar-tailed Godwit population, including a changing age structure and decreasing adult survival. From the latter development, we conclude that there is ample reason for concern about the future of *L. l. baueri*, particularly as loss and degradation of intertidal wetlands in the Yellow Sea continue at an alarming rate (Murray *et al.* 2014; Melville *et al.* 2016). Ongoing monitoring of survival (via marked individuals), age structure, and total population

numbers (winter and summer) in New Zealand will reveal the demographic consequences of the recent drop in survival, and whether it is eventually corrected or is a prelude to another significant population decline.

Acknowledgements

This project is indebted to many volunteers who assisted with trapping, counting, and resighting over more than two decades; chief among these is A. Habraken for his singular resighting effort. We thank C.E. Studds and R.A. Fuller for the use of unpublished population trend data. The Ornithological Society of New Zealand (OSNZ) kindly made available census and capture data. Godwit captures were in part funded and performed under New Zealand Department of Conservation Research and Development contracts 3739–01 and 3599 and under animal ethics approval by Massey University and Otago University. Captures in the Auckland region were supported by the Pukorokoro Miranda Naturalists Trust. JRC was supported by a Massey University Doctoral Scholarship, a Career Development Bursary from the British Ornithological Union, and an ALW Open Program postdoctoral research grant awarded to TP by the Netherlands Organisation for Scientific Research (NWO). The survival analysis by TL was made possible by an NWO Rubicon grant awarded to TL and by funding from BirdLife Netherlands and WWF-Netherlands to the Chair in Global Flyway Ecology occupied by TP at the University of Groningen. TP was additionally supported by an NWO TOP-grant ('Shorebirds in space', NWO-854.11.004). PFB was supported by a FRST Postdoctoral Fellowship, a Marsden Fund grant administered by the Royal Society of New Zealand, and the David and Lucile Packard Foundation through the Pacific Shorebird Migration Project. We thank R. Gill for helpful comments on the manuscript. Jesse R. Conklin and Tamar Lok contributed equally to this paper.

References

- Abadi, F., Botha, A., and Altwegg, R. (2013). Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: does it matter? *PLoS One* **8**, e62636. doi:10.1371/journal.pone.0062636
- Amano, T., Székely, T., Koyama, K., Amano, H., and Sutherland, W. J. (2012). A framework for monitoring the status of populations: An example from wader populations in the East Asian–Australasian flyway. *Biological Conservation* **143**, 2238–2247. [See also 2012 addendum.] doi:10.1016/j.biocon.2011.06.006
- Baker, A. J., González, P. M., Piersma, T., Niles, L. J., do Nascimento, I. D. S., Atkinson, P. W., Clark, N. A., Minton, C. D. T., Peck, M. K., and Aarts, G. (2004). Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society B: Biological Sciences* **271**, 875–882. doi:10.1098/rspb.2003.2663
- Bamford, M., Watkins, D., Bancroft, W., Tischler, G., and Wahl, J. (2008). 'Migratory Shorebirds of the East Asian–Australasian Flyway: Population Estimates and Internationally Important Sites.' (Wetlands International–Oceania: Canberra)
- Barter, M. (2002) Shorebirds of the Yellow Sea: importance, threats and conservation status. Available at http://www.wetlands.org/Portals/0/publications/Book/WI_ShorebirdsYellowSea_2002.pdf [Verified 19 January 2015].
- Barter, M. (2003). The Yellow Sea – a race against time. *Wader Study Group Bulletin* **100**, 111–113.
- Battley, P. F., and Piersma, T. (2005). Body composition and flight ranges of bar-tailed godwits (*Limosa lapponica baueri*) from New Zealand. *The Auk* **122**, 922–937. doi:10.1642/0004-8038(2005)122[0922:BCAFRO]2.0.CO;2
- Battley, P. F., Schuckard, R., and Melville, D. S. (2011) Movements of Bar-tailed Godwits and Red Knots within New Zealand. Science for Conservation No. 315. New Zealand Department of Conservation.
- Battley, P. F., Warnock, N., Tibbitts, T. L., Gill, R. E. Jr, Piersma, T., Hassell, C. J., Douglas, D. C., Mulcahy, D. M., Gartrell, B. D., Schuckard, R., Melville, D. S., and Riegen, A. C. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology* **43**, 21–32. doi:10.1111/j.1600-048X.2011.05473.x
- BirdLife International (2015) Species factsheets: IUCN Red list for birds. (BirdLife International) Available at <http://www.birdlife.org/datazone/speciesfactsheet.php?id=3005> [Verified 4 December 2015]
- Boyd, H., and Piersma, T. (2001). Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus islandica* wintering in Britain, 1969–1995. *Ardea* **89**, 301–317.
- Burnham, K. P., and Anderson, D. R. (2002) 'Model Selection and Multi-model Inference: A Practical Information-theoretic Approach.' 2nd edn. (Springer: New York)
- Choi, C.-Y. (2015) The northward migration stopover ecology of Bar-tailed Godwits and Great Knots in the Yalu Jiang Estuary National Nature Reserve, China. PhD Thesis, Massey University, Palmerston North, New Zealand.
- Choi, C.-Y., Battley, P. F., Potter, M. A., Ma, Z., and Liu, W. (2014). Factors affecting the distribution patterns of benthic invertebrates at a major shorebird staging site in the Yellow Sea, China. *Wetlands* **34**, 1085–1096. doi:10.1007/s13157-014-0568-4
- Choi, C.-Y., Battley, P. F., Potter, M. A., Rogers, K. G., and Ma, Z. (2015). The importance of Yalu Jiang coastal wetland in the north Yellow Sea to Bar-tailed Godwits *Limosa lapponica* and Great Knots *Calidris tenuirostris* during northward migration. *Bird Conservation International* **25**, 53–70. doi:10.1017/S0959270914000124
- Choi, Y. R. (2014). Modernization, Development and underdevelopment: reclamation of Korean tidal flats, 1950s–2000s. *Ocean & Coastal Management* **102**(Part B), 426–436. doi:10.1016/j.ocecoaman.2014.09.023
- Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., and Pradel, R. (2009a). U-CARE: Utilities for performing goodness of fit tests and manipulating Capture–Recapture data. *Ecography* **32**, 1071–1074. doi:10.1111/j.1600-0587.2009.05968.x
- Choquet, R., Rouan, L., and Pradel, R. (2009b) Program E-SURGE: a software application for fitting multievent models. In 'Modeling Demographic Processes in Marked Populations.' (Eds D.L. Thomson, E. G. Cooch and M.J. Conroy) pp. 845–865. (Springer: New York)
- Conklin, J. R., and Battley, P. F. (2011). Impacts of wind on individual migration schedules of New Zealand bar-tailed godwits. *Behavioral Ecology* **22**, 854–861. doi:10.1093/beheco/arr054
- Conklin, J. R., Battley, P. F., Potter, M. A., and Fox, J. W. (2010). Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nature Communications* **1**, 67. doi:10.1038/ncomms1072
- Conklin, J. R., Battley, P. F., and Potter, M. A. (2013). Absolute consistency: individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS One* **8**, e54535. doi:10.1371/journal.pone.0054535
- Conklin, J. R., Verkuil, Y. I., and Smith, B. R. (2014) Prioritizing migratory shorebirds for conservation action on the East Asian–Australasian Flyway. WWF-Hong Kong, Hong Kong.
- Garnett, S. T., Szabo, J. K., and Dutton, G. (2011) Action plan for Australian birds 2010. CSIRO, Melbourne.
- Gill, R. E. Jr, and Handel, C. M. (1990). The importance of subarctic intertidal habitats to shorebirds: a study of the central Yukon-Kuskokwim Delta, Alaska. *The Condor* **92**, 709–725. doi:10.2307/1368690
- Gill, R. E. Jr, and McCaffery, B. J. (1999). Bar-tailed godwits *Limosa lapponica* in Alaska: a population estimate from the staging grounds. *Wader Study Group Bulletin* **88**, 49–54.
- Gill, R. E. Jr, Tibbitts, T. L., Douglas, D. C., Handel, C. M., Mulcahy, D. M., Gottschalck, J. C., Warnock, N., McCaffery, B. J., Battley, P. F., and Piersma, T. (2009). Extreme endurance flights by landbirds crossing the

- Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society B: Biological Sciences* **276**, 447–457. doi:10.1098/rspb.2008.1142
- Gill, R. E. Jr, Douglas, D. C., Handel, C. M., Tibbitts, T. L., Hufford, G., and Piersma, T. (2014). Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific. *Animal Behaviour* **90**, 117–130. doi:10.1016/j.anbehav.2014.01.020
- Handel, C. M., and Gill, R. E. Jr (2010). Wayward youth: trans-Beringian movement and differential southward migration by juvenile Sharp-tailed Sandpipers. *Arctic* **63**, 273–288. doi:10.14430/arctic1492
- Hargrove, J. W., and Borland, C. H. (1994). Pooled population parameter estimates from mark-recapture data. *Biometrics* **50**, 1129–1141. doi:10.2307/2533449
- Hassell, C. (2013). Recent longevity records of waders in Roebuck Bay, NW Australia. *Wader Study Group Bulletin* **120**, 225–226.
- Hua, N., Tan, K., Chen, Y., and Ma, Z. (2015). Key research issues concerning the conservation of migratory shorebirds in the Yellow Sea region. *Bird Conservation International* **25**, 38–52. doi:10.1017/S0959270914000380
- Iwamura, T., Possingham, H. P., Chadès, I., Minton, C., Murray, N. J., Rogers, D. I., Tremblay, E. A., and Fuller, R. A. (2013). Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20130325. doi:10.1098/rspb.2013.0325
- Laake, J. L. (2013) RMark: an R interface for analysis of capture–recapture data with MARK. Available at <http://www.afsc.noaa.gov/publications/procrpt/pr2013-01.pdf> [Verified 14 December 2015].
- Lebreton, J.-D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118. doi:10.2307/2937171
- Leyrer, J., van Nieuwenhove, N., Crockford, N., and Delany, S. (2014) ‘Proposals for Concerted and Cooperative Action for Consideration by CMS COP 11, November 2014.’ (BirdLife International and International Wader Study Group) Available at http://www.cms.int/sites/default/files/document/COP11_Inf_44_Proposals_for_Concerted_and_Cooperative_Action_Bird_Species_for_Consideration_by_COP11_0.pdf [Verified 4 December 2015].
- MacKinnon, J., Verkuil, Y. I., and Murray, N. (2012) IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). Occasional Paper of the IUCN Species Survival Commission No. 47. IUCN, Gland, Switzerland and Cambridge, UK.
- McCaffery, B. J., and Gill, R. E., Jr (2001) Bar-tailed godwit (*Limosa lapponica*). In ‘The Birds of North America. Vol. 581.’ (Eds A. Poole and F. Gill). (The Birds of North America, Inc.: Philadelphia)
- Meltofte, H., Piersma, T., Boyd, H., McCaffery, B., Ganter, B., Golovnyuk, V. V., Graham, K., Gratto-Trevor, C. L., Morrison, R. I. G., Nol, E., Rösner, H., Schamel, D., Schekkerman, H., Soloviev, M. Y., Tomkovich, P. S., Tracy, D. M., Tulp, I., and Wennerberg, L. (2007). Effects of climate variation on the breeding ecology of Arctic shorebirds. *Bioscience* **59**, 1–48.
- Melville, D., Ying, C., and Ma, Z. (2016). Shorebirds along China’s Yellow Sea coast face an uncertain future – a review of threats. *Emu*. doi:10.1071/MU15045
- Minton, C., Taylor, S., Jessop, R., Gibbs, H., Habraken, T., and Schuckard, R. (2010). Amazing initial results from the deployment of engraved leg flags on Bar-tailed Godwits *Limosa lapponica* in Victoria, Australia. *Stilt* **58**, 10–12.
- Minton, C., Gosbell, K., Johns, P., Christie, M., Klaassen, M., Hassell, C., Boyle, A., Jessop, R., and Fox, J. (2011). Geolocator studies on Ruddy Turnstones *Arenaria interpres* and Greater Sandpipers *Charadrius leschenaultii* in the East Asian–Australasia Flyway reveal widely different migration strategies. *Wader Study Group Bulletin* **118**, 87–96.
- Moores, N., Rogers D. I., Rogers, K., and Hansbro, P. M. (2016) Tidal-flat reclamation and shorebird declines in Saemangeum and the Republic of Korea. *Emu* **116**. doi:10.1071/MU16006
- Murray, N. J., Clemens, R. S., Phinn, S. R., Possingham, H. P., and Fuller, R. A. (2014). Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Frontiers in Ecology and the Environment* **12**, 267–272. doi:10.1890/130260
- Murray, N. J., Ma, Z., and Fuller, R. A. (2015). Tidal flats of the Yellow Sea: A review of ecosystem status and anthropogenic threats. *Austral Ecology* **40**, 472–481. doi:10.1111/aec.12211
- O’Brien, S., Robert, B., and Tiandry, H. (2005). Consequences of violating the recapture duration assumption of mark–recapture models: a test using simulated and empirical data from an endangered tortoise population. *Journal of Applied Ecology* **42**, 1096–1104. doi:10.1111/j.1365-2664.2005.01084.x
- Piersma, T., and Gill, R. E. Jr (1998). Guts don’t fly: small digestive organs in obese bar-tailed godwits. *The Auk* **115**, 196–203. doi:10.2307/4089124
- Piersma, T., Lok, T., Chen, Y., Hassell, C. J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D. S., Zhang, Z.-W., and Ma, Z. (2016). Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *Journal of Applied Ecology*. doi:10.1111/1365-2664.12582
- R Core Team (2013) ‘R: A Language and Environment for Statistical Computing.’ (R Foundation for Statistical Computing: Vienna, Austria.)
- Rakhimberdiev, E., van den Hout, P. J., Brugge, M., Spaans, B., and Piersma, T. (2015). Seasonal mortality and sequential density dependence in a migratory bird. *Journal of Avian Biology* **46**, 332–341. doi:10.1111/jav.00701
- Robertson, H. A., Dowding, J. E., Elliot, G. P., Hitchmough, R. A., Miskelly, C. M., O’Donnell, C. F. J., Powlesland, R. G., Sagar, P. M., Scofield, R. P., and Taylor, G. A. (2013) Conservation Status of New Zealand Birds, 2012. Available at <http://www.doc.govt.nz/Documents/science-and-technical/nztc4entire.pdf> [Verified 3 December 2015].
- Rogers, K. G., and Gosbell, K. (2006). Demographic models for red-necked stint and curlew sandpiper in Victoria. *Stilt* **50**, 203–214.
- Sæther, B.-E., and Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653. doi:10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2
- Sagar, P., Shankar, U., and Brown, S. (1999). Distribution and numbers of waders in New Zealand, 1983–1994. *Notornis* **46**, 1–44.
- Southey, I. (2009) Numbers of Waders in New Zealand 1994–2003. Research & Development Series No. 308. New Zealand Department of Conservation, Wellington.
- Tomkovich, P. S., and Soloviev, M. Y. (2013) Breeding bird conditions in the circumpolar Arctic during 2011. Available at <http://arcticbirds.net/review2011.pdf> [Verified 3 December 2015].
- Tomkovich, P. S., Porter, R. R., Loktionov, E. Y., and Niles, L. J. (2013). Pathways and staging areas of Red Knots *Calidris canutus rogersi* breeding in southern Chukotka, Far Eastern Russia. *Wader Study Group Bulletin* **120**, 181–193.
- Wetlands International (2013) Waterbird population estimates fifth edition. Available at <http://wpe.wetlands.org/> [Verified 14 December 2015].
- White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. doi:10.1080/00063659909477239
- Wilson, J. R., Nebel, S., and Minton, C. D. T. (2007). Migration ecology and morphometrics of two bar-tailed godwit populations in Australia. *Emu* **107**, 262–274. doi:10.1071/MU07026
- Wilson, H. B., Kendall, B. E., Fuller, R. A., Milton, D. A., and Possingham, H. P. (2011). Analyzing variability and the rate of decline of migratory shorebirds in Moreton Bay, Australia. *Conservation Biology* **25**, 758–766. doi:10.1111/j.1523-1739.2011.01670.x