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Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird

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Ecological mismatches between reproductive events and seasonal resource peaks are frequently proposed to be a key driver of population dynamics resulting from global climate change. Many local populations are experiencing reduced reproductive success as a consequence of mismatches, but few mismatches have led to species-level population declines. To better understand this apparent paradox, we investigated the breeding phenology and chick survival of two disjunct populations of Hudsonian godwits *Limosa haemastica* breeding at Churchill, Manitoba and Beluga River, Alaska. Only one population experienced a mismatch: godwits bred nearly one week after the onset of the invertebrate peak at Churchill because of asynchronous climatic change occurring throughout their annual cycle. However, chicks were not uniformly affected by the mismatch — growth rates and survival of young chicks were not correlated with invertebrate abundance, but older chicks tended to suffer lower survival rates on days of low invertebrate abundance. Ecological mismatches thus resulted in a complex array of consequences, but nonetheless contributed to reductions in chick survival. In contrast, godwits at Beluga River hatched their chicks just before the invertebrate peak, such that the period of highest energetic need coincided with the period of highest invertebrate abundance. As a result, growth rates and survival of godwit chicks were unaffected by invertebrate abundance. Godwits at Beluga River were able to properly time their reproduction because of predictable rates of climatic change and strong selection imposed by high predation on late-hatched chicks. Taken together, our results suggest that population-specific, local-scale selection pressures play a critical role in determining the degree and severity of ecological mismatches. The potential for global climate change to induce species-level population declines may therefore be mediated by the spatial variation in the selection pressures acting across a species' range.

Ecological mismatches are commonly cited as a consequence of global climate change (Dunn and Winkler 2010, Ovaskainen et al. 2013). Mismatches occur when a population's reproductive events are mistimed relative to the peak availability of food resources, causing young to be raised under low resource availability (Durant et al. 2007). Mismatches are proposed to be strong drivers of population dynamics and are an emerging issue of conservation concern (Møller et al. 2008, Jones and Cresswell 2010). However, empirical evidence for mismatches leading to population declines is limited, and a recent meta-analysis found that the population dynamics of most mismatched species have not been detrimentally affected (Dunn and Møller 2014). The discrepancy between theory and empirical results highlights the need to identify the environmental factors causing mismatches and understand the potential effects of mismatches on both local- and large-scale population dynamics.

Part of the difficulty in identifying the causes and consequences of climate-induced mismatches lies in determining how synchronous a population and its food resources should be. The timing of reproductive events is

intricately linked with reproductive decisions being made by other species across multiple trophic levels within a community (Both et al. 2009). Thus, an array of environmental conditions that may be unrelated to climate change or the phenology of food resources for a species' offspring can determine the optimal timing of reproduction. For instance, food resources for adults during the pre-breeding period can limit when animals are capable of reproducing (Högestedt 1974). Predators are also known to play a strong role in structuring species' reproductive decisions, from the timing of reproduction, to provisioning rates, and the duration of development (Martin 2015). The optimal timing of reproduction can therefore fluctuate across years depending on the interplay among competing environmental and ecological factors (Drent and Daan 1980).

Ultimately, local conditions may be the most powerful determinants of ecological mismatches (Revilla et al. 2014). If so, it may be difficult to extrapolate the consequences of local-scale mismatches to project their effects on larger-scale population dynamics (Hodgson et al. 2011). The role of local conditions in causing mismatches could thus help explain the apparent discrepancy between the large number

of species experiencing mismatches and the relatively small number of cases where population declines have resulted from these mismatches (Dunn and Winkler 2010, Dunn and Møller 2014). However, past field studies have primarily focused on mismatches at a local scale — comprising at most a few tens of kilometres (Both et al. 2009) — with little information about the extent to which mismatches are occurring across a species' range.

The breeding season is also only one component of a species' annual cycle, and may play a limited role in regulating its population size. For instance, population dynamics of migratory Icelandic black-tailed godwits *Limosa limosa islandica* are driven by density-dependent processes operating during both the breeding and non-breeding seasons (Gill et al. 2001). In other cases, events occurring outside the breeding season have even been shown to obscure the consequences of variation in reproductive success (Reed et al. 2013a). It is therefore also necessary to put a species' reproductive timing within the context of other selection pressures acting throughout its life cycle (Rakhimberdiev et al. 2015).

To gain a better understanding of the causes and consequences of ecological mismatches, we conducted a three-year study of two disjunct breeding populations of a long-distance migratory shorebird, the Hudsonian godwit *L. haemastica* (hereafter, 'godwits'). Our goals were to 1) determine whether factors leading to ecological mismatches are common across a species' range or unique to specific regions, and 2) place a population's reproductive timing within the context of its annual cycle by coupling data on reproductive timing with measurements of individual- and population-level variation in migratory timing. Godwits exhibit a suite of traits that are hypothesized to be risk factors for vulnerability to ecological mismatches (Both et al. 2010): individual birds migrate extremely long distances, nest in highly seasonal Arctic and Boreal wetlands, lay a single, four-egg clutch each year, and have high annual adult survival with long generation times that may limit their ability to adapt to mismatches evolutionarily (Walker et al. 2011, Senner et al. 2014). Historical data have provided evidence for divergent trends in first arrival dates for our two study populations over the past four decades (Senner 2012), and dramatic climatic changes throughout the ranges of both populations are projected to accelerate in the coming century (IPCC 2014). Godwits thus offer a valuable study system that may provide insights into the causes and consequences of ecological mismatches.

To obtain a mechanistic understanding of ecological mismatches, we connected individual-level physiological processes with population-level changes in annual-cycle timing. To do this, we first measured the effects of weather conditions and invertebrate phenology on the growth and survival of chicks. Then we related inter-annual variation in local invertebrate phenology with historical climatic trends, godwit first arrival dates and reproductive timing. Based on long-term trends in first arrival dates at the breeding grounds (Senner 2012), we predicted that only the Churchill population would be exposed to an ecological mismatch, with low invertebrate abundance limiting chick growth and survival, and generating strong selection for earlier breeding. Our field study is one of the first attempts

to combine such individual- and population-level measures for two disjunct migratory bird populations and will help to identify those populations most vulnerable to ecological mismatches.

Methods

Study species

We studied godwits within two of their three disjunct breeding populations — the southcentral Alaska population at Beluga River, Alaska (61°21'N, 151°03'W) and the western Hudson Bay population at Churchill, Manitoba (58°93'N, 93°80'W; Walker et al. 2011). The two populations share similar migratory routes, but differ in the location of their nonbreeding sites, as well as migratory timing and breeding phenology (Senner 2012). Despite differences in range and phenology, reproductive effort is similar in both populations: females initiate nests within 5–7 days of arrival and lay a single clutch of four eggs, both parents jointly incubate the eggs for 22–23 days, and both parents attend to the nidifugous young for about three weeks. A replacement clutch may be laid if the first clutch is depredated early in incubation, but only a single brood is produced per season (Senner et al. 2014).

The two populations of godwits have also been exposed to different climate change regimes in recent decades. Southcentral Alaska has warmed steadily year-round, leading to an increase of +3°C in mean annual temperatures since 1950 (Serreze et al. 2000). Climate change in western Hudson Bay is more complicated; a slow warming trend persisted through the late 1990s (Hinzman et al. 2005), followed by a dramatic increase in warming in the 2000s (Kaufman et al. 2009). Despite an overall trend for climatic warming, temperatures in some months are currently cooling (Gagnon and Gough 2005). The climate change regimes experienced by the two populations differ along their migration routes as well. Alaskan godwits migrate northward through mid-continental North America during April, and have experienced consistent warming regimes along their entire migration path. Hudson Bay godwits migrate along the same route a month later, but encounter stable or cooling climatic regimes. This combination of factors has caused the two populations to diverge in their migratory phenologies: godwits now arrive nearly nine days earlier in southcentral Alaska, but almost 11 days later in western Hudson Bay than they did four decades ago (Senner 2012).

Field methods

We simultaneously monitored the breeding ecology of godwits at Beluga River and Churchill for the three-year period from 2009–2011. The two sites are close to the geographic centres of each population's breeding range. Our study sites were 8 km² at Beluga River and 15 km² at Churchill, and both supported large breeding populations of godwits, with densities of 5.0 and 2.3 breeding pairs per square kilometre, respectively (Senner unpubl.). Both sites were dominated by sedges *Carex* sp. and dwarf birch

Betula nana, but were otherwise ecologically dissimilar: the Churchill site is located within a large, open fen, while the Beluga River site is situated in a muskeg bog (Swift 2016).

We surveyed breeding godwits from adult arrival in spring until southward departure at the end of the breeding season. We located as many nests as possible and monitored each nest every 2–3 days until it hatched or failed. At hatch, we captured nestlings by hand at the nest and marked each bird with a unique alpha-numeric flag and a USGS or CWS metal band on the tibiotarsus. Some nests were not found before hatch, but chicks were captured opportunistically from mobile broods; estimated hatching dates for chicks caught off nest were calculated by comparing their body mass to standardized growth curves for known age young.

We randomly selected one chick per brood for telemetry monitoring with a 0.62 g Holohil or 0.65 g ATS radio transmitter. We clipped the downy feathers from a small area of the back and attached radios above the uropygial gland with cyanoacrylate glue. We located radio-marked chicks every 2–3 days until the chick had died or fledged. To monitor chick growth, we recaptured chicks once per week throughout the brood-rearing period. Weekly captures are adequate for accurate assessment of growth rates, but minimize the potential for adverse handling effects (Sharpe et al. 2009). Chicks undetected after three consecutive days were considered dead. We considered a chick to have successfully fledged if it survived to an age of 21 days; godwits usually fledge at 28 days, but 21 days was the average lifespan of our radios (range = 17–30 days) and the age when most adult godwits start to abandon their broods (Walker et al. 2011, Senner unpubl.).

Weather variables

We tested daily measures of minimum temperature, precipitation, and wind speed as correlates of intra- and inter-annual variation in growth and survival of godwit chicks given their likely effects on chick thermoregulation and invertebrate availability (Schekkerman et al. 2003). Daily weather records were taken from the closest weather stations – Anchorage, Alaska (50 km from the Beluga River field site) and Churchill, Manitoba (26 km from the Churchill field site) – and accessed through NOAA's Climate Data Online webpage. The weather station data were an index of the ambient conditions experienced by godwits at our field sites, but there is little topographic variation in the two regions, and we expected climatic conditions to be similar between our field sites and the weather stations. The same weather stations also provided the historical climate data for the 35-year period from 1974–2008 that we used to hindcast long-term changes in the timing of peak invertebrate abundance prior to the initiation of our study.

Resource phenology and abundance

To assess invertebrate phenology, we randomly selected two representative godwit territories and measured invertebrate biomass along 100-m transects deployed on each territory. Each transect consisted of five pitfall traps cleared each morning at 07:30 am from 2 May – 10 July at Beluga and

26 May – 16 Aug at Churchill (70 and 83 days, respectively). Pitfall traps were 10 cm wide, 15 cm deep, and filled with 4 cm of 75% ethanol to ensure that invertebrates were both trapped and preserved. Pitfall traps may underestimate the abundance of some classes of invertebrates, but have been successfully used in other studies of Arctic-breeding shorebirds (Schekkerman et al. 2003, Meltotte et al. 2007). We compared the results from our daily traps with samples collected from a more extensive network of five, 1000-m transects comprised of 11 traps each that were spread across both study areas and cleared weekly. Invertebrate phenology was statistically similar across both sets of transects within a site and we thus only present results from traps checked daily (Supplementary material Appendix 1 Table A1). After collection, invertebrates were identified to (sub)Order and their body length measured to the nearest 0.5 mm. Dry mass of invertebrates was calculated using published estimates of taxa-specific length–mass relationships (Rogers et al. 1977, Ganihar 1997). Godwit young are gape-limited, so we restricted our analyses to size-classes of invertebrates that could potentially be consumed by chicks (length: 2–9 mm; Schekkerman and Boele 2009).

Statistical analyses

Growth and condition analysis

To develop a mechanistic understanding of godwit reproductive performance, we examined how environmental covariates affected chick growth and survival. First, we created site-specific growth curves using the 'nlme' function in the package 'nlme' (Pinheiro et al. 2015) and a logistic growth equation in program R (ver. 3.0.1, <www.r-project.org>). The logistic growth function calculates age-specific mass (W_t) by:

$$W_t = A / (1 + \exp(-K(t - i)))$$

where A = asymptotic body mass of adults, K = the logistic growth coefficient, t = age in days, and i = the inflection point for maximal growth ($0.5A$ in the logistic function). To reduce the number of estimable parameters, we opted to fix A at the mean body mass for adult godwits at each site (Austin et al. 2011). Female godwits are slightly larger than males (Walker et al. 2011), but the sexes of godwit young are indistinguishable at hatch and we set the asymptotic body mass as the mean mass of adults from each population, based on a sample with equal numbers of males and females (Beluga: 249 g, $n = 72$; Churchill: 239 g, $n = 62$).

Second, we calculated a body-condition index (BCI) for each individual at each recapture by dividing the observed increase in body mass since last capture by the expected gain in mass based on our site-specific growth curves (Schekkerman et al. 2003). To test the factors most strongly affecting a chick's BCI, we first determined the appropriate timescale over which to relate environmental conditions to chick body condition using linear models in the R-package 'lme4' (Bates et al. 2014). We tested models that included a suite of environmental covariates – minimum temperature, wind speed, precipitation, and invertebrate biomass – averaged over the period since an individual's previous capture (6–7 days), three days prior to the recapture, two days prior, and

the day of the recapture as predictor variables. We also tested models with individual and year as random effects, but the models performed better without random effects (Supplementary material Appendix 1 Table A4). Then, using the time period with the best explanatory power, we tested which of the environmental covariates included in that time period's global model best explained chick body condition. We also included hatching date and nesting attempt (first nest versus re-nest) as predictor variables. However, due to collinearity, both variables could not be included in the same model. We therefore tested each factor separately as predictor variables and included the factor with the strongest relationship with the dependent variable in the final candidate model set. All other variables were not significantly collinear. After standardizing our predictor variables (Gelman 2008), we developed our set of candidate models by testing among all possible combinations of our predictor variables. In this and all subsequent analyses, we performed model selection using Akaike's information criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2001). If no single model had a model weight (w_i) > 0.90 , we identified the most important predictor variables through model averaging using the package 'MuMIn' (Barton 2015). Variables with coefficients whose 95% confidence intervals did not include zero were considered biologically relevant (Grueber et al. 2011).

Survival analysis

We used a two-step analysis to identify factors affecting survival of nests and chicks. In the first step, we estimated temporal and age-related trends in the daily survival rate (s) of **nests and chicks separately** with the 'nest survival' procedure for ragged telemetry data in PROGRAM Mark (ver. 5.1; White and Burnham 1999, Mong and Sandercock 2007). We selected candidate models to explain trends in s by testing all possible combinations (and interactions) between year, chick age, hatching date or nesting attempt, and four temporal models – linear, quadratic, time-dependent and constant. Seasonal probability of survival was calculated from daily survival rates for a 23-day incubation period for the nests and a 21-day pre-fledging period for chicks; variance of extrapolated estimates was calculated with the delta method (Powell 2007). We were unable to use model selection to directly compare survival rates between sites due to differences in the timing and duration of the breeding season. We thus opted to test for site differences in chick survival with post hoc tests in PROGRAM Contrast (Sauer and Williams 1989).

In the second step of our survival analysis, we assessed the potential effects of daily weather and body condition on chick survival. To include temporally varying individual covariates, we employed Andersen–Gill models (a type of proportional hazards model; Therneau and Grambsch 2000) in the R-package 'survival' (Therneau and Lumley 2015), which estimate the instantaneous risk that an individual will die during consecutive time intervals. Andersen–Gill models can accommodate time-varying individual covariates, as well as both left-censored data, due to individuals entering the study at separate times, and right-censored data, due to individuals with unknown fates or gaps in their resighting history, making them suitable for known fate data from field studies using radio telemetry (Johnson et al. 2004).

Godwit young leave the nest within 24 h of hatch, but are unable to fully thermoregulate until ~5–6 days of age (Visser and Ricklefs 1993). It is therefore possible that the same environmental conditions on a given day could present different mortality risk for chicks of different ages. Accordingly, age appeared in a number of our top models for both sites in PROGRAM Mark (Supplementary material Appendix 1 Table A6). Therefore, in the second step of our survival analysis, we separately tested for those factors affecting mortality risk for young chicks that required brooding by parents (≤ 6 days) versus older chicks capable of homeothermy (> 6 days). Our monitoring of chicks was conducted every 2–3 days, and thus we assessed the mortality risk for all individuals during consecutive 3-day intervals, from hatch until the age of 6 days for young chicks, and from 6–21 days for old chicks. We related an individual's mortality risk to its BCI during each 3-day period, as well as the average environmental conditions – minimum temperature, wind speed, precipitation, and invertebrate biomass – it experienced during those three days; we also included an individual's hatching date or nesting attempt as a predictor variable.

Estimates of energy expenditure

Following the results of our survival analyses, we conducted a post hoc analysis of variation in chick energetic requirements throughout the brood-rearing period. We estimated maintenance metabolic rates based on environmental conditions after Cartar and Morrison (1997: Eq. 2):

$$MMR_t = C_{est} \times (T_b - T_{es})$$

where MMR_t = maintenance metabolic rate in watts (W) at age t ; C_{est} = thermal conductance at age t ; T_b = body temperature; and T_{es} = ambient operative temperature accounting for wind speed. We determined age-specific values of C_{est} for godwit chicks using our site-specific growth curves (Williams et al. 2007). We then calculated MMR_t using ambient conditions for each day of the brood-rearing period in our study (Beluga: 31 May – 10 Jul; Churchill: 30 Jun – 3 Aug) and tested for differences in MMR_t between the two study sites using a linear regression with site as the predictor variable. Similarly, we employed our growth curves to calculate godwit chick resting metabolic rates at time t (RMR_t ; Williams et al. 2007). To assess the energetic requirements imposed by environmental conditions, we subtracted RMR_t from the average estimates of MMR_t from each study site and converted the difference from W to kJ. Assuming the average energy density of arthropod prey to be 23 kJ g⁻¹ dry mass (Robel et al. 1995), we then estimated how many additional invertebrates a chick would have to consume to meet these higher energetic requirements using the average dry mass of insects collected during our study. Last, using age-specific foraging rates of black-tailed godwit chicks as a proxy (Schekkerman and Boele 2009), we determined how many minutes a godwit chick would have to spend foraging to capture the additional quantity of invertebrates. Chicks feeding on invertebrates can have reduced digestive efficiency compared to other diets (Albano et al. 2011), but the low foraging efficiency and relatively short foraging bouts

of precocial shorebird chicks in Arctic/Boreal environments likely minimize the potential for physiological bottlenecks to bias our estimates (Krijgsveld et al. 2003, Budden and Wright 2008).

Hindcasting of ecological mismatches

Last, we tested whether ecological mismatches occurred within our study areas, both during our study and historically. At both of our field sites, nest initiation dates were highly synchronous and all first nests were laid within a 7-day period. Thus, to identify current mismatches, we used linear models to compare daily invertebrate abundance during the 28-day period – the typical period required by a godwit chick to mature until fledging (Walker et al. 2011) – following the hatch of the first godwit nest with daily invertebrate abundance during the 28-day period with the highest average daily invertebrate abundance. To identify historical mismatches, we used generalized linear models with the ‘glm’ function and a quasi-Poisson distribution to determine which climatic variables best predicted observed daily invertebrate biomass: average minimum, maximum and mean temperature; mean wind speed; total precipitation; dew point; mean air pressure; and degree days summed since 1 Jan. We used the resulting regression equations and historical climatic conditions to hindcast seasonal predicted peaks in invertebrate abundance at both sites over the past four decades (Tulp and Schekkerman 2008).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.d4m77>> (Senner et al. 2016).

Results

Nest survival

In our three-year study of two breeding populations of Hudsonian godwits, we located and monitored the fate of 57 nests at Churchill, Manitoba and 70 nests at Beluga River, Alaska. In all cases, failed nests were lost to predation events, and not abandonment. Seasonal patterns in nest survival at both sites were best explained by an interaction between year and a quadratic function (Supplementary material Appendix 1 Table A2), where daily nest survival was highest at the start and end of the nesting season (Fig. 1). At Churchill, the projected probability of nest survival for a 23-day exposure period averaged less than 0.20 (0.173 ± 0.146 , $n = 3$ years), while the probability of nest survival averaged higher than 0.60 at Beluga River (0.640 ± 0.285 , $n = 3$ years; Table 1).

Chick growth

We attached radio transmitters to 59 chicks at Beluga River and 33 chicks at Churchill. Growth rates of godwit young differed among years at both sites (Fig. 2; Supplementary material Appendix 1 Table A3). Logistic growth coefficients tended to be higher at Churchill ($K = 0.13 \pm 6.84 \times 10^{-7}$) than Beluga River ($K = 0.12 \pm 2.5 \times 10^{-3}$), but were not significantly different (ANOVA, $F_{1,4} = 0.11$, $p = 0.75$).

Growth rates of godwit young were affected by different environmental conditions at each site. At Beluga River, chick growth was best explained by environmental conditions averaged over the period since the previous capture ($w_i = 0.58$; Supplementary material Appendix 1 Table A4), with the minimum AIC_c model including the effects of

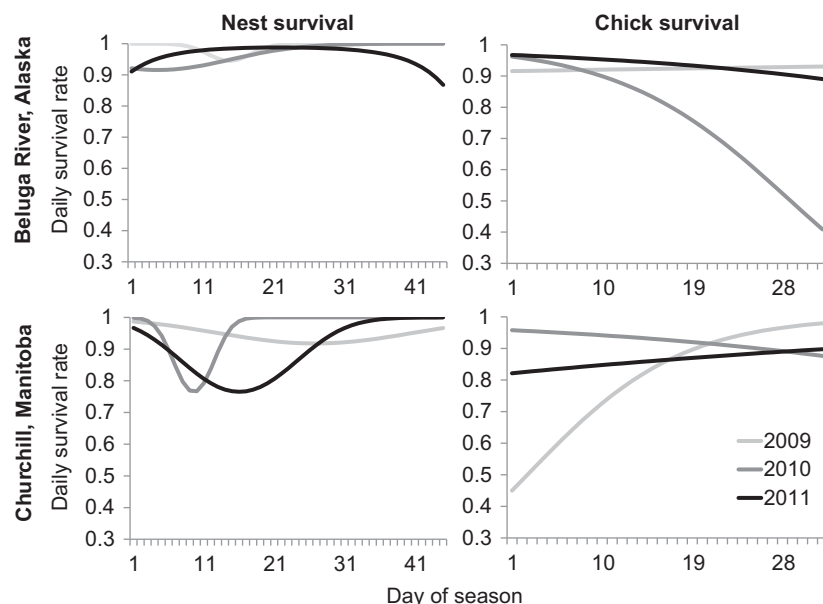


Figure 1. Seasonal variation in daily survival rates of Hudsonian godwit nests and chicks hatched at Beluga River, Alaska and Churchill, Manitoba, 2009–2011. For nests, daily survival rates (s) were taken from a model where seasonal trends were modelled as a quadratic function of day of season in each year (year \times quad), whereas for chicks, s was modelled as a linear function of day of season in each year (year \times lin). For nests, Day 1 was 5 May for Beluga River and 7 June for Churchill; for chicks, Day 1 was 31 May for Beluga River and 1 July for Churchill.

Table 1. Probability of survival for nests and chicks of Hudsonian godwits breeding at Churchill, Manitoba and Beluga River, Alaska, 2009–2011. Survival rates were estimated using constant survival models.

Site	Year	Estimate	SE	n
Probability of nest survival (23 days)				
Churchill	2009	0.17	0.14	15
	2010	0.32	0.29	26
	2011	0.04	0.02	16
	Pooled	0.17	0.15	57
Beluga River	2009	0.71	0.27	23
	2010	0.56	0.29	22
	2011	0.65	0.27	25
	Pooled	0.64	0.29	70
Probability of chick survival (21 days)				
Churchill	2009	0.06	0.03	6
	2010	0.23	0.13	16
	2011	0.04	0.01	11
	Pooled	0.13	0.07	33
Beluga River	2009	0.18	0.11	17
	2010	0.03	0.01	18
	2011	0.27	0.16	24
	Pooled	0.15	0.09	59

nesting attempt and minimum temperature ($w_i = 0.09$; Supplementary material Appendix 1 Table A5). However, model averaging failed to identify any biologically relevant variables (Supplementary material Appendix 1 Table A6). For Churchill, conditions on the day of recapture best explained a chick's body condition ($w_i = 0.64$; Supplementary material

Appendix 1 Table A4), and the minimum AIC_c model contained hatching date, minimum temperature, and precipitation as biologically relevant covariates ($w_i = 0.44$; Supplementary material Appendix 1 Table A5). Hatching date ($\beta = -0.26$, $SE = 0.12$, $CI = -0.55$, -0.05) and precipitation ($\beta = -0.06$, $SE = 0.03$, $CI = -0.12$, -0.01) had negative effects on chick growth, whereas minimum temperature had a positive effect ($\beta = 0.03$, $SE = 0.03$, $CI = 0.003$, 0.08 ; Supplementary material Appendix 1 Table A6). Chicks hatched on the last day of the hatching period (day 18) had a $> 30\%$ reduction in growth rates compared to those hatched on the day 1.

Chick survival

At Churchill, 41.3% of chick deaths ($n = 27$) were attributed to apparent starvation or hypothermia, compared to 13.0% of chick deaths at Beluga River ($n = 46$). All other mortality of godwit chicks prior to fledging was due to predation. At Beluga River, chick survival differed between nesting attempts and among years ($w_i = 0.35$; Supplementary material Appendix 1 Table A7). Survival of chicks from first nesting attempts was moderate to high (0.29 ± 0.17 across all years), whereas survival of chicks hatched from re-nests was close to zero (0.01 ± 0.001 across all years). Seasonal mortality patterns were different at Churchill: there was no single best model of chick survival (Supplementary material Appendix 1 Table A7), and survival of chicks was similar between nesting attempts (Table 2). Overall chick survival did not

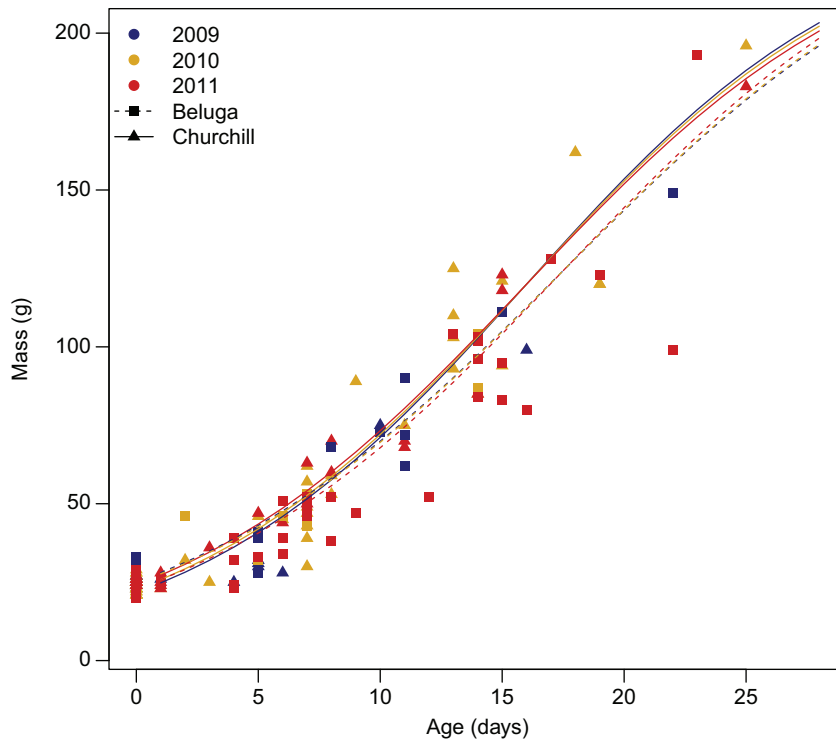


Figure 2. Annual growth curves for Hudsonian godwit chicks hatched at Churchill, Manitoba and Beluga River, Alaska, 2009–2011. Circles and solid lines are for Churchill chicks, triangles and dashed lines for Beluga River chicks (2009 = blue, 2010 = yellow, and 2011 = red). Growth curves were fit using the logistic growth function, where asymptotic mass of adults was fixed as a site-specific mass, and year was included as a random variable. We monitored survival of radio-marked chicks until 21 days and fledging occurred at 28 days.

Table 2. Model-averaged coefficients for factors affecting the mortality risk of young (≤ 6 days) and old chicks (> 6 days) of Hudsonian godwits hatched at Beluga River, Alaska and Churchill, Manitoba, 2009–2011. Mortality risk was assessed over consecutive 3-day periods using Andersen–Gill models and modeled separately for each field site.

Variable	β	SE	95% CI
Beluga River – young chicks			
Renest	0.91	0.48	0.13, 1.83
Invertebrates	–0.42	0.66	–2.30, 0.46
Wind speed	–0.41	0.50	–1.62, 0.19
Body condition index	0.00	0.41	–2.00, 2.07
Minimum temperature	–0.02	0.26	–1.35, 1.14
Precipitation	0.03	0.41	–0.66, 0.94
Beluga River — old chicks			
Renest	1.90	0.81	0.46, 3.43
Invertebrates	–0.03	0.29	–1.36, 1.04
Wind speed	–0.11	0.37	–1.66, 0.85
Body condition index	–0.35	0.52	–1.81, 0.33
Minimum temperature	–0.04	0.31	–1.47, 1.07
Precipitation	0.18	0.39	–0.47, 1.58
Churchill — young chicks			
Hatching date	–0.01	0.37	–1.72, 1.67
Invertebrates	0.88	1.01	–0.24, 3.26
Wind speed	0.24	0.59	–0.81, 2.44
Body condition index	1.05	1.57	–1.03, 5.38
Minimum temperature	–1.72	1.08	–3.80, –0.05
Precipitation	0.11	0.37	–0.53, 1.39
Churchill — old chicks			
Hatching date	–0.33	–0.69	–2.69, 0.72
Invertebrates	–1.23	1.76	–5.99, 0.90
Wind speed	1.33	1.04	–0.05, 3.44
Body condition index	–0.83	0.82	–2.62, 0.13
Minimum temperature	–0.67	1.00	–3.49, 0.56
Precipitation	1.62	1.77	–0.87, 5.81

differ significantly between sites (post hoc test, $\chi^2 = 0.03$, $DF = 1$, $p = 0.86$; Fig. 1; Table 1), but chicks from first nests at Beluga River had survival rates $2.4 \times$ higher than chicks from first nests at Churchill (0.29 ± 0.17 versus 0.12 ± 0.07 ; post hoc test, $\chi^2 = 4.39$, $DF = 1$, $p = 0.04$).

The Andersen–Gill models corroborated results from the known fate models for Beluga River and identified nesting attempt as the most important factor affecting chick

mortality. Models comparing the mortality risk of both young (≤ 6 days) and old (> 6 days) chicks were qualitatively similar and nesting attempt was the only biologically relevant variable in both model sets (Young: $\beta = 1.24$, $SE = 0.44$, $CI = 0.29, 2.19$; Old: $\beta = 1.90$, $SE = 0.68$, $CI = 0.46, 3.43$; Table 2, Supplementary material Appendix 1 Table A8). For Churchill, the factors affecting mortality risk differed between age classes. For young chicks, the lowest AIC_c model included the variables for mean invertebrate biomass and minimum temperature ($w_i = 0.11$; Supplementary material Appendix 1 Table A8), although only minimum temperature was biologically relevant ($\beta = -2.06$, $SE = 0.11$, $CI = -3.93, -0.27$; Table 2). For older chicks, the minimum AIC_c model included BCI, mean invertebrate biomass, minimum temperature, wind speed, and precipitation ($w_i = 0.09$; Supplementary material Appendix 1 Table A8). Invertebrate biomass was included in four of the top five models and was ~ 25 mg lower per transect during periods with mortality events versus periods without mortality events (Fig. 3, Supplementary material Appendix 1 Table A8). However, model averaging did not identify invertebrate biomass, or any other predictor variable, as biologically relevant (Table 2).

Environmental conditions and chick energetic requirements

Estimated maintenance metabolic rates (MMR) were, on average, 6% higher at Churchill than Beluga (1.93 ± 0.23 W versus 1.81 ± 0.16 W for chicks at 1 day; Supplementary material Appendix 1 Table A9) and $6.45 \times$ greater than RMR (range = 4.41 – 8.25 ; Fig. 4). Site differences in MMR indicated that, on average, chicks at Churchill would have to capture an additional 81 invertebrates at 1 day of age and 202 invertebrates at 10 days of age to meet their daily energetic needs, requiring an extra 20 min of foraging time compared to chicks at Beluga River. Moreover, on days when young chicks died in Churchill, 1-day old chicks required an extra 228 invertebrates and 56.9 min of foraging time compared with days when they survived. Conversely, because it was warmer on days when older

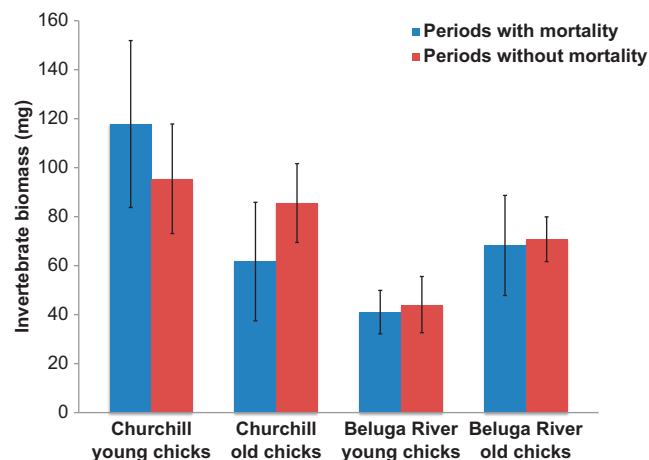


Figure 3. Differences in invertebrate abundance per transect between periods with and without mortality events for young (< 6 days) and older (> 6 days) chicks of Hudsonian godwits at Beluga River, Alaska and Churchill, Manitoba, 2009–2011.

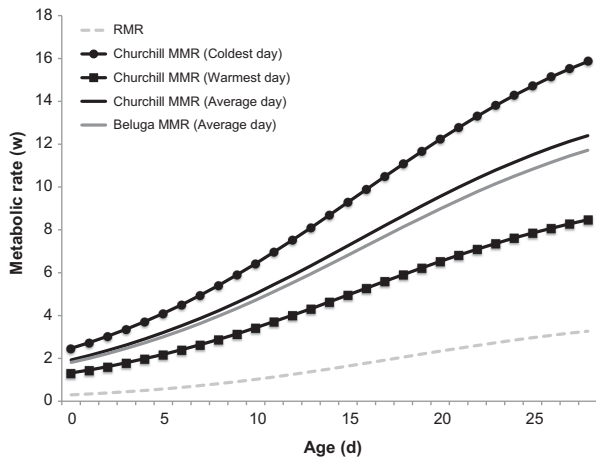


Figure 4. Estimated resting and maintenance metabolic rates for chicks of Hudsonian godwits at Beluga River, Alaska and Churchill, Manitoba, 2009–2011.

chicks died, 10-day old chicks required 39 fewer invertebrates and 2.9 min less foraging time than on days when they survived.

Current ecological mismatches in seasonal phenology

Godwit nests at Churchill hatched 5 ± 7 days ($n = 3$ years) after the onset of the 28-day peak phenological window of invertebrate biomass. In contrast, godwits at Beluga River hatched 8 ± 1 days ($n = 3$ years) before the onset of the peak phenological window. Daily invertebrate biomass was lower during the brood-rearing period than during the phenological peak in both populations (Fig. 5, Supplementary material Appendix 1 Table A10). However, period was not a biologically relevant predictor of invertebrate biomass at either Churchill or Beluga River (Supplementary material Appendix 1 Table A11).

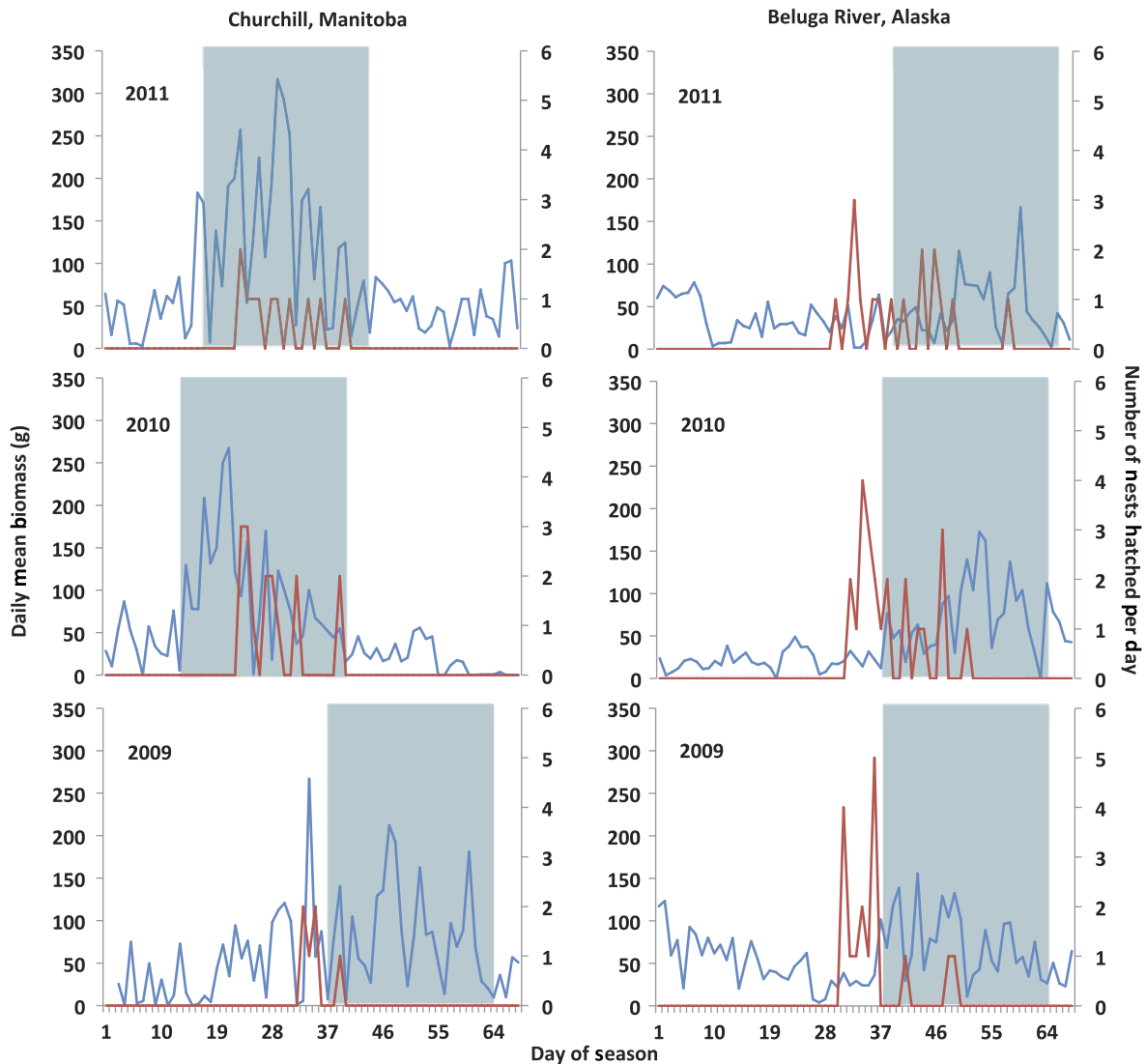


Figure 5. Chronological relationships between hatch dates of nests of Hudsonian godwits versus seasonal peaks in daily invertebrate abundance at (a) Churchill, Manitoba and (b) Beluga River, Alaska, 2009–2011. Blue line indicates daily measurements of invertebrate biomass per transect; red lines the daily number of godwit nests hatching; and the blue box the 28-day period of peak invertebrate availability.

Historical ecological mismatches in seasonal phenology

Different environmental conditions affected invertebrate abundance at each site, although our predictive power was limited. The best model at both sites had adjusted R^2 values of 0.27 and neither top model had $w_i > 0.90$ (Supplementary material Appendix 1 Table A12). We therefore used model-averaged coefficients for the hindcasting procedure (Supplementary material Appendix 1 Table A13). Hindcasting indicated that the date of peak invertebrate biomass has shifted earlier at Beluga River – peaks occurred 10.4 days earlier in 2011 than estimated during the early 1970s ($w_i = 0.51$) – but changed relatively little at Churchill ($AIC_c = 140.9$, $\Delta AIC_c = 2.2$, $w_i = 0.25$; Supplementary material Appendix 1 Table A14, A15).

Discussion

Ecological mismatches are frequently proposed as a threat to many species, but have yet to be implicated as driving widespread population declines. We found that the demographic performance and relative timing of reproduction differed between two populations of Hudsonian godwits. Godwits breeding at Churchill, Manitoba hatched their young as much as 11 days after the onset of the peak period of invertebrate abundance, which likely contributed to reductions in chick survival at the site. In contrast, godwits at Beluga River, Alaska hatched their chicks before the onset of the peak period of invertebrate abundance and maintained relatively high survival rates. Population-specific pressures occurring during northward migration and the breeding season are driving the divergent responses of godwit populations to global climate change (Senner 2012). As a result, the extent of the conditions determining each population's reproductive timing may be relatively limited in geographic scale. Our field study thus provides some of the first evidence that the potential for ecological mismatches to induce species-level population declines may be mediated by the size of a species' geographic range and spatial variation in the selection pressures acting across that range (Liebhold et al. 2004).

The characteristics of ecological mismatches

At Beluga River, hatch began about one week prior to the onset of the peak window in invertebrate abundance, such that the period of maximal chick growth coincided with the onset of peak invertebrate abundance. As a result, neither chick growth nor survival was affected by seasonal variation in invertebrate biomass. Instead, nesting attempt had a strong effect on chick survival. On average, renests hatched > 11 days later than first nests and few chicks from replacement clutches survived until fledging. Low survival of chicks from renests at Beluga River coincided with three events: hatching of nests of mew gulls *Larus canus*, which led to increased predation risk from foraging gulls; onset of the summer rainy season, which decreased the available time for chicks to forage; and an earlier cessation of parental care for broods from renests (Walker et al. 2011, Senner unpubl.). Given that the vast majority of chicks found dead in the study area appeared

to have died from predation, predator phenology was likely an important influence on the timing of breeding at Beluga River.

In contrast, godwits breeding at Churchill were mismatched with the seasonal peak in biomass of invertebrates, with the onset of hatch occurring up to 11 days after the onset of the period of peak invertebrate biomass in some years. The mismatch, however, did not uniformly affect all chicks: survival of young chicks (≤ 6 days) was unaffected by invertebrate abundance, but strongly negatively affected by periods of cold temperatures. Our results for older chicks (> 6 days) were more equivocal and limited by a small sample size due to attrition of young ($n = 18$), but suggest that survival of older chicks was negatively affected by low invertebrate abundance.

Our results at Churchill were likely driven by changes in the thermoregulatory capabilities and energy budgets of chicks during development. The absolute energetic requirements of young chicks are relatively low and most chicks hatched during the peak of invertebrate abundance, such that young chicks at Churchill were unlikely to starve under otherwise benign conditions (Williams et al. 2007). However, godwit chicks under 6-days of age are unable to fully thermoregulate at the cold temperatures regularly experienced during the Arctic summer (Visser and Ricklefs 1993, Williams et al. 2007) and are frequently brooded by their parents for warmth, especially during bouts of cold weather (Schekkerman et al. 2003, Schekkerman and Boele 2009). Increased brooding reduces the amount of time available for foraging, which can already comprise as much as 98% of the remaining daylight hours (Schekkerman and Boele 2009). In our study, the estimated MMR of 1-day old chicks was nearly 15% higher during periods when mortality events were recorded than during periods when chicks survived, and more than $9 \times$ higher than RMR. Meeting their energetic requirements during these periods would thus have required an extra 1 h of foraging to consume an additional 29 kJ. Irrespective of invertebrate abundance, chicks lacking sufficient reserves might be expected to starve or succumb to hypothermia under such inclement conditions.

Older chicks, on the other hand, are fully homeothermic, but have higher energetic requirements and had to largely meet those requirements outside the peak period of invertebrate abundance, meaning they were potentially more susceptible to starvation. For instance, the RMR of a 10-day old chick is $3.5 \times$ higher than that of a 1-day old chick, while that of a 21-day old chick is $8.3 \times$ higher than that of a 1-day old chick. These age-specific differences in metabolism require 10-day and 21-day old chicks to increase their energetic intake by 63 and 187 kJ, respectively, over 1-day old chicks. Older chicks were thus more likely to be food limited and tended to die during periods with low invertebrate abundance, irrespective of the ambient temperature. As such, older chicks were likely the ones most directly affected by the ecological mismatch.

Our results for godwits at Churchill, however, did not support all of the predictions of the mismatch hypothesis (Dunn et al. 2011) – we found no link between invertebrate biomass and chick growth, or between body condition and chick survival, nor did survival of godwit young

decline across the breeding season. Also, predation played a consistently strong role in determining chick survival rates. Nonetheless, our failure to support these predictions makes sense in the context of our other results. For instance, growth rates responded almost immediately to changes in environmental conditions, and we likely recaptured chicks too infrequently to adequately assess how their body condition may have affected survival. Similarly, because growth responded rapidly to environmental conditions, days with low invertebrate biomass may have caused rapid deterioration in chick condition. As a result, if chicks died before they could be recaptured on days when invertebrate biomass was truly low, we may have failed to detect the effects of body condition on survival. Furthermore, nearly half of all chicks that failed to fledge died before the age of 5 days. Given these high rates of early-life mortality and the strong synchrony in timing of hatch, it would have been difficult to detect declines in survival rates across the season. Last, the strong links between environmental conditions and both chick growth and survival indicates that the relationship between predation and survival was mediated by a chick's condition, suggesting that depredated chicks were likely a nonrandom subset of the population (Whiteside et al. 2015).

The ecological mismatch at Churchill was thus a function of both environmental conditions and features of godwit breeding biology. While the Beluga River field site is located further north, it is part of the Boreal ecosystem, whereas the Churchill field site is a low-Arctic environment (Serreze et al. 2000, Gagnon and Gough 2005). Environmental conditions at Churchill are highly variable and the short summer season requires elevated growth rates fuelled by higher feeding rates to allow chicks to fledge before the onset of cold weather. Any reduction in the quality of the resource environment is therefore likely to have a negative effect on chick survival (Schekkerman et al. 2003, but see McKinnon et al. 2013). When combined with the low nest survival and infrequent renesting after nest loss (only 22% of Churchill females renested after nest loss, $n = 36$; Senner unpubl.), even small mismatches can result in strong reductions in breeding success for godwits at Churchill. As such, Arctic populations may be more susceptible to the effects of climate change, not because of the occurrence of more rapid climatic changes at these latitudes, but because a population's margin for error is smaller than in more temperate regions (Bertheaux et al. 2004).

The causes of ecological mismatches

The underlying factors determining reproductive timing also differed between the two populations. Clutch initiation at Churchill is constrained by the timing of arrival for godwits at the breeding grounds, which has been delayed by nearly 11 days over the past four decades (Senner 2012). Delays in migratory phenology have resulted from asynchronous climate change regimes occurring throughout their annual cycle: stagnant or cooling trends characterize the northern portion of the population's migration route, while warming trends characterize the southern portion, as well as the breeding season at Churchill itself. Spatial heterogeneity in global climate change dictate that while the timing of peak invertebrate abundance has likely not changed in Churchill,

godwits now arrive and initiate their clutches later than in the past, causing them to be mismatched with local invertebrate phenology.

The timing of reproduction for godwits at Beluga River is less constrained. Godwits breeding at Beluga River experience synchronous warming regimes throughout their annual cycle and have accelerated both their timing of arrival and clutch initiation in recent decades (Senner 2012). However, selection for an earlier onset of reproduction may be driven only indirectly by climate change: low survival of chicks hatching from renests is the strongest factor determining the reproductive success of godwits at Beluga River. Thus, this population's apparent ability to 'respond' to recent climatic changes may actually be an indication that other selection pressures are acting strongly, albeit pushing godwits in the same direction as would the effects of climate change.

Combined, our findings strongly suggest that the forces determining the timing of reproductive events are population-specific, and not necessarily climate-related. Few other studies have directly compared trends in reproductive timing across multiple populations of the same species, nor the degree to which those trends match changes in local resource phenology (Dunn and Møller 2014). Nonetheless, our study joins a growing body of evidence documenting variation in the degree to which separate populations are responding to climate change (Visser et al. 2003, Both et al. 2006, Hodgson et al. 2011, Burger et al. 2012). This spatial variation in demographic responses suggests that many widespread species may experience climate change heterogeneously across their range, with some sub-populations being strongly affected and others less so (Dennis et al. 2010).

Consequences of ecological mismatches

If ecological mismatches can lead to reductions in chick survival, why do so few mismatches seem to result in population declines at the species level (Dunn and Møller 2014)? One potential solution to this paradox is that density-dependence can act more strongly outside of the chick-rearing period, meaning that an ecological mismatch occurring at a breeding site merely reduces the number of individuals competing for resources elsewhere in the annual cycle (Gill et al. 2001, Reed et al. 2013a, b, Dunn and Møller 2014). This may not be the case for Hudsonian godwits, though. Reversible state effects are reversible changes in fitness-related traits resulting from life-history tradeoffs that can carry-over to affect an individual's performance and fitness during future portions of its annual cycle (sensu Senner et al. 2015). In other systems regulated by density-dependent processes during other portions of the annual cycle, reversible state effects initiated in the non-breeding season are significant drivers of variation in reproductive success during the subsequent breeding season (Studds and Marra 2005). In our study, however, reversible state effects did not alter the reproductive success or survival of adults, indicating that density-dependence is not a strong regulator of population dynamics for Hudsonian godwits (Senner et al. 2014). Our results therefore suggest an additional possibility: if ecological mismatches are driven by local-scale, population-

specific processes, the effects on species-level declines will be proportional to the size of a species' range and spatial homogeneity in the selection pressures across that range.

Previous work has suggested that range size is one of the dominant factors determining the level of spatial synchrony across populations (Liebhold et al. 2004). Nevertheless, many studies have used field data taken at limited temporal or spatial scales to generate predictions encompassing longer periods at larger scales (Diez et al. 2012). Such efforts often fail to capture the full breadth of environmental variation that may affect population dynamics across a species' range (Hodgson et al. 2011). North temperate species and long-distance migratory birds with broad geographic ranges and large population sizes may thus not be the best study species with which to determine the full spectrum of potential consequences resulting from ecological mismatches. Accordingly, despite the mismatch in Churchill, godwit population trends appear to be generally stable at the species level (Andres et al. 2012, but see Bart et al. 2007). Instead, endemic or rare species may be far more likely to suffer species-level population declines stemming from mismatches. Perhaps unsurprisingly, endemic species with narrow ranges are projected to be most likely to face climate-induced extinctions (Urban 2015). To predict the potential impacts of climate change for any one species, we therefore need detailed information about not only the direct effects of climate change on a suite of populations across that species' range, but also what non-climatic selection pressures those populations are facing. Detailed population data are difficult to collect, but could help identify those species truly at risk of succumbing to climate-induced extinctions.

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Statement of animal rights – All applicable institutional and national guidelines for the care and use of animals were followed.

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Supplementary material (available online as Appendix oik-03325 at <www.oikosjournal.org/appendix/oik-03325>). Appendix 1.