Loss of periodicity in breeding success of waders links to changes in lemming cycles in Arctic ecosystems

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Lemming population cycles in the Arctic have an important impact on the Arctic food web, indirectly also affecting breeding success in Arctic-nesting birds through shared predators. Over the last two decades lemming cycles have changed in amplitude and even disappeared in parts of the Arctic. To examine the large scale effect of these recent changes we re-analysed published data from the East Atlantic Flyway (EAF), where a relationship between lemming cycles and wader breeding success was earlier found, and new data on breeding success of waders in the East Asian–Australasian Flyway (EAAF).

We found that 1) any long-term periodicities in wader breeding success existed only until the year 2000 in the EAAF and until the 1980s in the EAF; 2) studying these patterns at a smaller spatial scale, where the Siberian–Alaskan breeding grounds were divided into five geographical units largely based on landscape features, breeding success of waders from the EAAF was not correlated to an index of predation pressure, but positively correlated to Arctic summer temperatures in some species. We argue that fading out of lemming cycles in some parts of the Arctic is responsible for faltering periodicity in wader breeding success along both flyways. These changed conditions have not yet resulted in any marked changing trends in breeding success across years, and declining numbers of waders along the EAAF are therefore more likely a result of changing conditions at stop-over and wintering sites.

Several studies found breeding success of Arctic migratory waders (shorebirds) and geese to be linked to variation in lemming abundance (Summers and Underhill 1987, Martin and Baird 1988, Bêty et al. 2001, Blomqvist et al. 2002). This argument relies on the alternative prey hypothesis (Roselaar 1979, Summers 1986), which suggests that lemming cycles in the Arctic are responsible for fluctuations in the success of locally breeding geese and waders. Lemming numbers typically show three to four-year cycles and are potentially regulated by food-plant availability (bottom–up) and their predators, such as Arctic fox *Vulpes lagopus,* stoat *Mustela erminea* and snowy owl *Bubo scandiacus* (top–down). Whether lemming cycles are bottom–up or top–down controlled is in dispute (Andersson and Erlinge 1977, Turchin et al. 2000, Gilg et al. 2003, Krebs 2011). The alternative prey hypothesis suggests that predators, after having increased in numbers during a lemming peak, will switch to chicks and eggs of waders and geese when lemmings are scarce, lowering these birds' breeding success (Summers 1986, Dhondt 1987, Bêty et al. 2001, Kausrud et al. 2008, Lecomte et al. 2008).

Periodicity in lemming abundance is shown in parts of the Arctic (Ims et al. 2013, Reid et al. 2013). However, cycles have changed, and even disappeared in some parts over the past two decades. Collapsing cycles were first reported from Fennoscandia (Kausrud et al. 2008), followed by reports on their disappearance from areas in Greenland (Gilg et al. 2009) and Yamal Peninsula, northwestern Siberia (S. Mechnikova pers. comm.), whereas on Wrangel Island, Russia, a change in the length of cycles was reported (Menyushina et al. 2012). Although lemmings may have drifted in and out of cycles previously (Ims et al. 2008), similarly changing population cycles in other Arctic animal species (e.g. voles, black grouse *Tetrao tetrix* and forest insects) suggests the involvement of a common, large-scale effect, such as climate change (Ims et al. 2008). In the case of lemmings, changing snow conditions in winter are assumed to be key to these population dynamic changes (Kausrud et al. 2008, Ims et al. 2011), with cascading knock-on effects on linked species (Schmidt et al. 2012). Nonetheless, evidence of returning vole cycles in south Finland in the early 2000s, after being absent for five years (Brommer et al. 2010), and variation in patterns of periodicity between climatologically different regions in Finland (Korpela et al. 2013) have been suggested to refute this theory (Brommer et al. 2010).

Worldwide, waders are of particular conservation concern owing to their long distance migration, low reproductive

rate and dependence on specific habitats that are globally deteriorating (Fernandez and Lank 2008, Cox 2010). Degradation and loss of stopover and wintering habitats are widely considered to be the cause of their generally declining numbers (Norris 2005, Fernandez and Lank 2008, Rogers et al. 2010). Yet, climatic changes at the breeding grounds, and the interaction of climate and existing predator–prey cycles, is increasingly being considered to potentially play a role (Zöckler et al. 2000, Newton 2006, Fraser et al. 2013). Given the rapid economic developments along the East Asian–Australasian Flyway (EAAF, Fig. 1A) and the changing climatic and biotic conditions on the Arctic breeding grounds, there is notably great conservation concern for the 8 million and declining waders using this route (Bamford et al. 2008, Wilson et al. 2011, Cooper et al. 2012).

We investigated whether 1) lemming cycles on the breeding grounds, or the lack thereof, are reflected in the periodicity in breeding success of waders on the East Asian – Australasian Flyway (EAAF) and 2) whether predation pressure together with average summer temperatures across five geographic units within the Siberian–Alaskan breeding area may explain inter-annual variation in breeding success of waders from the EAAF. Along with the EAAF data we also re-analysed data from the East Atlantic Flyway (EAF, Fig. 1A), where a strong effect of lemming cycles on breeding success was previously shown (Blomqvist et al. 2002), to evaluate any changes in this effect over time.

Material and methods

Breeding success of waders

Published juvenile percentages as observed on the wintering grounds were used as estimators of breeding success of Arctic-breeding waders. Despite its limitations (Clark et al. 2004, McCaffery et al. 2006, Rogers et al. 2006), this is currently the most practical method for estimating breeding success especially in long-term monitoring of long-distance migrants (Minton 2003). Data was available in the EAAF for 1978–2013 in southeast Australia (SEA) for ruddy turnstone *Arenaria interpres*, red-necked stint *Calidris ruficollis*, curlew sandpiper *C. ferruginea*, sharp-tailed sandpiper *C. acuminata*, red knot *C. canutus* and bar-tailed godwit *Limosa lapponica* (Straw 2003, Minton et al. 2005, 2011a). For Broome and Eighty-mile Beach, north Western Australia (NWA), similar data was available for 1998–2013 for red-necked stint, curlew sandpiper and bar-tailed godwit (Minton et al. 2011a). We refer to the Australian and African non- breeding grounds (belonging to the EAAF and EAF, respectively) as 'wintering' areas throughout this paper, as these sites are used during the northern hemispheric winter. We chose only wader species for which breeding areas coincide with lemming abundance areas. These species breed in a vast area in the Russian– Alaskan tundra (especially curlew sandpiper and red-necked stint). However, we identified core breeding areas based on recoveries and flag-sightings. This data was obtained from Lappo et al. (2012) and Minton et al. (2011b) and matched with the five geographic regions identified below.

For the EAF, juvenile percentages of three wader species wintering in South Africa (curlew sandpiper, red knot and

sanderling) were obtained from Blomqvist et al. (2002) and include the years 1969–1986. For curlew sandpiper additional data from 1947–2005 from an autumn stop-over site in Ottenby, southern Sweden, was used (Barshep 2011).

### Identification of geographic regions

Lemming population cycles tend to be synchronous across regions with relatively uniform landscape structure (Angerbjorn et al. 2001, Chernyavsky and Lazutkin 2004) (but see Henden et al. (2009) for periods where populations were less synchronous in Fennoscandia). Accordingly, we divided the tundra zone of eastern Siberia and northwestern north America into five geographical regions: East Taimyr (from the mouth of the Verkhnyaya Taimyra River in the central Taimyr Peninsula to the Anabar River), Lena Delta (area between the Anabar and Yana Rivers), East-Siberian Plain (from the Yana to Kolyma River), Chukotka (from Chaun Bay to the Bering Strait) and Alaska (Fig. 1B). For each we obtained lemming abundance by combining information from observation points within each region, as described below. Most of these regions have different landscapes: gently sloping hilly landscape predominates at Taimyr, flat marshy tundra on the East-Siberian plains and mountains in Chukotka. The Lena Delta with adjacent areas as well as Alaska have a more complex composition of landscapes with huge deltas, hilly areas and mountain ranges.

In some cases, clear natural borders exist between the neighbouring regions – Alaska and Chukotka are separated by the Bering Strait, the western edge of the Chukotka region generally coincides with the border between the mountainous and flat plain landscapes. Borders between the other areas are more arbitrary but have been chosen such as to best separate the various wader populations. Also the western border of the East Taimyr region is arbitrarily chosen as 100°E, but it also coincides with the westernmost area where shorebirds of the EAAF are known to breed.

Lemming abundance and predation index

For the EAAF analysis most lemming abundance data were collected in the framework of the Arctic Birds Breeding Conditions Survey (ABBCS), covering the entire Arctic breeding area of the waders within the EAAF over the period 1989–2013 (all original data available at <www.arcticbirds.net>). Data for 1978–1988 and additional information to complement the data from ABBCS was obtained from the literature (Dorogoi 1988, Kuryshev and Dorogoi 1989, Chernyavsky and Lazutkin 1999, 2004, Koroleva 2002, Volpert and Shadrina 2002, Pozdnyakov 2004, Fischer et al. 2010).

All lemming abundance data were indexed on a scale from 1–3, corresponding to low, average and high, although intermediate values could be obtained when local scores within a region were averaged (Supplementary material Appendix 1). When quantitative information (mostly trapping data) was available, the three levels corresponded to 0–3, 4–10 and over 11 specimens captured per 100 trapdays. This ranking system largely follows the one used by Kokorev and Kuksov (2002), who additionally used a 'very low' and 'very high' category which we combined with 'low' and 'high', respectively. When quantitative information was

(A)

(B)

Tundra Legend

	Alaska
	Chukotka
	East-Siberian
	Lena Delta
	East Taimyr
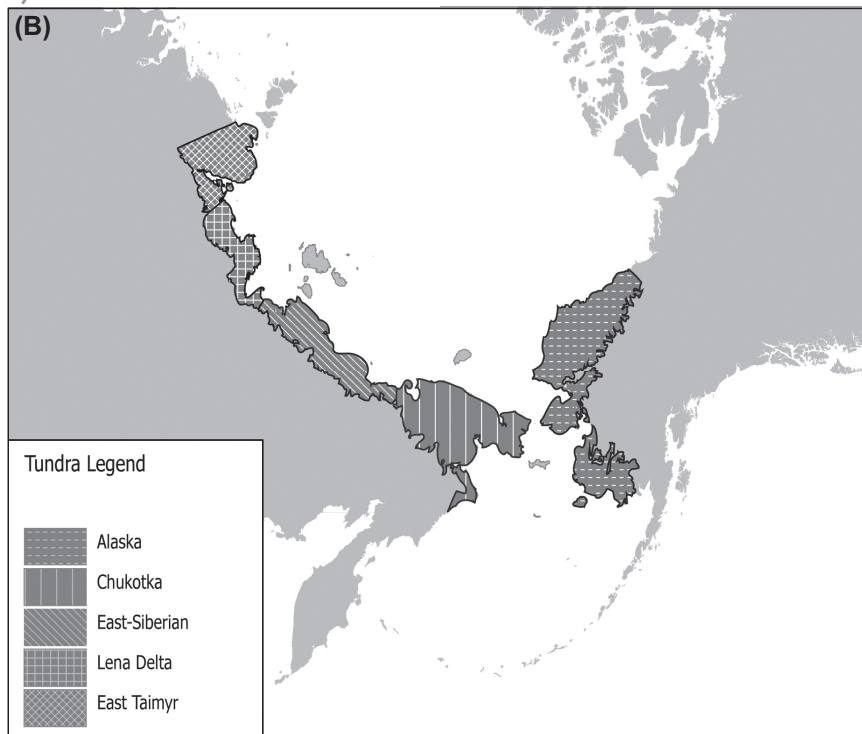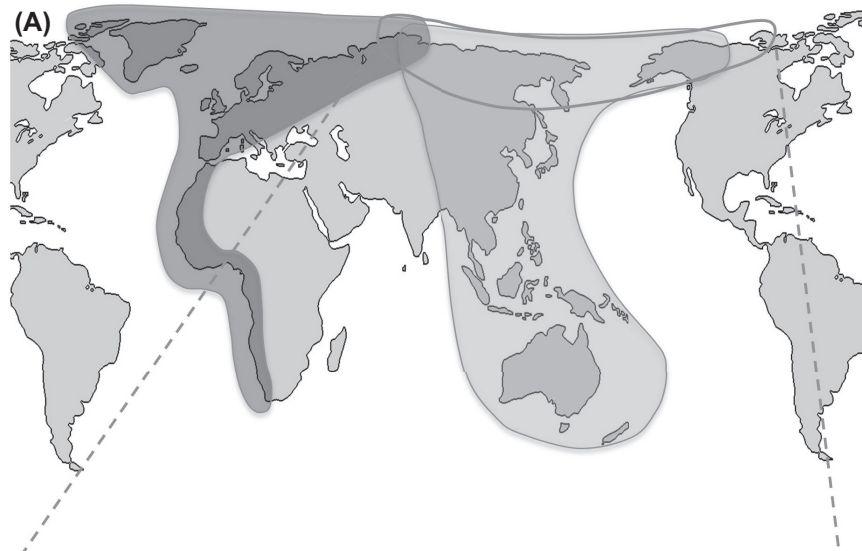
East Taimyr
Red-necked Stint
Curlew Sandpiper

Chukotka
Red-necked Stint
Red Knot

Alaska
Bar-tailed
Godwit
(SEA)

East Siberian Plains
Ruddy Turnstone
Sharp-tailed Sandpiper
Bar-tailed Godwit (NWA)
Curlew Sandpiper

Lena Delta
Red-necked Stint
Curlew Sandpiper

Figure 1. (A) Descriptions of the East Asian–Australasian Flyway (EAAF, light grey) and the East Atlantic Flyway (EAF, dark grey) for waders discussed in this paper. (B) The five geographic regions identified within the Siberian–Alaskan high-Arctic breeding range of waders from the EAAF. For each region the species of waders that find their core breeding range within that region are indicated. For bar-tailed godwit, which forms two different populations, the major non-breeding ground in Australia is mentioned in brackets (SEA for southeast Australia and NWA for north Western Australia).

lacking assignment of rank was based on the mutual agreement of two experts (MS and PT), who evaluated qualitative information available in breeding conditions reports in the ABBCS database. For the EAF analysis, lemming abundance data for the breeding grounds on Taimyr Peninsula covering the period from 1947 until 1995 were obtained from Blomqvist et al. (2002) and for 1996–2010 from the ABBCS.

Predation index (P) was calculated following Blomqvist et al. (2002) using the lemming abundance index (ranging from 1–3) in the previous (X_{t-1}) and the present year (X_t):

$$P = \frac{\left(X_{t-1} - X_t + 3\right)}{2}$$

This index (ranging from 0.5–2.5) is based on the assumption that in years with low lemming abundance following lemming peaks, predators will be abundant and divert their predation from lemmings to bird eggs and chicks.

Temperatures on the EAAF breeding grounds

Daily average temperature data (number of readings per day span from six in earlier years to 24 in recent years) from 15 May to 31 July over the years 1978–2012 from all available weather stations in the area from east Taimyr to Alaska (Global surface summary of the day at NOAA/ National Climatic Data Centre <ftp://ftp.ncdc.noaa.gov/ pub/data/gsod>) were used to create daily air temperature surface maps using the Manifold 8 GIS system. The interpolation algorithm was gravity (Manifold's implementation of inverse distance interpolator), with a search radius of 500 km and using a maximum of ten stations. Next, the surface maps were overlayed with the breeding ranges of each wader species from the EAAF and surface values averaged within these ranges, resulting in a daily temperature value for each species. Daily values were subsequently averaged to obtain the mean for the second half of May and monthly means for June and July.

Statistical analyses

For all wader populations along both the EAAF and the EAF, except for red knot from SEA because of data shortage, we used autocorrelation and partial autocorrelation functions (ACF and PACF, respectively) to test for periodicity in breeding success (i.e. juvenile percentages), using the *acf* function in the *stats* package of R. ACF is used to describe the correlation of a variable with itself at two points in a time series. PACF describes the correlation between a variable and itself in two different time points, once correlation between all successive lags are controlled, and is used to determine which time lags are involved in the generation of the cycles observed in the ACF (Crawley 2012b). To investigate a potential link between periodicity in breeding success and lemming cycles, a similar analysis was also performed on lemming abundance indices for the geographical areas mentioned above.

These correlation techniques assume that the statistical properties of the time series are stationary (i.e. consistent over time), an assumption which is often violated in ecological systems (Cazelles et al. 2008). To reveal whether periodicity in breeding success changed over time for wader populations

along both the EAAF and the EAF we used two different approaches: 1) a moving window of 20 years, starting in the first year of the time series, to test the changes in the autocorrelation over time and (2) wavelet analysis. Wavelet analysis has been shown to be optimal for detecting changes in ecological time series, as it can deal with aperiodic, noisy and varying signals (Torrence and Compo 1998). However, long data sets are required for a reliable wavelet analysis, which we thus limited to species with data sets exceeding 30 years in length. Data was sufficiently long in three species from the EAAF (curlew sandpiper, sharp-tailed sandpiper and red-necked stint, all from SEA) and in only one species from the EAF (curlew sandpiper from Sweden). Wavelet analysis was performed using the *wt* function in the *biwavelet* package in R, using all default settings, including 'morlet' as the mother wavelet (Gouhier 2004). A regular χ^2-test was used for significance testing. Periodicity estimates at the start and end of time series are fraud with error, which is recognised by *biwavelet* calculating a 'cone of influence' for each wavelet analysis identifying the region in a time series in which edge effects become important.

A similar analysis was also performed on the lemming indices in three breeding areas for waders of the EAAF for which the time series were sufficiently long (East Taimyr, Chukotka and East Siberian plains) as well as Taimyr Peninsula, the breeding area of curlew sandpiper from the EAF. Wavelet analysis requires uninterrupted data series, yet, for two years in Chukotka (1995 and 1999), two years in east Taimyr (1982 and 1984) and three years in the East Siberian plains (1985, 2002 and 2003) gaps in the data series occurred. In these cases we trialed all possible combinations of lemming indices (1, 2 and 3) across the missing years to test, and in all three cases indeed confirm, the robustness of the trend. We therefore completed these missing values with an average index (2).

Dispersion parameter in the breeding success data (ϕ = deviance divided by the degrees of freedom of the residuals) was high in all cases due to many low juvenile percentages. We therefore used a quasi-binomial logistic model (Crawley 2012a) when analysing breeding success in relation to temperature and predation index. For each bird population along the EAAF we ran a model with the annual proportions of juveniles from wintering wader populations, weighted for total sample size, as the dependant variable, predation index as categorical predictor, and average temperatures in late May (T_{may},°C), June (T_{june},°C) and July (T_{july},°C) as continuous predictors. We also ran a model for curlew sandpiper from Sweden (EAF) with predation index as categorical variable. All predictor values in the EAAF models were standardized (i.e. Z-transformed), to ease assessment of their contribution to the ultimate model. We limited core breeding area for all populations except curlew sandpiper and red-necked stint to one of the five geographic regions identified above (Fig. 1B). For curlew sandpiper and red-necked stint predation index was averaged across the various geographic regions where they breed prior to standardization. Although weakening the correlation, this step was essential due to the vast range of breeding locations of these species across the Russian tundra. For each population, model selection was achieved through ANOVA F-tests (as quasi binomial models do not provide log(likelihood) values

for the calculation of AIC). Subsequently, for each parameter in the final model we calculated the odds ratio (OR), which is the increase in breeding success for every unit of increase in the predictor variable (while holding all the other variables in the model at a fixed value). An OR > 1 indicates a positive, whereas an OR < 1 indicates a negative effect of the predictor variable.

All statistical analyses were conducted using R ver. 3.0.3 (<www.R-project.org/>). Significance level of all statistical tests was set at p = 0.05.

Results

Periodicity in breeding success

Autocorrelation in the juvenile percentages data on waders from both EAF and EAAF resulted in significant three-year periodicity, confirmed by partial autocorrelation, for red-necked stint from SEA only (Supplementary material Appendix 2).

Curlew sandpiper from Sweden belonging to the EAF showed only close to significant three-year periodicity (p = 0.08) and a highly significant nine-year periodicity. Red-necked stint from NWA showed a non-significant tendency for three year periodicity as well as curlew sandpiper and sanderling from South Africa (Supplementary material Appendix 3–4).

Applying a 20-years moving window on the juvenile percentage data for curlew sandpiper from Sweden revealed that only starting years in the late-1950s until early-1970s yielded a significant periodicity of three years. Also when applying wavelet analysis on the juvenile percentage data for curlew sandpiper from Sweden along the EAF, we again found a strong periodicity, changing from five years in the late-1950s to three years by the mid-1960s, followed by a gradual fading out after the late-1970s (Fig. 2).

In the EAAF, a 20-years moving window of autocorrelation in the red-necked stint dataset from SEA, showed a gradual weakening of the three-year periodicity, although also in early years, correlation was not significant. In the same species, wavelet analysis showed significant periodicity, changing from three to four, and again three years from the mid-1980s until approximately 2003. Curlew sandpiper and sharp-tailed sandpiper from SEA showed a significant periodicity for a very short time, ranging from two to four years between the late-1980s and early-1990s, however, when we divided the time series to 20-year windows, no significant autocorrelation emerged (Fig. 3).

Periodicity in lemming abundance

Autocorrelation analyses on lemming abundance data for the breeding grounds resulted in a significant three-year periodicity for Taimyr Peninsula only, East Siberian Plains data showing a non-significant tendency for three year periodicity (Supplementary material Appendix 5). Wavelet analysis disclosed a significant three-year periodicity in lemming abundance on Taimyr Peninsula, the breeding area of curlew sandpipers from Sweden, until the early-1990s (Fig. 2). Remarkably, this three-year periodicity was
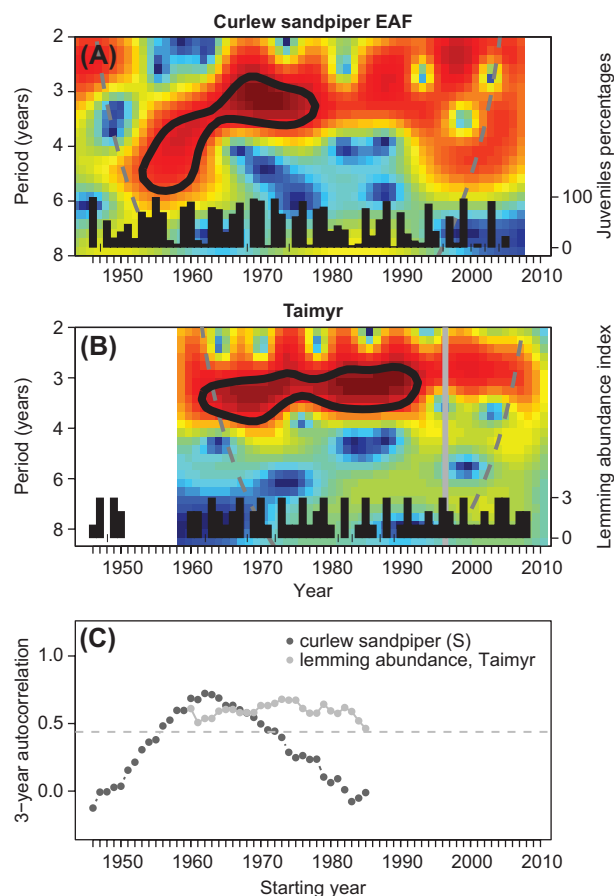

Figure 2. The wavelet power spectrum, showing the change in periodicity for (A) curlew sandpiper from the East Atlantic Flyway and (B) lemming abundance index on Taimyr Peninsula. The likelihood of periodicity increases from blue to red and the black contour marks areas with > 95% confidence. Grey broken line indicates the 'cone of influence'. Outside this area inferences are weak due to edge effects. Juvenile percentages (A) and lemming index (B) are presented in black bars (y-axes of the right). (C) Results of a 20-years moving window autocorrelation analysis for annual juvenile percentages of curlew sandpiper from the East Atlantic Flyway (EAF) and lemming abundance on Taimyr Peninsula, researching the presence of a three-year periodicity. Autocorrelation function for the three-year period in each 20-years window is plotted in the y-axis against the first year of the 20-years period in the x-axis (each data point represents the three year correlation coefficient of three-year periodicity in one 20-years window).

persistent also well after the periodicity in shorebird productivity had started to decline (Fig. 2).

Although neither a significant autocorrelation was found in the complete time series of lemming abundance in Chukotka nor for the 20-years moving window analysis on the same dataset, wavelet analysis showed a 3–4 year cycle in lemming abundance for a short period from the mid-1970s until the late-1980s. In East Taimyr and the East Siberian Plains, no significant periodicity was found for the 20-years moving window analysis, and very short period with approximate three year periodicity was detected around the late-1980s and late-1990s respectively for the wavelet analysis (Fig. 4). Also two short periods with four to six year periodicity were revealed in these areas, but these periods are
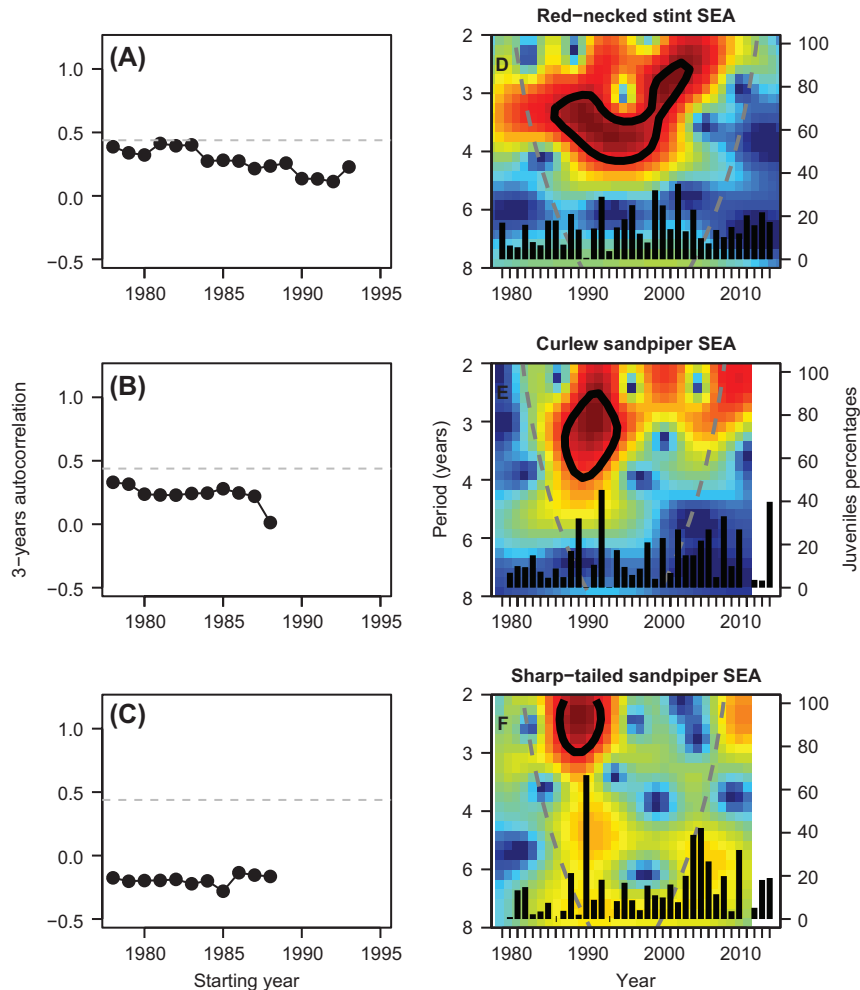
Figure 3. Three-year autocorrelation for juvenile percentages of waders from south east Australia (SEA) in the East Asian–Australasian Flyway (EAAF) in a 20-year moving windows (A–C) and wavelet analysis for the same species (D–F). In panels (A–C), autocorrelation coefficients for the three-year period in each 20-years window are plotted in the y-axis against the first year of the 20-years period in the x-axis (each data point represents the three year correlation coefficient of three-year periodicity in one 20-years window). In panels (D–F), the wavelet power spectrum, showing the change in periodicity in juvenile percentages. The likelihood of periodicity increases from blue to red and the black contour marks areas with >95% confidence. Grey broken line indicates the 'cone of influence'. Outside this area inferences are weak because of edge effects. Juvenile percentages for each species are represented with black bars (y-axes of the right).

outside the cone of influence and may therefore be subject to an edge effect and should be interpreted with caution.

Correlation between breeding success, summer temperatures and predation pressure

Most species in the EAAF do not correlate in their breeding success (Supplementary material Appendix 6) and we thus negate the possibility of one common, large-scale effect on the breeding success of these Arctic waders while on their breeding grounds. Summer temperatures had a significant positive effect on breeding success in five out of nine cases in our study species, with June and July having the strongest effects (Table 1). In two cases (ruddy turnstone from SEA and curlew sandpiper from NWA) some ORs for monthly temperature averages on the breeding grounds were < 1 indicating a negative effect of temperature on breeding success. However, the overall summer temperature effect was always positive (i.e. the net OR obtained by

multiplication of both ORs was > 1). The breeding success of bar-tailed godwit from NWA was not affected by temperatures whereas the population of the same species from SEA was affected by July temperatures. These two populations breed in widely separated Arctic areas, East Siberia and Alaska respectively, thus explaining these differences. Remarkably, the same applied to red-necked stints, where only the population from NWA was affected by May temperatures, although their breeding grounds are assumed to overlap. Conversely, for curlew sandpipers from SEA and NWA, which are also thought to belong to the same population, June temperatures had the most significant effect on birds from both wintering locations. Predation index did not have a significant effect on any species from the EAAF. In the EAF, using the 45 years of data available for curlew sandpiper from Sweden, we found a significant negative effect (i.e. OR < 1) with 50% reduction in breeding success due to predation pressure on Taimyr Peninsula (Table 1).
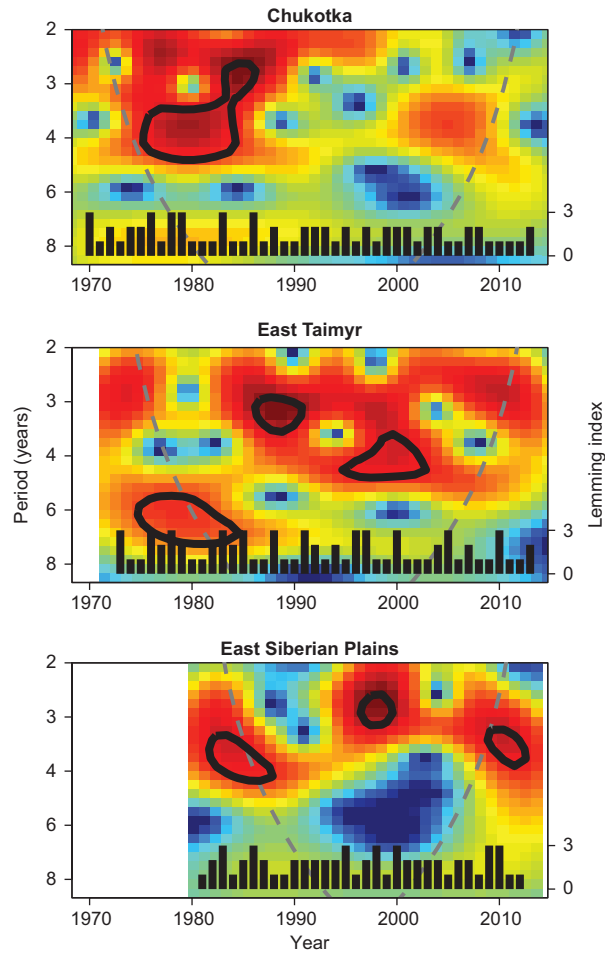
Figure 4. The wavelet power spectrum, showing the change in periodicity in lemming abundance index in three areas on the breeding grounds of waders from the East Asian–Australasian Flyway (EAAF). The likelihood of periodicity increases from blue to red and the black contour marks areas with > 95% confidence. Grey broken line indicates the 'cone of influence'. Outside this area inferences are weak because of edge effects.

Discussion

In contrast to the suggestions made by the alternative prey hypothesis and to the previous findings along the EAF (Blomqvist et al. 2002), we could not identify a strong, common link between breeding success in Australian wintering waders and predation pressures on their Arctic breeding grounds. Given presumed periodicity in lemming numbers and corresponding periodicity in predation pressure (Roselaar 1979, Summers 1986), periodicity in the breeding success of Arctic breeding birds is considered to be one of the hallmarks of the major impacts that lemming cycles have on Arctic ecosystems (Ims and Fuglei 2005). Our (re-) analysis of breeding success in waders along both the EAAF and the EAF now highlights that these cycles have changed in some populations in the last 30 years, alternating between periodic and aperiodic years, and may explain the lack of correlation between breeding success across the various wader species and populations in the EAAF (Supplementary material Appendix 6) and with lemming-linked predation indices from the breeding grounds (Table 1). Clearly, the interaction between lemmings-predators and waders is more complex than a simple predator–prey relationship. Waders are assumed to have a weaker link as they may be a secondary alternative prey in the presence of goose colonies (McKinnon et al. 2013). However, in the general absence of high density goose colonies in the eastern Russian Arctic, where our study species mainly breed, waders are most likely to be among the preferred alternative prey.

For the EAF, only the Swedish data set for curlew sandpipers is sufficiently long to allow a robust analysis of the possible change in periodicity in breeding success over time. The remarkable change in periodicity in this long term data set (Fig. 2), combined with 1) the tendency for a three-years periodicity in two species from South Africa during 1969–1986 (Supplementary material Appendix 4), and 2) the decreasing trends in periodicity in red-necked stint and the waning periodicity in curlew sandpiper and sharp-tailed sandpiper from SEA in the EAAF (Fig. 3A–B), infer a loss

Table 1. Odd Ratios for the best quasi-binomial logistic models relating juvenile ratios in wintering wader populations with predation index (P) and average monthly temperatures in May (T_{may}), June (T_{june}) and July (T_{july}) within the population's respective breeding region. Numbers in brackets are 95% confidence intervals. N is the total number of observations on which juvenile ratios were based across all years (No. of years) used in the model for which data was available for all four predictors. Data are presented for six species along the East Asian–Australasian Flyway (EAAF) wintering in south east Australia (SEA), three species along the EAAF wintering in north Western Australia (NWA), and one species along the East Atlantic Flyway (EAF) observed in Sweden. Hyphens indicate that the parameter was not selected into the final, best model.

	n	No. of years	P	T_{may}	T_{june}	T_{july}
EAAF						
SEA						
Curlew sandpiper	11406	15	–	–	**2.33** (1.56–3.66)	–
Ruddy turnstone	4454	19	–	–	**0.4** (0.2–0.7)	**3.0** (1.6–6.2)
Red-necked stint	59206	14	–	–	–	–
Sharp-tailed sandpiper	5626	23	–	–	–	–
Red knot	1786	23	–	–	–	–
Bar-tailed godwits	2571	17	–	–	–	**1.75** (1.2–2.5)
NWA						
Curlew sandpiper	1506	7	–	–	**2.63** (2.1–3.4)	**0.64** (0.5–0.8)
Red-necked stint	3248	8	–	**1.54** (1.2–1.9)	–	–
Bar-tailed godwits	4125	10	–	–	–	–
EAF						
Curlew sandpiper	4347	45	**0.5** (0.3–0.8)	–	–	–

of periodicity in breeding success of Arctic breeding waders in both flyways.

A problem with our analysis is that it is difficult, if not a statistical impossibility, to prove the absence (rather than the significant existence) of a pattern. The use of a qualitative, expert-opinion based index of lemming abundance may at least in part have contributed to weakened patterns. Yet, this does not explain why these patterns vary over time and space. Although our analysis suggests similarities in the effect of changing lemming cycles on waders of the EAF and EAAF, there may be inherent differences between their typical breeding areas that may anyhow result in a weaker periodicity for waders in the EAAF compared to the EAF. Lemmings are a characteristic feature within the lowlands of the central and northern belts of the Arctic tundra. Typically, their peak occurrences are least pronounced in the southern regions of their distribution and in valleys or coastal sections separated by mountains. It therefore seems that rather systematic periodicity of lemmings is an attribute of large uniform land masses like Taimyr Peninsula (Tomkovich unpubl.). Such is also evident from our analysis, where only lemming abundances in Taimyr Peninsula showed a persistent three-year periodicity.

Waders from the EAAF use more extensive breeding areas than species from the EAF. Finding correlations between breeding success of an entire population and predation index thus requires substantial spatial synchronization in lemming cycles and predator abundances. Although synchronization of lemming cycles has been shown for some areas in the Arctic (Angerbjorn et al. 2001), a phenomenon that is probably driven by predators' mobility and weather conditions across large spatial scales (Krebs et al. 2002), the likelihood of such synchronization is probably diminishing with an increase in area. Still, there we observed changes in periodicity over time and we should not rule that these could be due to change in climatic conditions in some areas, possibly altering patterns of synchrony (Krebs 2013), leading to weaker cycles on large spatial scales.

Despite the relatively short time series, notably for species from NWA, limiting the power of our analysis, our results demonstrate a positive effect of Arctic summer temperatures on breeding success for some waders in the EAAF as shown previously for waders in the EAF and the EAAF (Boyd et al. 2005, Tulp 2007). The three different spring/summer months included in our analysis represent different phases in the breeding season of Arctic waders. Temperatures in late May determine the timing of snowmelt and the rate of thawing. Prolonged snow cover affects the availability of nesting locations and food, and may delay breeding attempts (Niehaus and Ydenberg 2006). June and July are the peak egg laying and chick rearing periods respectively, during which high temperatures may positively affect breeding success (Krijgsveld et al. 2003, McKinnon et al. 2012).

Changes in lemming cycles have a cascading effect on linked species in the Arctic (e.g. resident grouse species, Kausrud et al. 2008). Recently, changing lemming cycles have been linked to decreasing populations of brent geese *Branta bernicla bernicla* wintering in Europe (Nolet et al. 2013). These changes were also suggested to affect red knot migrating through the United States (Fraser et al. 2013). However, there is little evidence of recent changes in lemming cycles across the Canadian Arctic and other studies point at changes occurring on the stopover areas of red knot in North America (Baker et al. 2004), in combination with Arctic snow conditions (McGowan et al. 2011) as the leading factor for population decline.

Here, we enhanced the analysis of former studies and suggest an effect of fading lemming cycles on Arctic breeding birds of the East Atlantic and the East Asian–Australasian Flyways. We argue that fading out of lemming cycles in some parts of the Arctic is responsible for faltering periodicity in wader breeding success along both flyways, and is a major factor for changing breeding conditions of Arctic nesting birds. These changed conditions have not yet resulted in any marked changes in trends on breeding success across years and declining numbers of waders along the EAAF are therefore more likely related to changing conditions at stop-over and wintering sites (Norris 2005, Fernandez and Lank 2008, Rogers et al. 2010) or yet undetected changes in breeding success on the Arctic breeding grounds.

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Supplementary material (available as Appendix oik.01730 at <www.oikosjournal.org/readers/appendix>). Appendix 1–6.

Oikos

Appendix 1

Lemming abundance indices for east Siberia (from central Taimyr to Bering Strait) and Alaska. Indices indicate lemming abundance as (1) low, (2) average and (3) high; although intermediate classifications are possible due to data averaging within regions. Numbers in superscript indicate sources.

Year	East Taimyr	Lena Delta	East-Siberian plain	Chukotka	Alaska	Taimyr Peninsula
2013	2^{10}	1^{10}	-	2^{10}	-	-
2012	1^{10}	1^{11}	1^{10}	1^{10}	$1.5^{8,10}$	-
2011	1^{10}	1^{11}	1^{10}	1^{10}	$1.5^{8,10}$	-
2010	3^{10}	3^{10}	3^{10}	1^{10}	$1.5^{8,10}$	3^{10}
2009	1^{10}	-	3^{10}	1^{10}	$1.5^{8,10}$	-
2008	1^{10}	1^{10}	1^{10}	2^{10}	$2^{8,10}$	2^{10}
2007	2^{10}	1^{10}	2^{10}	2^{10}	$1.5^{8,10}$	2^{10}
2006	1^{10}	1^{10}	2^{10}	1^{10}	$2^{8,10}$	1^{10}
2005	3^{10}	3^{10}	1^{10}	1^{10}	$1^{8,10}$	3^{10}
2004	2^{10}	3^{10}	2^{10}	2^{10}	$1^{8,10}$	3^{10}
2003	1^{10}	1^{10}	-	2^{10}	$2^{8,10}$	1^{10}
2002	1^{10}	1^{10}	-	1^{10}	$1^{8,10}$	2^{10}
2001	1^{10}	1^{10}	2^{10}	2^{10}	$1.5^{8,10}$	1^{10}
2000	3^{10}	3^{10}	3^{10}	2^{10}	$2.5^{8,10}$	1^{10}

Year	East Taimyr	Lena Delta	East-Siberian plain	Chukotka	Alaska	Taimyr Peninsula
1999	1[10]	2[10]	1[10]	-	2[8,10]	3[10]
1998	1[10]	1[10]	3[10]	1[10]	1.5[8,10]	1[10]
1997	3[10]	1[10]	2[10]	2[10]	1.5[8,10]	2[10]
1996	3[1]	3[1]	1[2]	1[10]	2.5[8,10]	3[10]
1995	1[10]	1[10]	3[2]	-	2.5[8,10]	1[9]
1994	2[10]	1[10]	2[2]	1[10]	1[8,10]	2[9]
1993	1[10]	2[10]	2[2]	2[10]	2[8,10]	1[9]
1992	2[10]	3[1]	2[2]	2[10]	1[8,10]	1[9]
1991	3[3]	3[1]	2[2]	2[10]	2[8,10]	3[9]
1990	1[3]	-	2[10]	1[10]	3[8,10]	1[9]
1989	1[4]	1[4]	1[5]	1[4]	2[8,10]	1[9]
1988	3[3]	3[1]	1[5]	2[4,6,7]	2[8,10]	1[9]
1987	1[3]	-	2[5]	1[4]	-	1[9]
1986	1[3]	-	3[7]	3[4]	-	1[9]
1985	3[3]	3[1]	-	1[4]	-	3[9]
1984	-	-	1[4]	1[4]	-	1[9]
1983	3[3]	-	3[4]	3[4]	-	1[9]
1982	-	3[1]	2[4]	1[4]	-	3[9]
1981	1[3]	-	1[4]	1[4]	-	1[9]
1980	1[3]	-	-	1[4]	-	1[9]
1979	2[3]	3[1]	-	3[4]	-	3[9]
1978	3[3]	-	-	3[4]	-	2[9]
1977	2[3]	-	-	1[4]	-	1[9]
1976	3[3]	3[1]	-	3[4]	-	3[9]
1975	1[3]	-	-	2[4]	-	1[9]

Year	East Taimyr	Lena Delta	East-Siberian plain	Chukotka	Alaska	Taimyr Peninsula
1974	1^3	-	-	2^4	-	1^9
1973	3^3	3^1	-	1^4	-	3^9
1972	-	-	-	2^4	-	1^9
1971	-	-	-	1^4	-	1^9
1970	-	-	-	3^4	-	3^9
1969	-	-	-	-	-	2^9
1968	-	-	-	-	-	1^9
1967	-	-	-	-	-	3^9
1966	-	-	-	-	-	2^9
1965	-	-	-	-	-	1^9
1964	-	-	-	-	-	2^9
1963	-	-	-	-	-	3^9
1962	-	-	-	-	-	1^9
1961	-	-	-	-	-	2^9
1960	-	-	-	-	-	2^9
1959	-	-	-	-	-	-
1958	-	-	-	-	-	-
1957	-	-	-	-	-	-
1956	-	-	-	-	-	-
1955	-	-	-	-	-	-
1954	-	-	-	-	-	-
1953	-	-	-	-	-	-
1952	-	-	-	-	-	-
1951	-	-	-	-	-	-
1950	-	-	-	-	-	2^9

Year	East Taimyr	Lena Delta	East-Siberian plain	Chukotka	Alaska	Taimyr Peninsula
1949	-	-	-	-	-	3[9]
1948	-	-	-	-	-	0[9]
1947	-	-	-	-	-	3[9]

[1] Pozdnyakov 2004; [2] Chernyavsky and Lazutkin 1999; [3] Koroleva 2002; [4] Chernyavsky and Lazutkin 2004; [5] Volpert and Shardina 2002; [6] Kuryshev and Dorogoi 1989; [7] Dorogoi 1988; [8] Fischer et al. 2010; [9] Blomqvist et al. 2002; [10] Arctic Birds Breeding Conditions Survey (ABBCS); [11] Vladimir Pozdnyakov (pers. comm).
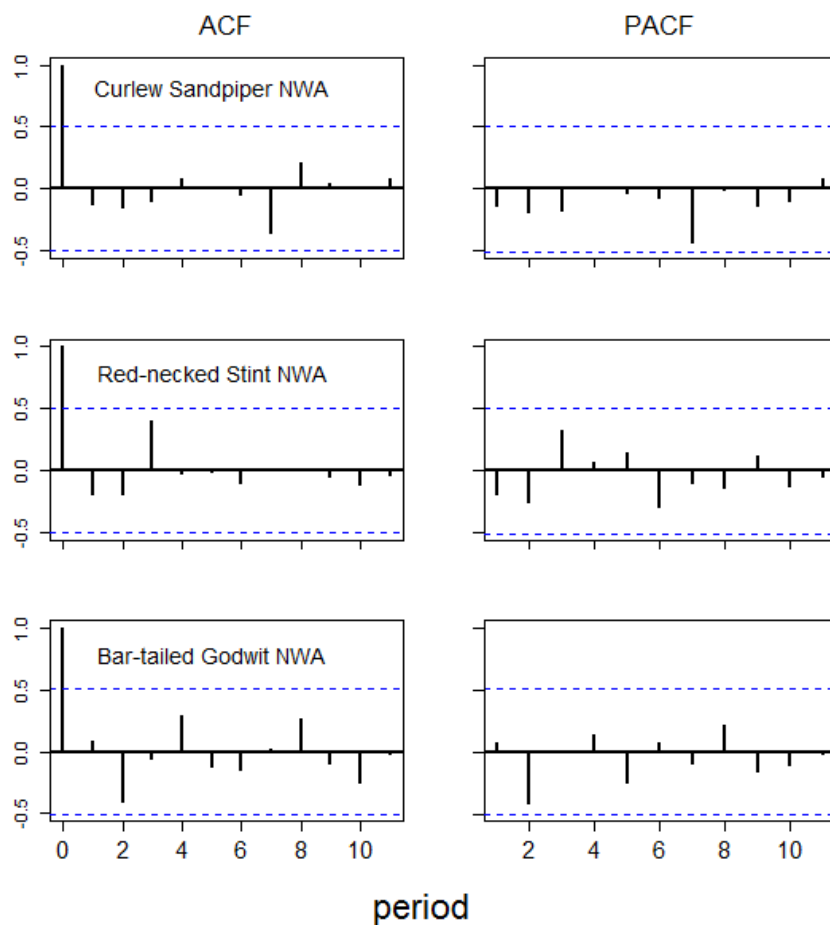
Appendix 2

Autocorrelation function (ACF, the correlation between a variable and itself in two different time points) and partial autocorrelation function (PACF, the correlation between a variable and itself in two different time points, once correlation between all successive lags are controlled) for annual juvenile percentages of waders from the East Asian–Australasian Flyway (EAAF). ACF (left panels) and PACF (right panels) between juvenile percentages for species from South East Australia (SEA) (species names depicted in panels) are plotted against time lag (years; a time lag of 0 years yielding a correlation coefficient of 1). Dashed lines indicate the confidence limit, values above these lines are significant ($p < 0.05\%$).
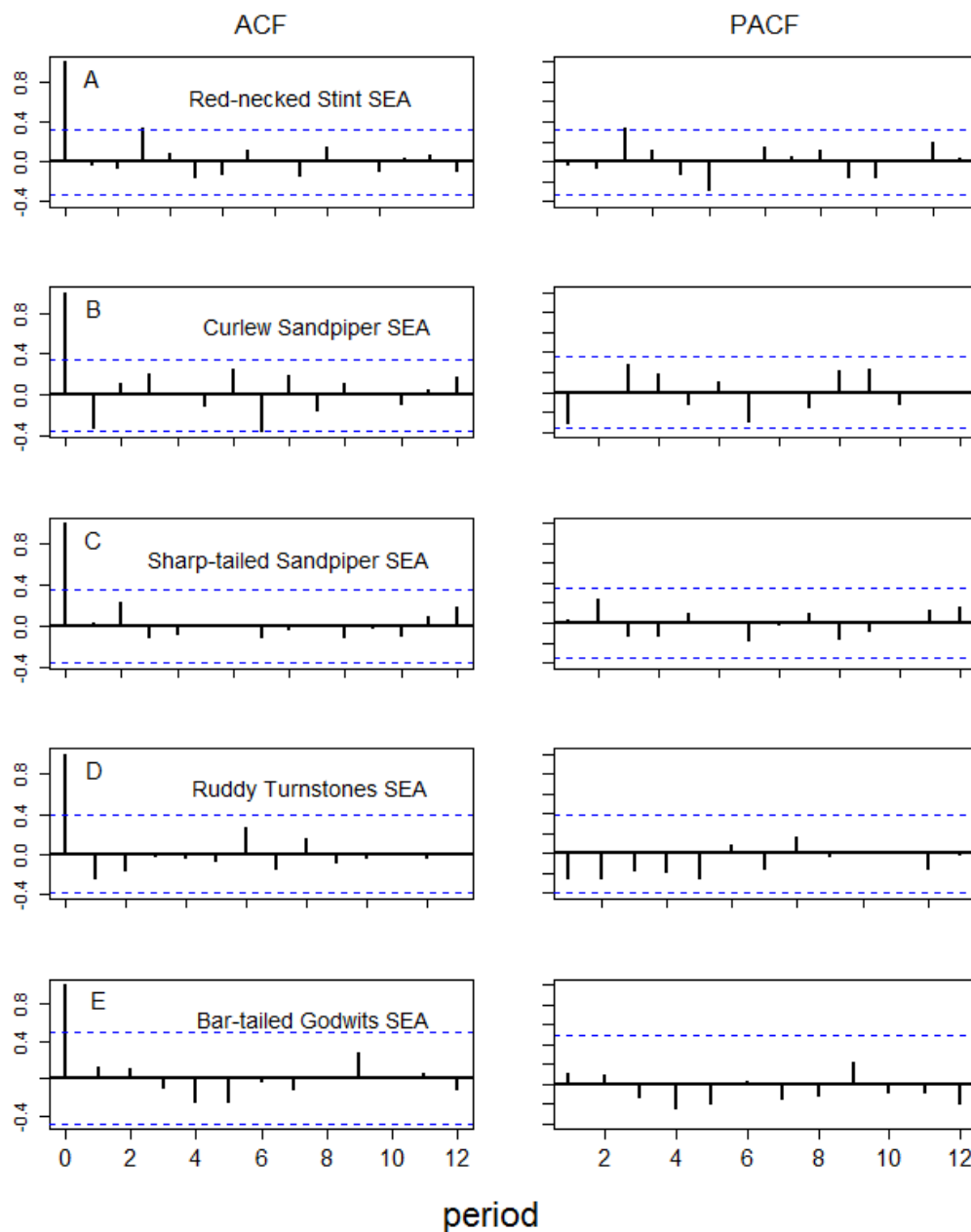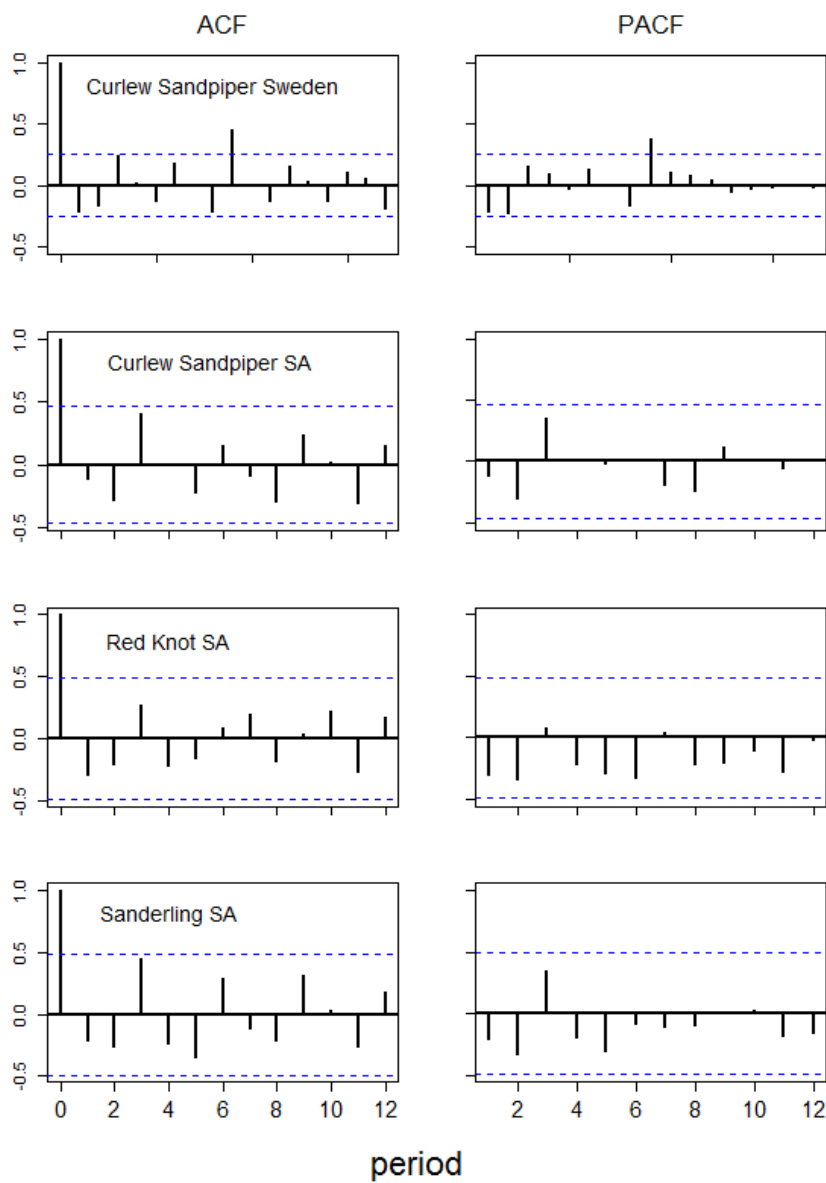
Appendix 3

Autocorrelation function (ACF, the correlation between a variable and itself in two different time points) and partial autocorrelation function (PACF, the correlation between a variable and itself in two different time points once correlation between all successive lags are controlled) for annual juvenile percentages of waders from the East Asian–Australasian Flyway (EAAF). ACF (left panels) and PACF (right panels) between juvenile percentages for species from north Western Australia (NWA) (species names depicted in panels) are plotted against time lag (years; a time lag of 0 years yielding a correlation coefficient of 1). Dashed lines indicate the confidence limit, values above these lines are significant ($p < 0.05\%$).
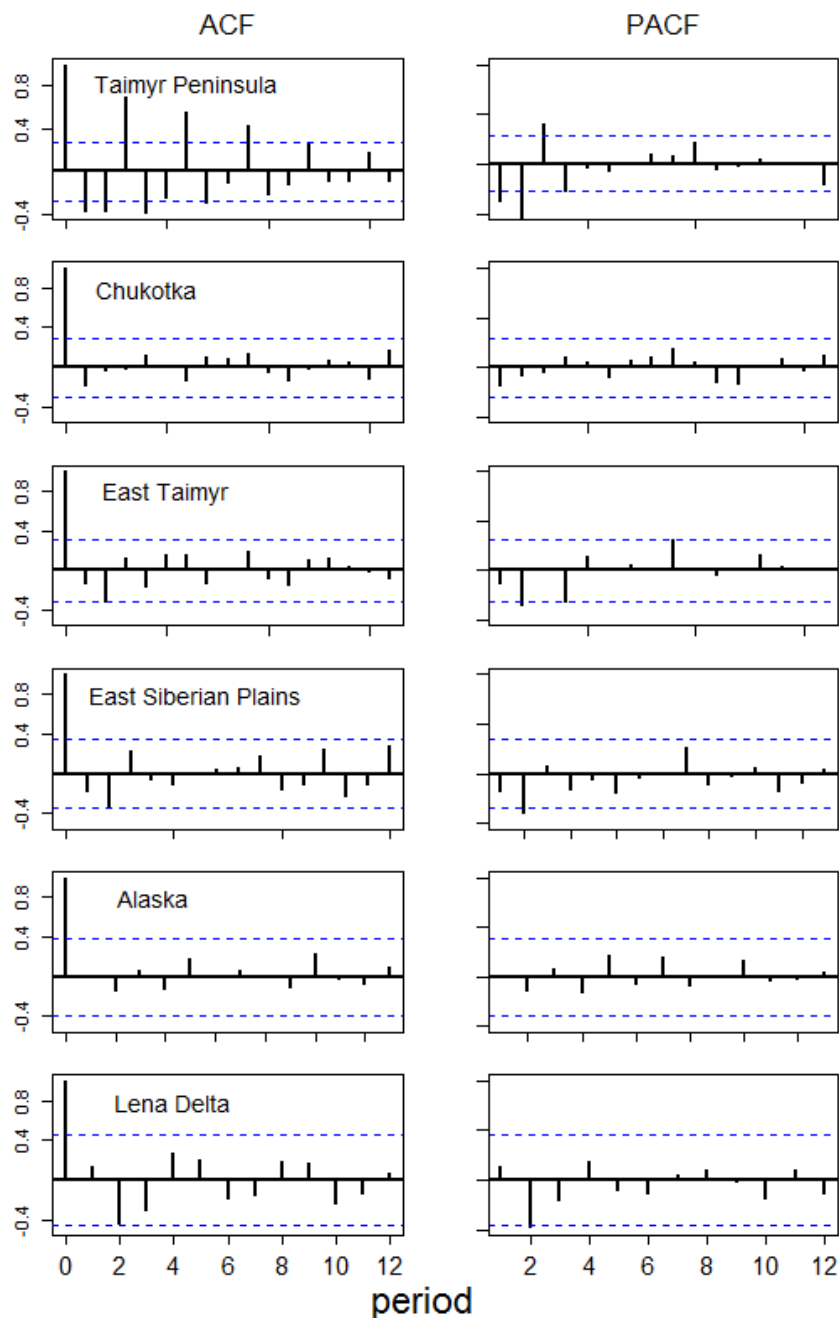
Appendix 4

Autocorrelation function (ACF, the correlation between a variable and itself in two different time points) and partial autocorrelation function (PACF, the correlation between a variable and itself in two different time points once correlation between all successive lags are controlled) for annual juvenile percentages of waders from the East Atlantic Flyway (EAF). ACF (left panels) and PACF (right panels) between juvenile percentages for species from Sweden and South Africa (SA) (species names depicted in panels) are plotted against time lag (years; a time lag of 0 years yielding a correlation coefficient of 1). Dashed lines indicate the confidence limit, values above these lines are significant ($p < 0.05\%$).

Appendix 5

Autocorrelation function (ACF, the correlation between a variable and itself in two different time points) and partial autocorrelation function (PACF, the correlation between a variable and itself in two different time points once correlation between all successive lags are controlled) for lemming abundance index in six breeding areas in the Alaskan–Siberian Arctic. ACF (left panels) and PACF (right panels) between lemming abundance for areas depicted in panels are plotted against time lag (years; a time lag of 0 years yielding a correlation coefficient of 1). Dashed lines indicate the confidence limit, values above these lines are significant (p < 0.05%).

Appendix 6

Correlation matrix for juvenile percentages of the East-Asian–Australasian Flyway.

(A) Spearman rank correlation matrix for juvenile percentages of species from south east Australia (SEA). Significant correlation after Bonferroni correction for multiple comparisons was found only between ruddy turnstone and curlew sandpiper (r = 0.78, p < 0.001).
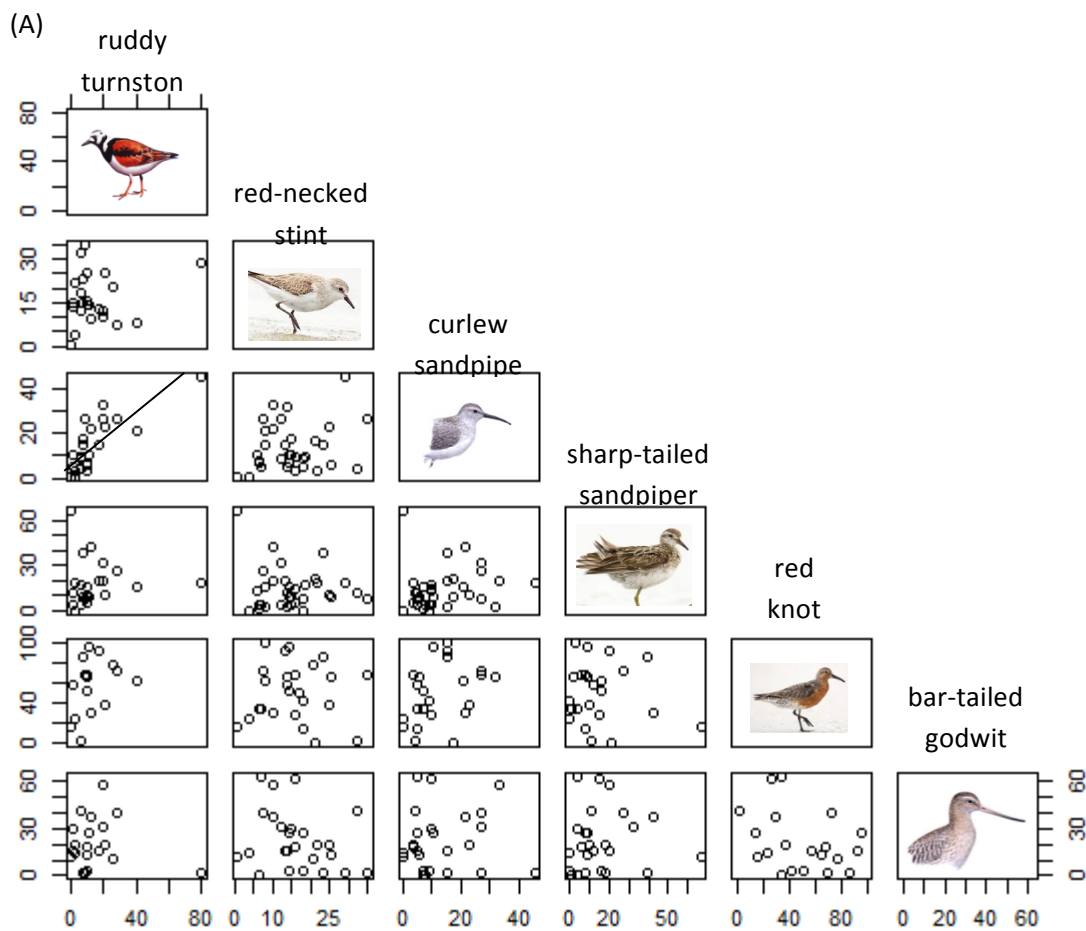
(B) Spearman rank correlation matrix for juvenile percentages of species from north Western Australia (NWA). None of the results were significant after Bonferroni correction for multiple comparisons.

(B) red-necked stint, curlew sandpipe, bar-tailed godwit