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Foraging ecology mediates response to ecological mismatch during migratory stopover

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Abstract. Impacts of ecological mismatches should be most pronounced at points of the annual cycle when populations depend on a predictable, abundant, and aggregated food resource that changes in timing or distribution. The degree to which species specialize on a key prey item, therefore, should determine their sensitivity to mismatches. We evaluated the hypothesis that the effects of ecological mismatch during migratory stopover are mediated by a species' foraging ecology by comparing two similar long-distance migratory species that differ in their foraging strategies during stopover. We predicted that a specialist foraging strategy would make species more sensitive to effects of mismatch with a historically abundant prey, while an active, generalist foraging strategy should help buffer against changing local conditions. We estimated arrival times, start of mass gain, and rate of mass gain during spring stopover in Delaware Bay, USA. At this site, shorebirds feed on a temporally aggregated food resource (horseshoe crab *Limulus polyphemus* eggs), the timing of which is linked to water temperature; red knot (*Calidris canutus rufa*) specializes on these while the ruddy turnstone (*Arenaria interpres*) feeds more generally. We used a hierarchical nonlinear model to estimate the effect of mismatch between shorebird arrivals and timing of crab spawning on the timing and rate of mass gain over 22 yr. In years with cooler water temperature, crabs spawned later, which was associated with later and faster mass gain for the knots. Turnstones exhibited less inter-annual variation in the timing and rate of mass gain than knots, and we found no relationship between mass gain dynamics and the availability of horseshoe crab eggs for this generalist species. Long-distance migrants rely on predictable resources en route and even when these linkages are simple and predictable, populations can be vulnerable to change; these results suggest that generalist foraging strategies may buffer migratory species against phenological mismatch. We provide a framework to evaluate population responses to changes in prey phenology at sites vulnerable to climatic change.

Key words: ecological mismatch; foraging specialization; migration; migratory stopover.

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Introduction

Migratory species depend on productive, seasonal habitats and may be vulnerable to phenological mismatches if environmental changes at breeding, nonbreeding, or stopover sites occur asynchronously (Walther et al. 2002, Robinson et al. 2009, Thorup et al. 2017). The negative impacts of these mismatches are most likely to be pronounced at points in the annual cycle when populations depend on historically predictable, aggregated food resources. Although theory predicts that mismatches should have negative population-level effects, empirical studies show mixed evidence for such effects (Stenseth and Mysterud 2002, Miller-Rushing et al. 2010). Understanding whether and how species can adjust to shifting annual cues and resource availability is critical for predicting species' responses to climate change.

One mechanism by which animals may respond to climate change is through flexibility in the timing of annual events (e.g., migration, breeding). For example, many Neotropical migratory songbirds have advanced the timing of pre-breeding migration and hence breeding over the past few decades in response to warming spring temperatures (Winkler et al. 2002). Similarly, migratory ungulates and geese time northward movements to track the onset of spring across the landscape (Bischof et al. 2012, Si et al. 2015). However, other studies have shown that individuals may not always be able to avoid mismatches, leading to insufficient resources during migration (Post et al. 2008) or the breeding season (Plard et al. 2014, Senner et al. 2016). Mismatches often occur because heterogeneous patterns of warming and cooling across the landscape lead to situations in which conditions at departure sites are poor indicators of conditions at the destination (Both et al. 2009, Jones and Cresswell 2010, Senner et al. 2016). Although much research effort has focused on mismatches caused by phenological shifts (i.e., directional changes in average conditions), increased climatic variability could also increase the frequency of ecological mismatches even in the absence of a sustained trend (Stouffer and Wetherald 2007, Holmes et al. 2016).

Environmental cues during the nonbreeding season influence the timing of migration and stopover, and if arrival to the breeding site is delayed, individuals might miss the optimal resource window for reproduction (Kokko 1999). Ecological mismatches have been largely studied during the breeding season, but seasonal resource availability is critical during migration. Pre-breeding migration typically occurs in a narrow time frame, and during stopover individuals have limited time to acquire fuel stores needed to continue migration (Nilsson et al. 2013). This narrow window must coincide with prey availability. Insufficient resources during migratory stopover could result in either delayed or underweight departure, both of which could have individual carry-over effects to the breeding season, with potential population-level demographic impacts (Newton 2006, Harrison et al. 2011, Lameris et al. 2017, Rakhimberdiev et al. 2018).

The degree to which mismatches negatively affect populations likely depends, in part, on species foraging ecology and breadth of diet. A generalist foraging strategy makes a species less reliant on the availability of a single key prey item while temporal overlap with prey is critical for specialist foragers. Generalist species are better able to cope with novel or unpredictable environments (Mayr 1965, Sol et al. 2002) and therefore should be less sensitive to the availability of a specific prey item. Species that rely on the availability of a specific prey item at any point of the annual cycle are more vulnerable to potential mismatches.

Arctic-breeding shorebirds rely on plentiful food at stopover sites to quickly accumulate large fat stores, which are necessary to continue their migration (Gudmundsson et al. 1991, Nilsson et al. 2013, Rakhimberdiev et al. 2018). These species have some of the longest known migrations and have experienced widespread declines in the past several decades (Piersma et al. 2014, Pearce-Higgins et al. 2017). Degradation of stopover sites has been implicated as a key contributor to observed declines (Baker et al. 2004, Studds et al. 2017). These species rely on predictable aggregations of abundant prey at stopover sites en route to replenish fat stores needed to complete their migratory journey (Piersma and Lindstrom 2004, Rakhimberdiev et al. 2018); therefore, matching of arrival timing and food availability at those sites may be critical for population stability.

In Delaware Bay, USA, a globally important stopover site for several migratory shorebirds, the eggs of spawning horseshoe crabs (*Limulus polyphemus*) provide a critical, but temporally variable and ephemeral, food resource during spring migration (Castro and Myers 1993, Haramis et al. 2007). Declining horseshoe crab abundance due to past unregulated harvest has been suggested as the cause of observed declines in the numbers of birds seen in Delaware Bay during stopover (Baker et al. 2004, Niles et al. 2008), especially the red knot (*Calidris canutus rufa*), which is listed as Threatened under the United States Endangered Species Act (79 FR 73705 73748). Although more recent studies indicate that deteriorating Arctic conditions may be an important driver of population declines (McGowan et al. 2011, Fraser et al. 2012, McGowan 2015, van Gils et al. 2016), conservation management actions in the Delaware Bay region have focused on restoring shorebird stopover habitat and maintaining horseshoe crab populations. As horseshoe crab and red knot populations recover with the aid of strict horseshoe crab harvest regulations (McGowan et al. 2015), the ability of birds to reach adequate departure mass may be important for population stability (Baker et al. 2004). In addition to the overall abundance of eggs, timing of horseshoe crab spawn plays a key role in determining the availability of adequate food resources in Delaware Bay. Horseshoe crabs spawn once a year during the spring high tides in May and early June (Smith et al. 2002), coinciding with shorebird stopover in mid- to late May (Niles et al. 2008). Timing of spawn is linked to lunar periods and water temperature, with the largest spawn typically on the full moon high tide when water temperature is ≥15°C (Smith et al. 2002, Smith and Michels 2006). Over the past 20 yr, spring water temperatures have fluctuated in Delaware Bay (Appendix S4: Fig. S3) and annual variability in global temperature and precipitation is predicted to increase with climate change (Stouffer and Wetherald 2007, Holmes et al. 2016). Cooler temperatures have been anecdotally linked to observed delays in crab spawn and concerns about whether shorebirds are able to gain mass at the necessary rate.

Here, we evaluate the hypothesis that the effects of mismatch on stopover ecology differ by species' foraging strategy. We predicted that, when compared to a specialist, a generalist forager would show less among-year variation in the timing and rate of mass gain during stopover in the face of temporal variation in water temperature and show no relationship between dynamics of mass gain and the availability of a single prey item. To test our hypothesis, we considered two long-distance migratory shorebirds, the red knot and the ruddy turnstone (*Arenaria interpres*). Both species breed in the Arctic with medium- to long-distance migrations and use Delaware Bay as a primary spring stopover. At this site, both red knot and ruddy turnstone primarily consume horseshoe crab eggs (Gillings et al. 2007, Haramis et al. 2007, Mizrahi and Peters 2009), although at other sites they consume a variety of invertebrate prey, including crustaceans, mollusks, polychaetes, and insects (González et al. 1996, Nettleship 2000, Baker et al. 2001, Cohen et al. 2010, Martínez-Curci et al. 2015). Ruddy turnstone have a more diverse and opportunistic diet than red knot and will also scavenge carrion and human garbage (Gill 1986). Additionally, when foraging for horseshoe crab eggs, red knot consume eggs on the sand surface or upper layer of sand (1–3 cm) while ruddy turnstone actively dig for buried eggs, effectively increasing resource availability (Tsipoura and Burger 1999, Gillings et al. 2007). We predicted that, due to these differences in foraging ecology, red knot would show more variation in the timing and rate of mass gain than ruddy turnstone and that mass gain dynamics for red knot, but not ruddy turnstone, would be dependent on the timing of horseshoe crab spawning. The results of this research will help advance our ability to assess and predict a population's vulnerability to climate change-induced mismatches in resource availability with annual cycle timing, especially for migratory species.

Methods

Focal species

Red knot and ruddy turnstone are medium-sized sandpipers with global distributions. The Atlantic flyway populations of both species breed in the Canadian Arctic and overwinter at coastal sites ranging in latitude from the Gulf coast of the United States to northern Argentina; some red knot overwinter as far south as Tierra del Fuego, Argentina (Nettleship 2000, Baker et al. 2001, Perkins et al. 2007, Lathrop et al. 2018). Northward migration begins in late April/early May, with most birds arriving to Delaware Bay in mid- to late May and staying for 1–2 weeks before continuing north to begin breeding in early June (Smith et al. 2010). Evidence suggests that most Arctic-breeding shorebirds are income breeders and fuel stores acquired during migratory stopover are largely depleted during the final flight to the breeding grounds (Klaassen et al. 2001, Morrison and Hobson 2004), although some reserve fuel stores from migration may be needed upon first arrival (Morrison et al. 2007). The optimal temporal window for breeding in the Arctic is short, and therefore, punctual arrival is important for successful breeding (Meltofte et al. 2007).

Study site and field methods

Birds were captured in mixed foraging flocks using cannon nets during the spring stopover period between 1 May and 5 June in Delaware, USA, from 1997 to 2018, weighed with a digital scale accurate to the nearest 0.1 g and marked with Incoloy U.S. Geological Survey (USGS) leg bands and—beginning in 2004—Darvic leg flags inscribed with unique field-readable alphanumeric codes (Clark et al. 2005). The number and timing of catches varied among years. From 2005 to 2018, beaches were also surveyed to resight individually flagged birds. Trained observers visited 10 study beaches distributed along the Delaware coast of Delaware Bay in 3-d sampling periods to scan flocks for flagged individuals.

Timing of shorebird arrival to stopover site

We used mark–resight data from flagged birds to estimate shorebird arrival probabilities over the course of the stopover season for each year using Jolly-Seber models (Fig. 1A). Details of model specification and goodness-of-fit tests for these are provided in Appendix S2. We estimated sampling period-specific entry probabilities across the season for each species in each year and derived the cumulative probability of arriving during or before each sampling period. We assumed that flagged individuals were a representative sample of the stopover population (flagged individuals are observed throughout foraging flocks on all study beaches) and used this cumulative probability as an index of the proportion of the stopover population that had entered the region by each period. To determine the proportion of horseshoe crab spawn available to shorebirds, we defined a cutoff date for each shorebird species in each year as the period by which 95% of the population had arrived at the stopover site. To compare these dates to horseshoe crab spawning activity, and for clarity of presentation, we converted 3-d shorebird sampling periods to days since 1 May using the middle day of each sampling period. Resighting data were not collected prior to 2005, so we used the median 95% cutoff period for each species to assess horseshoe crab spawning availability for 1997–2004. The timing of bird arrivals to the stopover site was fairly consistent across years from 2005 to 2018, and, therefore, we assumed that average timing of arrival was also consistent from 1997 to 2004.

Availability of horseshoe crab eggs

Horseshoe crab spawning activity was surveyed across 13 beaches in Delaware each year from 2003 to 2017. Observers counted the number of females on the high tide line per 1-m quadrat during each lunar period's high tide (from two nights prior to the full or new moon to two nights post) totaling ~12 surveys per beach per year. Survey design and methodology are described in detail by Smith et al. (2002). The statewide density of females is reported as an index of female spawning abundance (IFSA), which we use as a proxy for egg abundance (Zimmerman et al. 2016). Horseshoe crab spawning is monitored throughout the bay in both Delaware and New Jersey. Shorebirds forage on beaches in both states and move among sites in the Bay, generally concentrating at the sites with the greatest horseshoe crab spawning activity (Karpanty et al. 2006). For this study, shorebirds were captured in Delaware only, but both the abundance and timing of horseshoe crab spawning were comparable between states in each year (Appendix S4: Figs. S1 and S2) so we only included spawning surveys from Delaware in our analyses.

We used survey-specific IFSA from across the season to assess temporal patterns in spawning. For each year, we determined the proportion of cumulative total annual spawn that had occurred by each day. Horseshoe crab eggs accumulate on the beach and can remain available to birds on the mudflats and upper layer of sand; therefore, we assumed that spawning activity that occurred before bird arrival would still be available to foraging birds. We used a loess smoothing function to estimate the predicted proportion of spawn that occurred by each date and defined relative horseshoe crab egg availability to shorebirds as

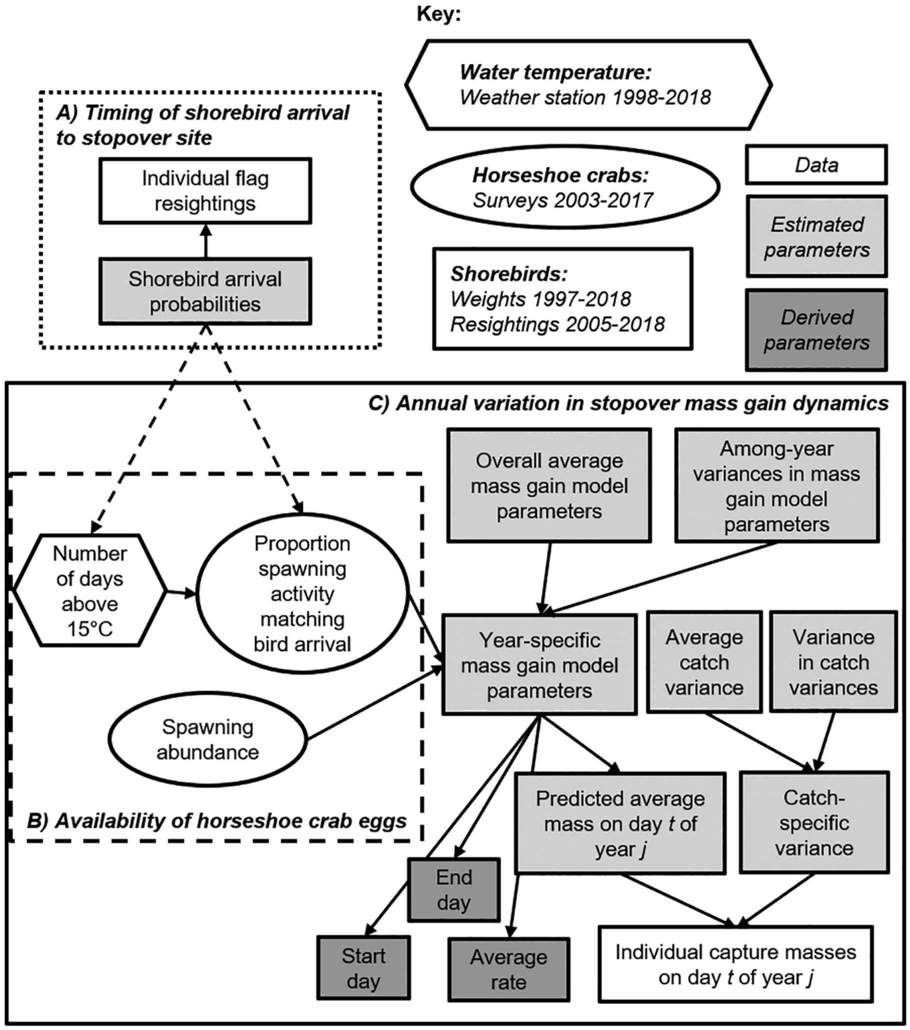

Fig. 1. Hierarchical model structure used to estimate the relationship between horseshoe crab egg availability and shorebird mass gain dynamics. Shorebird arrival probabilities were estimated using Jolly-Seber models (A). The relationship between water temperature and horseshoe crab spawn (B) and parameters governing shorebird mass gain dynamics (C) were estimated simultaneously in an integrated analysis.

the proportion of the total spawning activity that occurred by the 95% arrival cutoff date for each species in each year.

Timing of horseshoe crab spawn is dependent on environmental cues, with water temperatures above 15°C thought necessary for substantial spawning activity to occur (Smith and Michels 2006). For each year, we determined the number of nights with average water temperatures above 15°C prior to the date by which 95% of birds had arrived, which we expected to explain some annual variation in horseshoe crab egg availability (Fig. 1B). We obtained water temperature data collected by an offshore station in Lewes, DE (station ID 8557380), from the NOAA Center for Operational Oceanographic Products and Services. We used hourly water temperatures from 1 May to 15 June to estimate daily average water temperature for those dates from 1998 to 2018. Temperature data were unavailable from this station for 1997 and 2017. We estimated the relationship between the number of nights with average water temperature above 15°C with the relative amount of horseshoe crab spawn available to shorebirds using a linear model, with both variables scaled and centered for analysis.

Annual variation in stopover mass gain dynamics

We analyzed capture masses of 13,046 red knots and 12,476 ruddy turnstones from 239 catches (114 catches of red knots, 125 catches of ruddy turnstones) over 22 yr in Delaware (Appendix S1: Table S1). Because this analysis estimates mean masses of each catch, we only included catches with at least 25 individuals weighed to ensure sufficient sample size for an unbiased estimate of central tendency. The number of individuals weighed on a single occasion ranged from 25 to 479 for red knot (median = 77) and from 25 to 584 for ruddy turnstone (median = 75). The number of catches in a year ranged from 1 to 9 for red knot and 1 to 10 for ruddy turnstone; we only estimated year-specific parameters for years with >3 catches but all data were used to estimate global mean parameters.

Average capture masses increased nonlinearly throughout the stopover period, so we modeled the mean mass of individuals of each species captured on a given day as a nonlinear effect of day of the stopover period (1 May = day 1) using a four-parameter logistic curve:

$$\mathrm{mass}_{day,t} = \mathrm{Max}_t + \frac{\mathrm{Min}_t - \mathrm{Max}_t}{1 + \left(\frac{\mathrm{day}}{p_t}\right)^{r_t}}$$

where $\mathrm{mass}_{\mathrm{day},t}$ is the mean mass of all birds captured on a given day in year t, Max_t is the maximum average mass in year t, and Min_t is the minimum average mass in year t. The scaling parameters p_t and r_t dictate the shape of the curve; r_t is the maximum rate of mass gain in year t; and p_t is the inflection point, that is, the day on which the maximum rate of mass gain occurred. We fit the mass gain model separately for each species.

To assess among-year variation in mass gain dynamics, we used a hierarchical annual random-effects model (Fig. 1C) analyzed in a Bayesian framework to estimate overall means and year-specific deviations for the maximum mass (Max_t), minimum mass (Min_t), maximum rate of mass gain (r_t), and inflection point (p_t). We estimated year-specific model parameters by defining a prior distribution for the global average value of each parameter and the variance around that average, which were used to define the normal distribution from which the year-specific values were drawn, for example:

$$\mu_{\mathrm{Min}} \sim \mathrm{Unif}(80, 150)$$
$$\sigma_{\mathrm{Min}} \sim \mathrm{Unif}(0, 50)$$
$$\mathrm{Min}_t \sim \mathrm{Normal}(\mu_{\mathrm{Min}}, \sigma_{\mathrm{Min}})$$

where μ_{Min} is the global average minimum mass, σ_{Min} is the among-year standard deviation in minimum masses, and Min_t is the estimated minimum mass in year t. All four mass gain model parameters were estimated using this general structure. We used weakly informative Uniform priors for the average minimum and maximum masses based on documented masses for each species (Nettleship 2000, Baker et al. 2001) to keep posterior sampling within reasonable values (minimum = 80 g, maximum = 300 g). Weakly informative Uniform priors were also used for the average rate and inflection point parameters (r_t: Unif(0, 20); p_t: Unif(0, 40)).

We calculated the derivatives of each annual mass gain curve to estimate the mass gain start day, end day, and average rate of mass gain in that window for each species in each year (Fig. 1C). We defined the start and end day of mass gain as the days with the maximum and minimum second derivative of the predicted curve, respectively (Appendix S1: Fig. S1). This method approximates the dates on which the population experienced the greatest changes in the rate of mass gain, which we interpret to correspond to the beginning and end of the period of peak refueling.

We assumed individual masses of birds weighed on a given day were normally distributed around daily predicted means with a catch-specific variance. Observed within-catch variance varied across the season and among years, due to continued influx of new (lighter) individuals as the season progressed, so we estimated this variance as a random effect of catch unconstrained by day or year. We assigned a Uniform (0, 50) prior distribution to the average and a Gamma (1, 0.01) prior distribution to the among-catch variance. To assess our assumption that within-catch masses were normally distributed, we used posterior predictive checks to estimate the sum of squared residuals for the observed individual masses and a predicted ideal data set (Kéry 2010), which indicated that this assumption was reasonable with a Bayesian *P*-value of 0.50 for red knot and 0.49 for ruddy turnstone.

Red knot are slightly larger than ruddy turnstone, so to facilitate comparison of annual mass gain dynamics on a common scale, we present the annual variation in model parameters using the coefficient of variation (CV = σ/mean) and report rates of mass gain scaled to average minimum mass. We evaluated our prediction that red knot (specialist) would exhibit greater among-year variation in mass gain dynamics than ruddy turnstone (generalist) by assessing the overlap of the posterior distributions for CV of the inflection point and rate parameters.

Effect of resource availability on mass gain dynamics

We specified covariates on growth model parameters to estimate the effect of the relative horseshoe crab egg availability on the timing and rate of mass gain by shorebirds. Because year-specific mass gain model parameters were assumed to be normally distributed around the global average, the effects of ecological covariates were estimated using linear models with normal errors and identity links. We simultaneously estimated the relationship between water temperature and overall horseshoe crab abundance with the availability of horseshoe crab spawn and the effect of horseshoe crab egg availability on shorebird mass gain dynamics in an integrated analysis (Fig. 1).

We predicted that both the timing and the rate of mass gain were associated with the relative amount of horseshoe crab eggs available during the stopover period for red knot (specialist), but not ruddy turnstone (generalist). We tested for an effect of both overall spawning abundance and the relative horseshoe crab egg availability on both the year-specific inflection point and maximum rate of mass gain. We also included an interaction term between abundance and availability of horseshoe crabs, which we interpret as the relative abundance of eggs available to the birds. We used indicator variable selection to simultaneously estimate parameter values and the probability that each covariate was an important predictor. For each covariate, we estimated a binary indicator variable γ. We defined a joint slab-and-spike prior on coefficient (β) estimates, such that the estimate would equal 0 if γ was equal to 0 and be drawn from an uninformative prior distribution otherwise.

$$\gamma_1 \sim \text{Bernoulli}(0.5)$$
$$\beta_1 \sim \begin{cases} \gamma_1 = 0 & \text{Normal}(0, 10^{-10}) \\ \gamma_1 = 1 & \text{Normal}(0, 10^{3}) \end{cases}$$

The proportion of Markov chain Monte Carlo (MCMC) iterations in which $\gamma = 1$ is interpreted as the inclusion probability for that covariate. We report covariate effects as the posterior means (β), the proportion of the posterior distribution with the same sign as the mean (f), and the inclusion probability (γ).

MCMC estimation

We fit all models using R 3.5.1, JAGS 4.3, and the jagsUI package (Plummer 2003, Kellner 2015, R Core Team 2016). We generated three MCMC chains of 100,000 iterations each with 10,000 iterations in the adaptive phase and discarded the first 50,000 samples as burn-in values, which was sufficient to ensure convergence for all parameters ($\hat{R} < 1.1$). JAGS model code is provided in Appendix S3.

Results

Timing of shorebird arrival to stopover site

We found consistent timing of arrival to the stopover site for both species (Fig. 2). For both species, 95% arrival generally occurred by the seventh sampling period (26–28 May), sometimes occurring as early as the sixth sampling period (23–25 May) for red knot, but no later than the eighth sampling period for both species (29–31 May). See Appendix S2 for details of all Jolly-Seber model results.

Availability of horseshoe crab eggs

The amount of horseshoe crab spawn available to the birds varied among years and was dependent on water temperature. The proportion of horseshoe crab spawn that occurred by peak shorebird arrival ranged from 0.23 (2003) to 0.74 (2004), with a median of 0.58 for both shorebird species, but there was not a detectable trend in degree of mismatch between horseshoe crab spawning and shorebird arrival over the past 20 yr. Water temperature was a positive

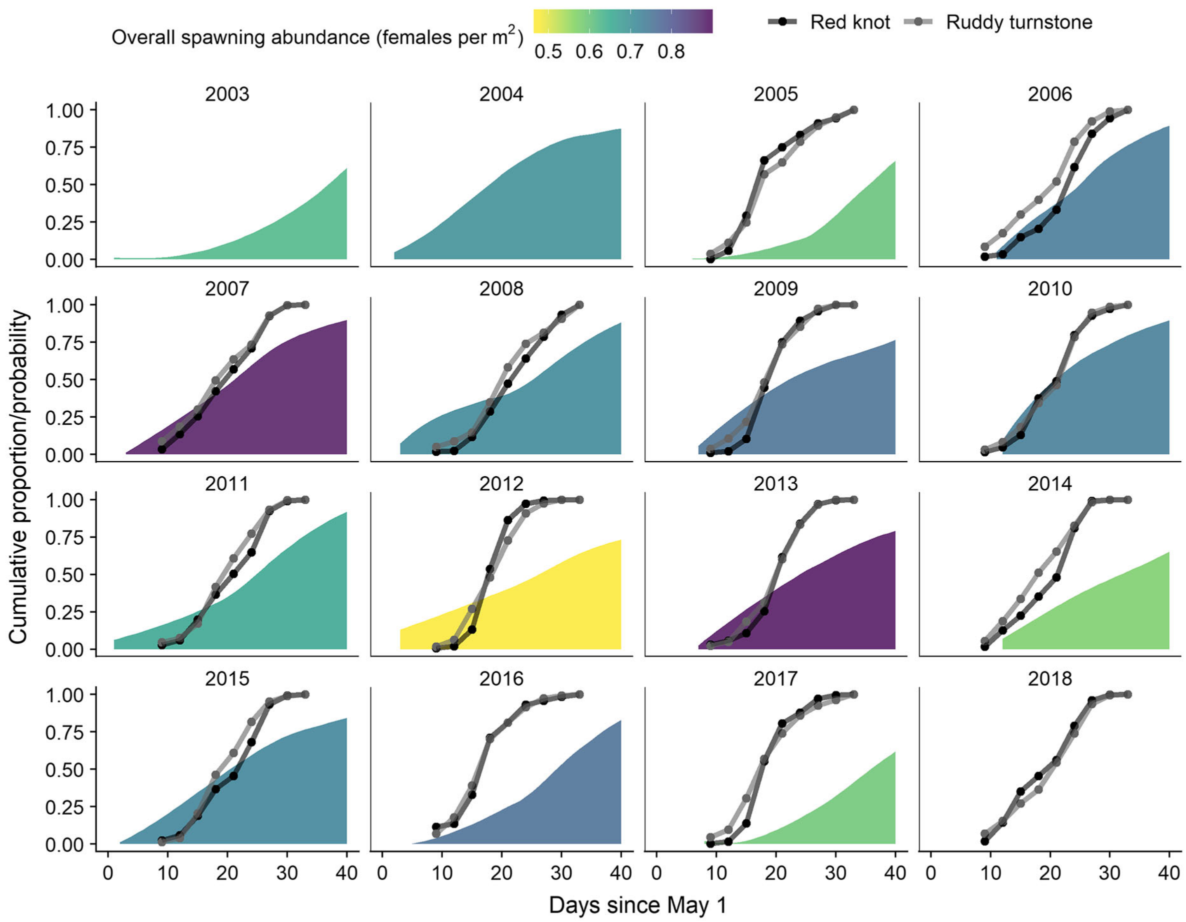

Fig. 2. Timing of horseshoe crab spawn and shorebird arrival to the stopover site. Shaded regions show the cumulative proportion of horseshoe crab spawning activity that occurred by each day. The color of those regions represents the total spawning abundance (IFSA) for that year (yellow, low; purple, high). Black and gray lines indicate the estimated cumulative proportion of flagged birds arrived by each day (gray, ruddy turnstone; black, red knot).

predictor of the proportion of spawn available to shorebirds ($\beta = 0.64$; 0.15, 1.16; in red knot model and $\beta = 0.60$; 0.12, 1.07; in ruddy turnstone model).

Annual variation in stopover mass gain dynamics

Red knots gained mass more quickly and over a shorter time period than ruddy turnstones (Table 1; Appendix S1: Fig. S2). Scaled to the average minimum mass, the maximum rate of mass gain for red knot was equal to an increase of 10% of minimum average body mass per day and that of ruddy turnstone was equal to an increase of 7.4% per d. Red knot mass gain also typically happened over fewer days than ruddy turnstone; the median number of days of the peak refueling period was 6.3 (2.5, 14.5) for red knot and 9.1 (6.5, 14.9) for ruddy turnstone.

As predicted, red knots exhibited more among-year variation in year-specific model parameters than ruddy turnstones, measured as the among-year CV of estimates (Table 1, Fig. 3). This difference was most pronounced for the year-specific maximum rate. This parameter varied by 81% among years for red knot (95% credible interval [CRI]: 29%, 220%), but only by 27% for ruddy turnstone (95% CRI: 0.15%, 45%); in only 3% of MCMC iterations was the maximum

Table 1. Model estimates for overall average and among-year coefficient of variation (CV) in mass gain model parameters, reported as posterior mean and lower and upper bounds of the 95% credible interval (CRI).

Species	Model parameter	Average			Among-year CV		
		Mean	LCRI	UCRI	Mean	LCRI	UCRI
Red knot	Minimum average mass	116	109	123	0.097	0.049	0.161
	Maximum average mass	179	170	189	0.068	0.026	0.115
	Inflection point	22.1	20.8	23.6	0.127	0.078	0.195
	Maximum rate	11.7	4.0	19.1	0.811	0.290	2.182
	Start day	18.7	12.7	20.9	...	...	...
	End day	24.4	22.6	26.9	...	...	...
	Average rate of mass gain	6.9	2.9	11.0	...	...	...
Ruddy turnstone	Minimum average mass	98.9	96.3	101.6	0.032	0.008	0.064
	Maximum average mass	160.7	153.8	168.7	0.034	0.002	0.080
	Inflection point	24.0	23.0	25.1	0.115	0.055	0.251
	Maximum rate	7.3	5.3	9.8	0.271	0.148	0.446
	Start day	18.7	16.6	20.3	...	...	...
	End day	27.3	25.9	28.9	...	...	...
	Average rate of mass gain	4.1	3.2	5.2	...	...	...

Notes: Minimum and maximum average mass are reported in grams. The inflection point (day on which maximum rate of mass gain occurred), start day, and end day are reported as the day in May. Maximum rate of mass gain and average rate of mass gain are reported in g/d. Start day, end day, and the average rate of mass gain were derived from the logistic model and among-year CV was not estimated for these parameters (as indicated by ellipses). LCRI, lower bounds of the 95% credible interval; UCRI, upper bounds of the 95% credible interval.

slope CV for knot lower than turnstone. Both species had similarly low among-year variation in the inflection point of the mass gain curve (red knot CV = 0.13; 0.08, 0.20; ruddy turnstone 0.12; 0.06, 0.25).

The average rate of mass gain was positively associated with start day for both species, indicating faster average refueling rates in years when mass gain started later in the season (Fig. 4). The start day of mass gain was also positively associated with the end day but was not associated with the predicted maximum average mass.

Effect of food availability on mass gain dynamics

In cooler years with later horseshoe crab spawning, red knots gained mass at a faster rate and the inflection point occurred later in the season (Table 2). The interaction term between statewide spawning abundance (IFSA) and overlap with shorebirds, that is, the relative availability of horseshoe crab eggs, was the strongest predictor of red knot maximum rate of mass gain, indicating that red knots gained weight at a slower rate in years with greater relative horseshoe crab egg availability. Importantly, this interaction was almost three times as likely to be included as a predictor of mass gain in knots (0.36) than turnstones (0.13).

Discussion

We evaluated the hypothesis that the effects of ecological mismatch on stopover mass gain dynamics are dependent on foraging strategy by comparing how yearly variation in the timing of food abundance affected the timing and rate of mass gain for a specialist and generalist species. We found support for our predictions that both the timing and rate of mass gain were linked to timing of food abundance for the specialist but not the generalist forager. Additionally, red knot (the specialist) exhibited larger among-year variation in the rate of mass gain, suggesting greater sensitivity to local conditions. Ruddy turnstone mass gain dynamics were more consistent across years and not associated with abundance or availability of horseshoe crab spawn, which aligns with our prediction that as generalist foragers they are less sensitive to availability of this food resource.

The hierarchical modeling approach used here allowed us to evaluate year-specific mass gain dynamics while borrowing information across years, which helped compensate for uneven sampling and sparse data in some years. Similarly, the integrated analysis of the effect of water temperature on the timing of horseshoe crab spawn allowed us to effectively impute some missing

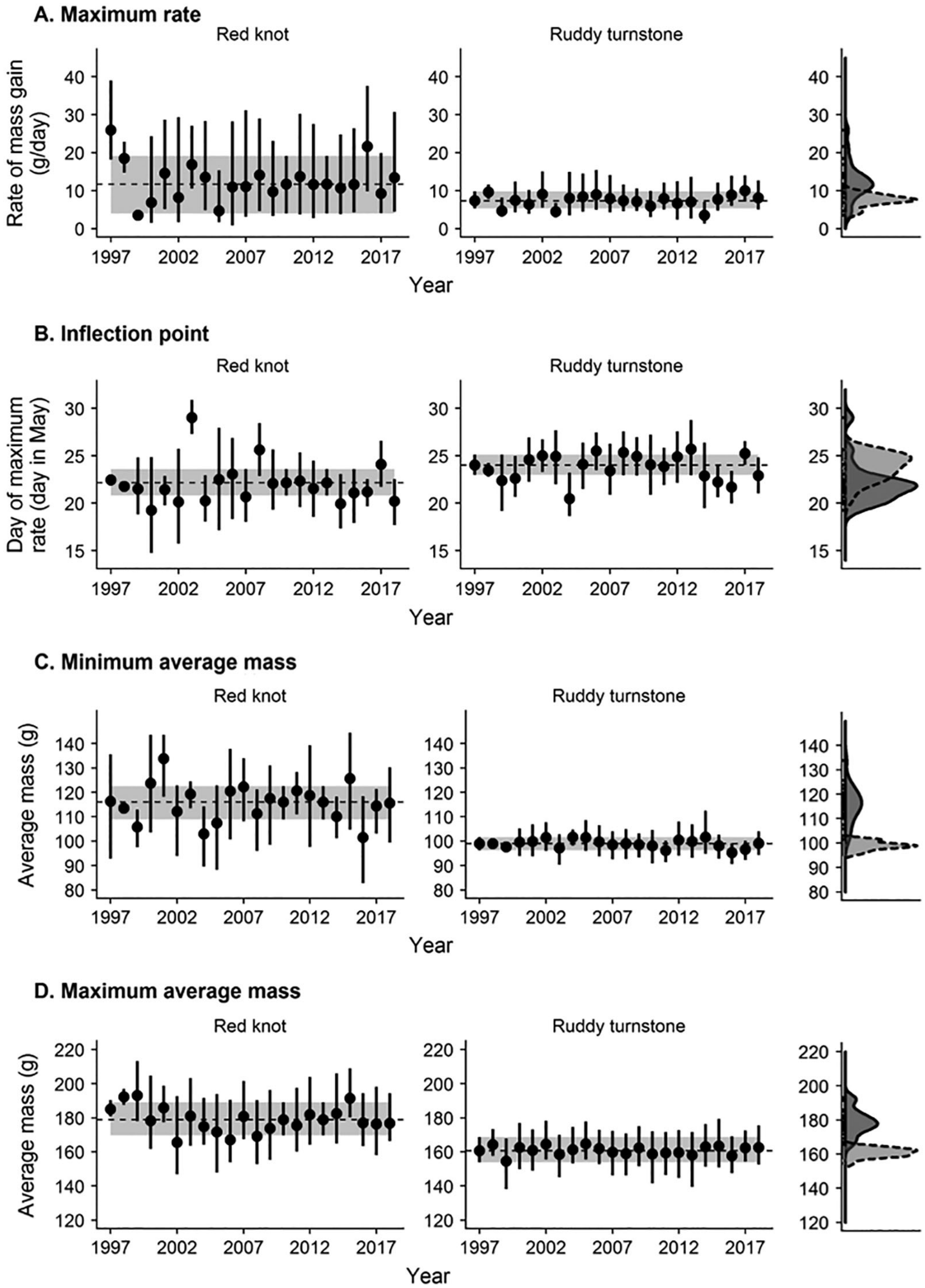

Fig. 3. Annual variation in mass gain model parameters for red knot and ruddy turnstone. Points and vertical lines show the posterior mean and 95% credible interval (CRI) for estimated maximum rate of mass gain (A), inflection point of the mass gain curve (B), minimum average mass (C), and maximum average mass (D) for each year. Dashed horizontal lines and shaded region represent the global average parameter value and 95% CRI. Kernel densities of estimated annual means are shown on the right (ruddy turnstone: dashed line, light gray; red knot: solid line, dark gray).

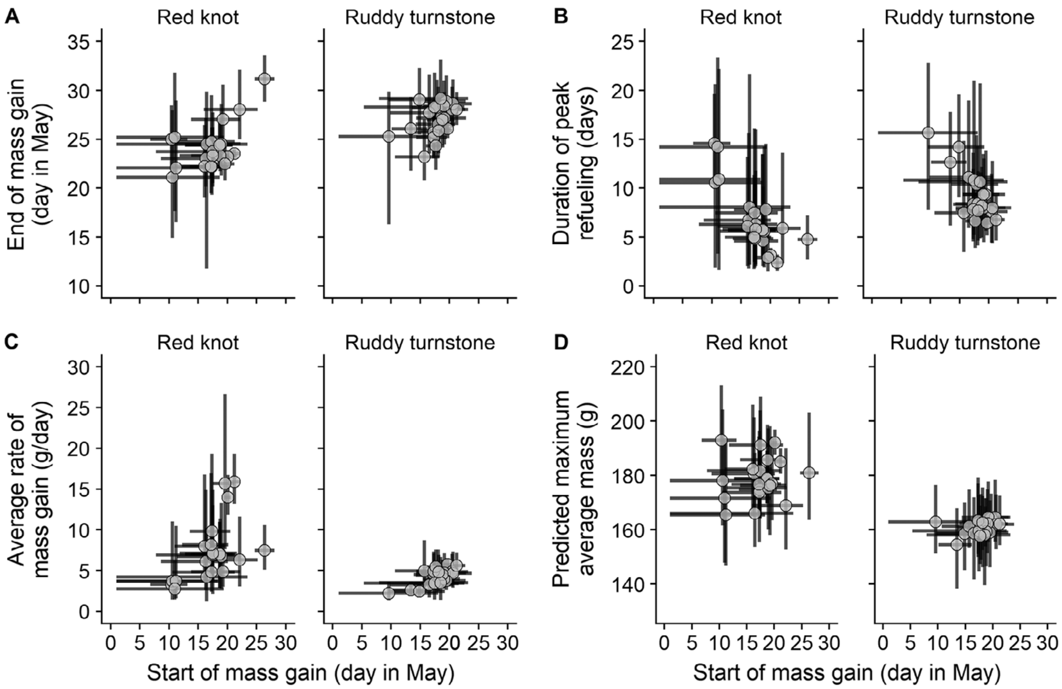

Fig. 4. Association between the day on which peak refueling began and the day on which it ended (A), the duration of the peak refueling period (B), the average rate of mass gain (C), and the predicted maximum average mass (D).

Table 2. Estimated effects of the timing and abundance of horseshoe crab spawning on mass gain model parameters for red knot and ruddy turnstone.

Species	Model parameter	Covariate	Mean	LCRI	UCRI	γ	*f*
Red knot	Maximum rate	Abundance	3.4	−9.6	15	0.21	0.72
	Maximum rate	Timing	−4.1	−15	6.1	0.18	0.80
	Maximum rate	Abundance × timing	−8.1	−22	3.6	0.36	0.92
	Inflection point	Abundance	−0.35	−2.2	1.5	0.03	0.66
	Inflection point	Timing	−1.4	−2.7	0.01	0.14	0.97
	Inflection point	Abundance × timing	0.82	−1.2	2.9	0.04	0.80
Ruddy turnstone	Maximum rate	Abundance	0.83	−1.7	3.9	0.13	0.75
	Maximum rate	Timing	0.34	−1.9	2.9	0.09	0.63
	Maximum rate	Abundance × timing	−0.69	−4.3	2.5	0.13	0.68
	Inflection point	Abundance	−0.06	−1.3	1.2	0.06	0.55
	Inflection point	Timing	−0.52	−1.7	0.63	0.08	0.83
	Inflection point	Abundance × timing	0.38	−1.2	1.9	0.08	0.70

Notes: Parameter estimates are reported as the means and 95% credible intervals (LCRI, UCRI) of the posterior distributions. Inclusion probability (γ) is the proportion of MCMC iterations in which that covariate was included as a predictor. *f* is the proportion of the posterior distribution that is the same sign as the posterior mean. LCRI, lower bounds of the 95% credible interval; UCRI, upper bounds of the 95% credible interval.

data. However, this approach propagates all uncertainty through each level of the modeling hierarchy and, in years with sparse shorebird mass data, this can result in substantial uncertainty in model parameter estimates. Wide credible intervals around these estimates may have contributed in part to low inclusion probabilities for the covariates associated with horseshoe crab abundance and timing of spawn. Additionally, the horseshoe crab spawning survey used here measures spawning females, which we use as a proxy for egg abundance, rather than the abundance and availability of horseshoe crab eggs directly throughout the season. However, we still found evidence of a relationship between mass gain dynamics—especially the maximum rate of mass gain—and the relative availability of horseshoe crab eggs for red knot and a much weaker relationship for ruddy turnstone. This indicates that these two species, similar in many other aspects of their ecology, are responding differently to changes in local conditions during migration.

For this study, we captured shorebirds foraging along the Delaware coast of Delaware Bay, but shorebirds use beaches in New Jersey and Delaware interchangeably during stopover. Although individuals move among beaches, likely tracking food availability (Karpanty et al. 2006), this analysis is focused at the level of the population; such individual movements should not influence our ability to estimate changes in the population average mass across the season. Previous analyses of red knot mass gain in Delaware Bay have pooled capture masses from both states (Atkinson et al. 2007, Gillings et al. 2009), indicating no substantive difference in mass gain dynamics. Additionally, both the timing and overall abundance of horseshoe crab spawning activity are highly correlated between states (Appendix S4: Figs. S1, S2). Therefore, we believe the data used here are sufficient to make inference about stopover dynamics and the ecological differences between these two species.

Ruddy turnstone seemed unaffected by annual variation in horseshoe crab egg availability, likely because their generalist foraging strategy allows them to exploit a variety of prey more easily. Additionally, ruddy turnstone foraging behaviors are more active and aggressive (e.g., digging up buried eggs), which increases the relative availability of horseshoe crab eggs. In contrast, red knot only consume eggs readily available in the upper layer of sand (Gillings et al. 2007). Red knot undergo extreme physiological changes during migration, including a reduction in gizzard size which must be regrown before consuming hard-shelled prey (van Gils et al. 2005), which are their primary prey at other sites worldwide (Piersma and Drent 2003). As a result, upon first arrival knots are especially reliant on the high-quality soft-shelled horseshoe crab eggs which may be consumed regardless of gizzard size (van Gils et al. 2003). To our knowledge, there is no evidence that ruddy turnstone experience similar physiological changes, which may also in part explain their ability to maintain a consistent rate of mass gain regardless of horseshoe crab spawning dynamics. It is also possible that ruddy turnstone are using a hop strategy (Warnock 2010) during northward migration, making more stops with short-distance flights in between, as opposed to the jump strategy used by red knot at this site. In general, ruddy turnstone have a broader arrival window than red knot and gain less mass relative to their minimum arrival mass (Appendix S1), which may indicate differences in migration strategy between these two species. Use of Delaware Bay as one of several stopover sites, instead of as the primary stop between nonbreeding and breeding sites, would allow for more flexibility in response to variation in the abundance and timing of horseshoe crab spawning. Although ruddy turnstone are known to perform long-distance flights in the East Asian Australasian Flyway (Minton et al. 2011), without further evidence from this flyway it is possible that the results presented here also reflect differences in migration strategy.

Our estimated minimum and maximum average masses correspond with the minimum and maximum published masses for these species (red knot 125–205 g; Baker et al. 2001; ruddy turnstone 84–190 g; Nettleship 2000). Birds are arriving at Delaware Bay close to their minimum possible mass and, after only a few weeks, departing close to the maximum possible, approximately doubling their body mass. This underscores the importance of prey availability at this stopover site. Although this analysis indicated substantial uncertainty in maximum average mass due to sparse data toward the end of the season in most years, the overall average maximum mass for red knot predicted from this analysis (178 g) agrees with predictions of optimal red knot departure mass made by Baker et al. (2004). That study, based on red knot physiology and optimal fuel load following Kvist et al. (2001), estimated that a departure mass of 180 g is necessary for sufficient fat stores to reach the

Arctic breeding grounds in a single flight. This threshold mass of 180 g has been used in conservation management planning to assess flyway population health in Delaware Bay (McGowan et al. 2011), which this study reaffirms. We note, though, that this analysis focuses on the population while others have investigated departure weight on the individual level (Baker et al. 2004, McGowan et al. 2011). A population average departure mass of 180 g will result in some individuals below that threshold, which could lead to negative individual carry-over effects. Additionally, for this study we mostly captured shorebirds in foraging flocks, which inherently biases our sampling to those birds still actively refueling and excludes those that have reached their departure masses and are preparing to continue migration. For these reasons, we are cautious to interpret estimates of minimum or maximum average mass and focus instead on the dynamics of the timing and rate of mass gain, which should be unaffected by the above concerns.

In cooler years, when the relative availability of horseshoe crab eggs was below average, red knot experienced a later onset of mass gain and gained mass more rapidly. This indicates some flexibility in the rate of mass gain and suggests that birds may increase the rate of fat deposition in years with later food availability to avoid delayed departure from the stopover site. Optimal migration theory predicts strong selective pressure on optimizing fuel deposition rates during migratory stopover (Hedenström and Alerstam 1997), and evidence indicates that Arctic-breeding shorebirds operate primarily under time constraints during northward migration (Zhao et al. 2017). Our observation that red knots increased mass gain rates in mismatch years, as opposed to maintaining a lower rate of mass gain but delaying departure from the stopover site, aligns with such a time-constrained strategy. In addition to a narrow time window for breeding, shorebirds are also constrained by a fixed single-clutch size (usually four eggs) and have little flexibility in their breeding strategy to compensate for unfavorable conditions encountered during migration (Arnold 1999). The potential impacts of climate-induced changes in phenology for breeding behavior have been well-documented (Both et al. 2005, Winkler et al. 2002), but increased frequency of mismatches, and potential associated physiological costs, may be especially detrimental to species like shorebirds with limited capacity to compensate at other points of the annual cycle.

Red knot refueling was slower in years with greater prey abundance and ruddy turnstone maintained a consistent rate of mass gain, suggesting that a slower mass gain is preferable and there may be a physiological cost of rapid refueling. Other studies have shown that individual mass predicts timing of departure from the stopover site and possibly breeding success, with heavier birds choosing more advantageous tailwinds and having a greater probability of being observed during the following autumn (Duijns et al. 2017). We found no evidence for population-level delays or lack of mass gain in mismatch years, but carry-over effects from mismatches may potentially be acting on individuals to reduce survival probability or breeding success. Preliminary work in this system indicates that after years in which the population experienced rapid mass gain, red knot apparent annual survival probability was lower (Tucker 2019). Future work investigating individual-level responses to mismatch would help in assessing potential carry-over effects, but such studies are difficult because within-season individual recaptures are typically rare in stopover systems. Alternative methods of weighing birds without physical capture may be needed, such as that used by Delingat et al. (2006).

This work provides a framework to evaluate population responses to changes in prey phenology at other stopover sites that may also be vulnerable to climatic change (Steen et al. 2018). Long-distance migrants rely on predictable resources en route and even when these linkages are simple, populations can be vulnerable to change (Runge et al. 2014). The predictability of prey availability at these sites facilitates specialization, but if the abundance or timing of resources becomes unpredictable, we expect generalists to be better able to cope. In this system, stochastic fluctuations in spring water temperature determine, in large part, the timing of prey availability. If there was a sustained cooling trend in water temperature, birds may be able to shift their migration timing to adapt. Although much of the literature on ecological mismatches focuses on directional shifts in phenology, climate models also predict increased variability in temperature and precipitation (Stouffer and Wetherald 2007, Holmes et al. 2016). This may be an increasingly common cause of mismatches in the future as conditions become more unpredictable.

Considering species traits such as foraging ecology is likely to be important in predicting population responses and understanding species persistence under global change (Foden et al. 2013, Pacifici et al. 2017). A diverse body of research has shown that species that specialize on habitat types, prey, or host plants are more vulnerable to changing environmental conditions, leading to disproportionate population declines (Clavel et al. 2011, Davey et al. 2012) while generalist species have greater flexibility to expand into and cope with novel environments (Jonsen and Fahrig 1997, Stefanescu et al. 2011). Even with closely related species that share many ecological and life-history traits, differences in foraging ecology may explain differences in distribution, population trends, and status. As the myriad effects of global climate change become more pronounced, species traits will be important in predicting which species will persist and, therefore, the impacts of such changes on ecological communities.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2898/full