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ORIGINAL PAPER

No effects of asynchrony between hatching and peak food availability on chick growth in Semipalmated Plovers (*Charadrius semipalmatus*) near Churchill, Manitoba

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Abstract

Birds rely on consistent patterns of food availability on their breeding grounds to successfully complete their breeding cycle. Due to ongoing warming of the sub-Arctic, there is potential for a mismatch between the peak in available invertebrate biomass and the peak in food demand for shorebird chicks. During the summers of 2010 and 2011, we investigated the relationship between temperature and benthic and terrestrial invertebrate biomass, measured using three sampling techniques in Churchill, Manitoba. We also investigated the relationship between timing of breeding of Semipalmated Plovers (*Charadrius semipalmatus*) and timing of peaks in invertebrate biomass. In 2011, chick growth rates were also measured to examine whether hatching in synchrony with the peak in invertebrate biomass during the brood rearing period affected growth rates. In 2010, emergent and core invertebrate biomass were negatively related to soil degree days, whereas in 2011, core biomass increased with soil degree days and pitfall biomass increased with air temperature. Total invertebrate biomass (summed over trap types) peaked from 25 to 31 days before the median chick hatch date in 2010 and 10 days after the median chick hatch date in 2011. In 2011 we did not detect any effects of asynchrony on the growth of Semipalmated Plover chicks. These results may indicate that food resources in their environment remain adequate throughout the breeding season, despite inter-annual fluctuations in the timing of invertebrate peaks.

Keywords *Charadrius semipalmatus* · Invertebrates · Shorebird · Chick growth · Phenology · Weather

Introduction

Migratory species time their movements in part to take advantage of seasonal flushes in food resources on their breeding grounds (Johansson and Jonzen 2012). The phenology of migration in many long-distance migrant birds is primarily driven by day length, an environmental factor that is not influenced by weather (Both and Visser 2005). As climate change affects northern latitudes at a more accelerated pace than southern latitudes, differential changes in climate may outpace the ability of populations to adapt to climate-induced changes in the timing of resource peaks on their breeding grounds (Both and Visser 2001; Stenseth and Mysterud 2002; Senner 2012). A delayed migratory response to changes in climate on the breeding grounds could result in a later start to breeding, lower breeding success, and a subsequent decline in population size (Both and Visser 2001; Drever et al. 2012).

Climate change induced gaps between the timing of hatch and peaks in food availability on the breeding grounds, hereafter "mismatch" (Stenseth and Mysterud 2002), has been noted as one the of the possible mechanisms driving population declines in insectivorous Arctic-nesting shorebird populations (Tulp and Schekkerman 2008). In the Arctic, short peaks in invertebrate abundance during mid-summer (MacLean and Pitelka 1971; McKinnon et al. 2012; Bolduc et al. 2013) are driven largely by temperature (Hodkinson et al. 1998; Danks 2004). Short summer and weather-related resource availability translates into a small window during which there is adequate food available for reproduction and the growth and survival of young. As such, birds breeding

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at northern latitudes are under intense pressure to acquire sufficient food to fuel them throughout the various stages of their breeding cycle (Morrison et al. 2007; Senner 2012). Thus, birds should time their breeding cycle so that chicks hatch just prior to the peak in invertebrate biomass (Meltofte et al. 2008).

During the breeding season in the sub-Arctic, Semipalmated Plovers (*Charadrius semipalmatus*) are opportunistic foragers that consume a variety of invertebrates from wet substrates, which is dependent largely (but not exclusively) on their availability and detectability (Skagen and Oman 1996; Rose and Nol 2010). Semipalmated Plover chicks are precocial, with a fledging period of 21 days (Nol and Blanken 2014). Unlike adults who often fly 3 km to forage (CAC pers. obs.), chicks generally forage within 200 m from their nest (CAC pers. obs., Armstrong and Nol 1993).

The objectives of this study were to: (1) investigate drivers of seasonal variation in the invertebrate biomass throughout the shorebird breeding season, (2) test for potential mismatch between peaks in invertebrate biomass and peaks in hatching of Semipalmated Plover chicks, and (3) assess the effects of a mismatch on chick growth rates. Determining the timing of prey availability and hatching dates is a necessary precondition for the mismatch hypothesis (Dunn et al. 2011).

Materials and methods

Study site

Data were collected during the summers of 2010–2011 between 29 May and 10 August in the Churchill, Manitoba (58°45′N, 94°04′W, Fig. 1) region. Invertebrate sampling was conducted at known Semipalmated Plover foraging sites. Semipalmated Plovers foraged both along the coast and at inland ponds on wet substrates free from vegetation. Coastal sites were < 500 m from Hudson Bay with no vegetation barrier between Hudson Bay and the foraging site. Coastal habitat zones were found at the supratidal zone along Hudson Bay, the substrate of which was saturated and high in organic content due to high amounts of macroalgal detritus from marine sources immediately surrounding the sampling locations but not constituting them. These zones were never submerged during the tidal cycle during the study period, and the shallow ponds and the soils surrounding them were potentially brackish due to sea spray from wind, storm events, or inputs from the decaying marine vegetation (Adams et al. 1992). Vegetation grew in low densities surrounding these areas, and

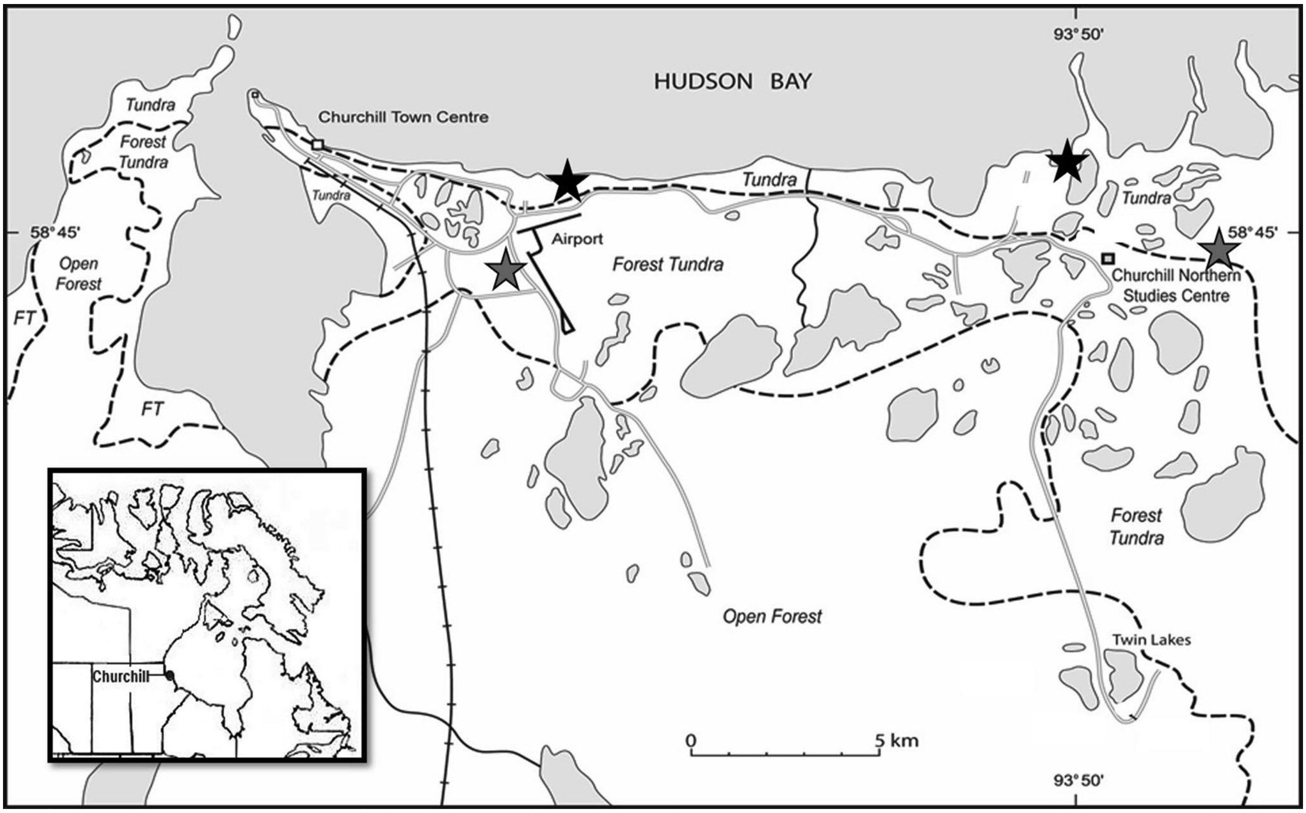

Fig. 1 Map of the Churchill, Manitoba study site. Black stars indicate coastal sites and gray stars indicate inland sites. Dashed lines separate major habitat types in the Churchill region

consisted of willow (*Salix* spp.), birch (*Betula* spp.) and sedges (*Cyperaceae*). The sizes of the ponds at these sites changed frequently, affected both by rainfall and evaporation during high temperatures. Inland freshwater ponds were > 500 m from the coast. Willow, birch and sedges grew in the wet mud and gravel on the shorelines of these ponds.

Invertebrate phenology and biomass

Invertebrate sampling techniques were chosen to include the diversity of invertebrates likely to be consumed by Semipalmated Plovers which are generalist foragers (Nol and Blanken 2014). Emergence traps and soil core samples were collected every three to four days in 2010, and every three days in 2011. In 2010, three inland and seven coastal sites were sampled for invertebrates with the aim of sampling as many representative feeding sites as possible. In 2011, two coastal and two inland sites were sampled every three days to minimize among site variability. At each site, three 5-cm deep soil core samples were collected using a 5-cm diameter tube (sample volume = 98.1 cm^3), in addition to samples from three emergence traps. In 2010, emergence traps consisted of plastic rectangular containers (volume = 600 cm^2), coated with vegetable oil in the interior to trap the emerging insects and to ease extraction. In 2011, we used aluminum pie plates with an exposed area of 314 cm^2. In 2011, a round white pitfall trap (11.5 cm diameter × 8.5 cm deep (total surface area was 103.9 cm^2) filled with soapy water, was set approximately 30 cm from each emergence trap. Pitfall traps were buried flush with the ground's surface. Emergence and pitfall traps were left at each sampling location for a period of 24 h and then brought back to the lab. Invertebrates were extracted from emergence traps using forceps and from pitfall traps by pouring their contents through coffee filters. All samples were then stored in 95% ethanol for later identification to Family, enumeration, and measurement. Invertebrates from core samples were extracted within 12 h of collection so that invertebrates were still alive, as movement facilitated detection. Each sample was placed into a white observation tray and components of the sample were separated with water and forceps. Samples were viewed in the tray for a maximum of 20 min, but if no invertebrates were seen after 5 min, observation ceased. Invertebrates were removed and stored in 95% ethanol for later identification to Family, enumeration, and measurement (to nearest 1 mm).

In the sub-Arctic, invertebrate peaks are commonly driven by large numbers of small invertebrates, therefore, abundance is a poor representation of how much energy may be available to shorebirds at a given time (White et al. 2007). As such, peaks were ascertained based on biomass (g/trap) determined using length:mass relationships from linear and polynomial regressions and power functions derived previously for invertebrates in similar sub-Arctic environments (L.P. Nguyen, unpubl. data).

Each time a core sample was collected and an emergence trap was set, soil temperature of the top 10 cm of the sampling location was measured to the nearest 0.1 °C, using a digital temperature probe. Daily mean and minimum air temperatures were obtained from Environment Canada (2013) for the Churchill, Manitoba airport weather station (Station A). Cumulative air degree days were calculated for each sampling day by summing temperatures for each day the mean air temperature was above zero, beginning with the first day when there was consistently no snow cover (15 May 2010 and 16 May 2011). Cumulative soil degree days were calculated similarly but starting with the first day of invertebrate sampling in each year (28 May 2010 and 29 May 2011).

Semipalmated Plover breeding phenology and chick growth.

Semipalmated Plover nests were located during the laying and incubation periods at coastal and inland locations (Nol and Blanken 2014). Areas with known nests or pairs from previous years were visited every 2–3 days. Nests were located for nearly every pair observed, and these nests were monitored every 2–3 days until no longer active. Clutch sizes were recorded and predicted hatch dates were estimated by counting ahead 24 days (the average incubation period for Semipalmated Plovers) from the clutch completion date (Nol and Blanken 2014). If a nest was found after the clutch had been completed, estimated clutch completion date was determined using the egg flotation method (Liebezeit et al. 2007), or by back-calculating from the hatch date if this was known.

During 2011, nests were visited at hatch so that each chick ($n = 58$) could be banded at age 0. Each chick's leg was banded with an aluminum-numbered band and each brood was assigned a unique combination of two color bands. After banding, each chick was weighed to the nearest 0.5 g using a 50-g Pesola scale. Broods were then relocated approximately every three days, until we could no longer locate them, or until chicks fledged.

Statistical analysis

Effects of location (coastal versus inland) and environmental temperature (air temperature, soil temperature, air degree days, and soil degree days) on invertebrate biomass were tested using multiple linear mixed-effects models. Biomass of each trap type (separately) was the dependent variable for all analyses. Because of differences in either sampling locations or trap size, the 2 years were analyzed separately. The effects of environmental temperature and location on biomass were modeled as fixed effects and site was included as a random effect because we had three replicate traps (for each type), per site. As air temperature, soil temperature, air degree days, and soil degree days were all highly correlated ($r > 0.62$), one weather variable for each model was selected based on the presumed relative importance of the substrate for invertebrate movement (e.g., core and emergent samples were predicted to relate most strongly to soil degree days, while the activity of invertebrates falling into pitfall traps was predicted to be most closely related to air temperature). All data were log-transformed before analysis to conform to normal distributions.

To assess the effects of asynchrony between peak in invertebrate biomass and chick hatching in 2011, peak in invertebrate biomass (summed across all trap types) within the hatching period were identified graphically. The peak was defined as the day on which invertebrate biomass was greatest between 7 and 25 July (hatch dates for the first and last nest to hatch, respectively). Growth curves (growth modeled on age alone) were generated using the package "drc" in Program R (Ritz and Streibig 2005). Preliminary model selection (Akaike Information Criterion, AIC) revealed the four parameter logistic model to be the best fit to the growth data over a series of other models. To assess the importance of asynchrony on chick growth, growth curves were then generated for chicks hatching within 5 days of the peak in invertebrate biomass and chicks hatching greater than 5 days before or after the peak and compared to growth modeled on age alone, using the package 'drc' (Ritz and Streibig 2005).

The model with the lowest AIC score was considered the best fitting model, and models with < 2 delta AIC from the top model were considered competitive (Burnham and Anderson 2002). Analyses were conducted using statistical program R (R Development Core Team 2015) and JMP (SAS Institute, Inc. 2014). Unless otherwise specified, all statistical tests were based on an alpha of 0.05.

Results

Churchill average air temperatures ranged from − 1.6 °C in May to 23.5 °C in August. Soil temperatures varied from − 0.4 °C in May to 20.5 °C in August. During invertebrate sampling minimum daily soil temperatures dropped below 0 °C in three days in May 2010, but not in 2011. Soil temperatures remained consistently above freezing during June, July and August in both years.

Invertebrate phenology and biomass

In 2010, 28 invertebrate families from eight orders were identified. Prey from the Order Diptera were the most abundant (66.4% of all invertebrate biomass) while prey from the Order Collembola were the second most abundant (18.7%). In 2011, 27 families from seven orders were identified. Diptera accounted for 39.6% of the overall invertebrate biomass, with Acarina and Coleoptera accounting for 19.6% and 12.3%, respectively. Family composition of invertebrates was similar between coastal and inland sites in both years, with no exclusively marine invertebrates collected at coastal sites. Based on biomass, Diptera (44.6%) were the dominant taxa in core samples followed by Oligochaeates (31.1%) and Collembola (22.7%). Emergence traps caught 59.7% Collembola, 28.3% Diptera and 8.1% Acarina. Finally, pitfall traps contained 43.2% Acarina, 35.0% Diptera, and 7.9% Hemiptera.

Of the three trap types, pitfalls yielded the highest invertebrate biomass (Table 1). Peaks of invertebrate biomass varied depending on year, trap type and location (Fig. 2). In 2010, there was only one distinct peak for both core and emergent traps, whereas in 2011 there were two distinct peaks in invertebrate biomass from both emergent and pitfall traps but these occurred at different times. There was one peak in invertebrates collected from core samples but this peak was only evident from samples collected from coastal sampling sites (Fig. 2).

Soil degree days was a significant negative predictor of biomass from core and emergent traps in 2010,

Table 1 Least-squared mean invertebrate biomass (± 95% CI, back-transformed from log values to g) per trap, from three invertebrate sampling techniques, for coastal and inland locations around Churchill, Manitoba (2010, 2011)

Trap type	2010		2011	
	Coastal	Inland	Coastal	Inland
Core (g)	0.004 (0.001–0.011)	0.001 (0.0002–0.008)	0.008 (0.001–0.058)	0.005 (0.0007–0.041)
Emergent (g)	0.24 (0.09–0.64)	0.18 (0.05–0.66)	0.91* (0.47–1.78)	0.21* (0.11–0.41)
Pitfall (g)	NA	NA	53.0* (28.3–99.2)	9.7* (5.2–18.1)

Asterisks indicate significant differences ($P < 0.05$) in invertebrate biomass between locations, within years

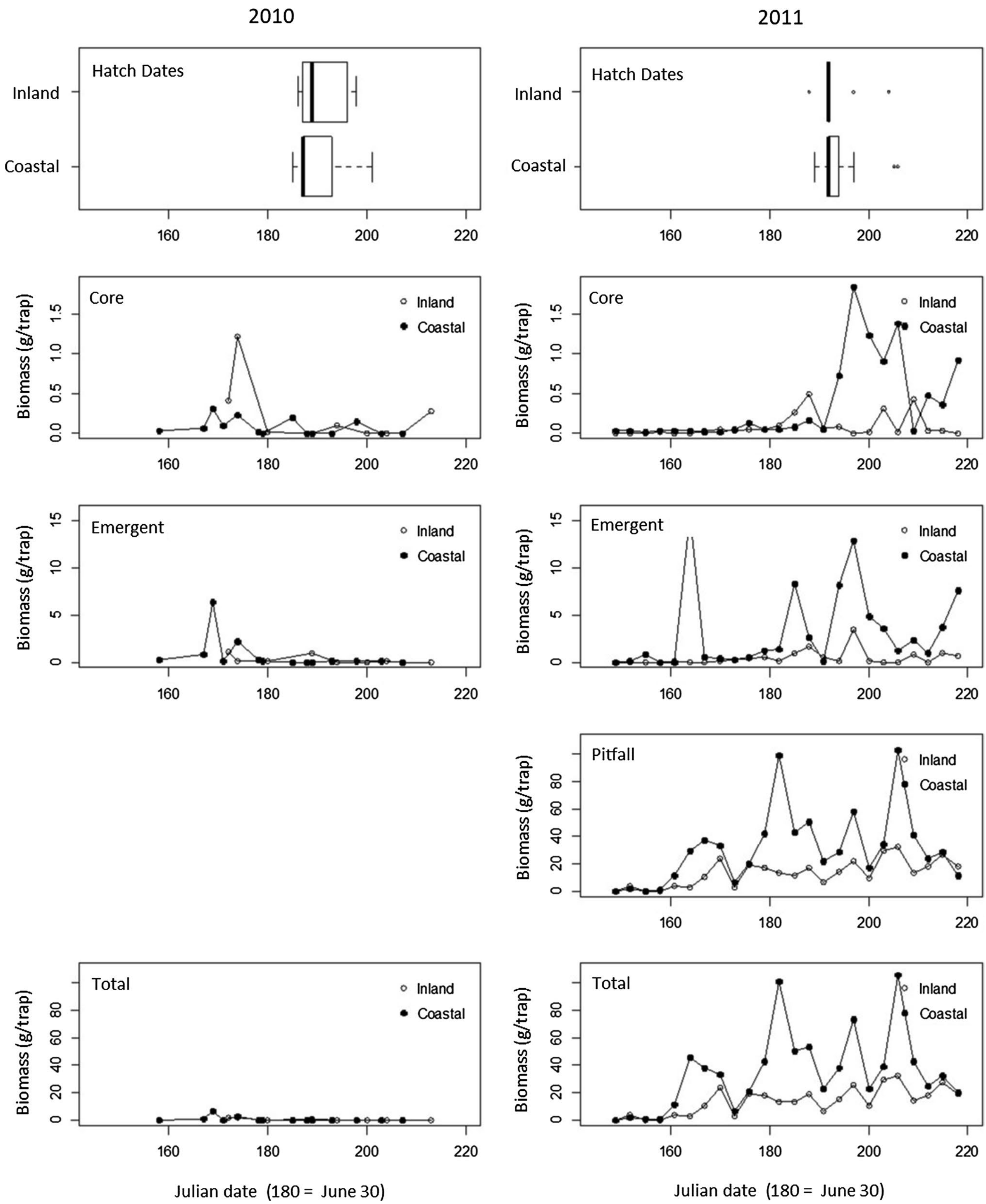

Fig.2 Boxplots of hatch dates for Semipalmated Plovers (*Charadrius semipalmatus*), and mean daily invertebrate biomass between 29 May and 10 August in 2010 and 2011 near Churchill, Manitoba. Boxplots present the median, 10th, 25th, 75th, 90th percentiles, and all outliers

Table 2 Parameter estimates from GLM to determine impacts of habitat and temperature on invertebrate biomass (log), collected from three trap types from sampling sites around the Churchill, Manitoba region

Year	Trap type	*n*	Intercept	Habitat *(Coast)	*P*	Temperature (°C)	*P*	Variance component site (%)
2010	Core[a]	37	– 5.02	0.31 (0.45)	0.45	**– 0.003 (0.001)**	**0.001**	9.9
	Emergent[a]	26	– 0.20	0.05 (0.29)	0.86	**– 0.004 (0.0006)**	**0.001**	33.0
2011	Core[a]	24	– 5.81	0.42 (0.49)	0.39	**0.002 (0.0006)**	**0.001**	25.4
	Emergent[a]	24	– 1.01	**0.72 (0.24)**	**0.003**	0.0006 (0.0004)	0.14	6.4
	Pitfall[b]	24	2.45	**0.85 (0.23)**	**0.001**	**0.07 (0.01)**	**0.0001**	9.8

Bolded values represent significant predictors ($P < 0.05$)

[a] Temperature is measured as soil degree days

[b] Air temperature

Table 3 Semipalmated Plover (*Charadrius semipalmatus*) nesting phenology for 2010 and 2011 near Churchill, Manitoba

	2010		2011	
	Coast	Inland	Coast	Inland
Earliest, latest and median clutch completion dates	10 June–2 July (20 June)	11–27 June (20 June)	13 June–6 July (25 June)	12–30 June (22 June)
N (nests)	30	11	27	11
Earliest, latest and median hatch dates	4 –20 July (12 July)	5–17 July (11 July)	8–25 July (17 July)	7–23 July (15 July)

while in 2011 this relationship was positive for core traps (Table 2). Air temperature was a significant positive predictor of pitfall trap biomass in 2011. There was significantly greater invertebrate biomass captured in emergence and pitfall traps at the coast than inland in 2011 (Tables 1, 2).

Semipalmated Plover breeding phenology and chick growth

Median hatch dates were similar between coastal and inland sites in both years, but median hatch dates were approximately 4 to 5 days later in 2011 than in 2010 for both sites (Table 3). In 2010, invertebrate biomass (summed across all trap types) peaked 31 days before the median hatch date of the chicks at the inland sites, and 25 days before the median hatch date at the coastal sites (Fig. 2). In 2011, peak invertebrate biomass occurred 10 days after the median hatch date at the inland sites, and 8 days after the median hatch date at the coastal sites (Fig. 1).

We measured the mass of 58 plover chicks on 107 occasions (average number of recaptures per chick: 1.8, range 1–5). Based on the 4-parameter logistic growth model (growth as a factor of age alone), growth was fastest at 7.4 days of age (Fig. 3). The mean chick mass at age 0 was 6.0 g and the mean mass at the asymptote of this model was 31.5 g, which is approximately 67% of the average adult body mass of 47 g (Teather and Nol 1997). We did not detect any effect of asynchrony between the timing of food peaks and hatch as growth rates of chicks that hatched within 5 days of the invertebrate peak did not differ from those that hatched outside of the peaks (ΔAIC = 2.82; Table 4, Fig. 3).

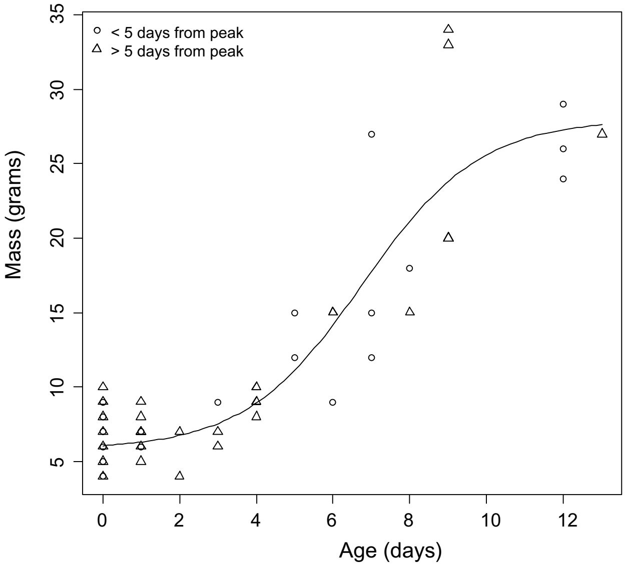

Fig. 3 Plot of the four-parameter logistic growth curve for all Semipalmated Plover (*Charadrius semipalmatus*) chicks that were measured in the 2011 breeding season near Churchill, Manitoba. Circles represent chicks that hatched within 5 days of the peak in invertebrate biomass, and triangles represent those that hatched greater than 5 days before or after the peak

Table 4 Comparison of growth models for chicks of Semipalmated Plovers (*Charadrius semipalmatus*)

Model	Number of parameters	AIC	Δ AIC
Age + synchrony (within 5 days)	3	491.99	3.04
Age	2	489.17	0

Discussion

Results from our invertebrate sampling suggest a high level of inter-annual variation in both the timing of resource peaks and their relationship with environmental variables. In Arctic and sub-Arctic regions, invertebrate activity begins in early spring in response to snowmelt due to temperatures remaining consistently above freezing (Danks 2004; Hoye and Forchhammer 2008a, b). In general, invertebrate activity increases as temperature increases throughout the season (Hodkinson et al. 1998; Hoye and Forchhammer 2008b; Bolduc et al. 2013). In 2011, our results from both core sampling and pitfall sampling were consistent with these general trends, with positive relationships with soil and air temperatures, respectively. However, once invertebrate activity is triggered by temperatures above 0°C, there is a flush of emergence, often followed by a drop in invertebrate emergence when the seasonal stock is depleted (Hoye and Forchhammer 2008a). This may explain the negative relationships documented in 2010 for both core and emergent sampling. Annual variation in phenology of insects and overall weather patterns can result in complex and inconsistent environmental effects (Bolduc et al. 2013). Indeed, relationships between environmental predictors and invertebrate biomass were significant in all but one of the five possible year/trap combinations, but the relationships were not consistent between years and did not have large explanatory power ($R_{\text{adj}}^2 < 24\%$). That the sampling methods we used collected such a diverse suite of invertebrate orders, each possibly with its own relationship to environmental variables, could explain these inconsistent environmental effects.

In 2010, there was only one distinct peak for both core and emergent traps, whereas in 2011 there were two distinct peaks in invertebrate biomass from both emergent and pitfall traps but these occurred at different times (Fig. 2). There was one peak in invertebrates collected from core samples but this peak was only evident from samples collected from coastal sampling sites (Fig. 2).

Our results also indicate considerable inter-annual variation in the number and timing of invertebrate biomass peaks between years. Whereas, we found one distinct biomass peak for core and emergent traps in 2010 and core traps in 2011 (coastal sites only), there were two distinct, but not simultaneous, peaks for emergent and pitfall traps in 2011. In 2011, the first peak from emergent traps appeared in early June, while the first peak from pitfall traps occurred much later. For both sampling methods the second peak occurred during the period when chicks were growing. Pitfall traps captured the highest biomass of invertebrates and the results with this trapping technique suggested that warmer air temperatures would allow for greater foraging success by plovers, due to greater invertebrate activity levels. As plovers are generalist foragers on the breeding grounds (Baker 1977; Nol and Blanken 2014) these multiple peaks and patterns in biomass may have provided a diversity of food throughout the nesting cycle.

Semipalmated Plover chicks hatched on average 25–31 days after the seasonal peak in invertebrate biomass in 2010, and 8–10 days before the seasonal peak in 2011. The number of days of mismatch between hatching of chicks and the seasonal peaks in food resources during the chick-rearing period, is comparable to results found in other studies (McKinnon et al. 2012). To support the mismatch hypothesis as an explanation for reduced reproductive success, there must be some observable effect of asynchrony between hatching and peaks in food resources on growth, survival, or recruitment. During the year in which growth of chicks was measured, all chicks hatched before the seasonal (and greatest) peak in total food resources. However, when the effects of asynchrony were tested based on the timing of hatch in relation to the peak of food that was identified within the hatching period, no effects of asynchrony on the growth of Semipalmated Plover chicks were detected. This is in contrast to several other studies of shorebirds that provide evidence that it is beneficial for chicks to hatch in synchrony with peaks in food availability to achieve an optimum rate of development (Schekkerman et al. 2003; McKinnon et al. 2012). Similarly, cool weather, assumed to result in less foraging time and lower food intake, was associated with reduced growth rates in Little Stint (*Calidris minuta*) (Tjorve et al. 2007) and declines in Dunlin (*Calidris alpina*) and Little Stint growth rates were associated with declines in invertebrate abundance (Tulp 2008).

That no effect of asynchrony was detected on chick growth in the Semipalmated Plover could indicate that their environment is relatively rich in terms of food availability even outside of our defined peaks in insect availability. No starving chicks were captured and this is consistent with this hypothesis. Inland sampling sites contained substantially lower invertebrate biomass than the coastal sites (at least based on emergent and pitfall sampling), consistent with what has been found previously in Churchill, Manitoba (Nol and Blanken 2014). Too few older chicks were captured at inland sites to make any valid comparisons of growth between habitats but no signs of starvation were detected there either.

High Arctic environments exert higher thermoregulatory demands on chicks than at sub-Arctic latitudes, and as such, they require a minimum daily intake of food to meet energetic requirements for growth and thermoregulation (Schekkerman et al. 2003). This could suggest that energetic requirements of chicks breeding in the sub-Arctic are not completely reliant on the peak, and that food levels would have to drop below some threshold for there to be a noticeable effect on chick growth and survival. Tulp (2008) found that Red Knot (*Calidris canutus*) chick growth rates dropped drastically when invertebrate biomass obtained in pitfall samples dropped below 100 mg/20 traps/day, while growth was considered normal at a minimum of 200 mg/20 traps/day, which was still well below their measured peak in invertebrate biomass. The pitfall traps used in this study had the same diameter surface exposed for potential prey (Tulp 2008) but captured biomass that was several orders of magnitudes more than this, even at inland sites. Thus, it may not be surprising that negative effects on chick growth were not detected. Even in the event of a true mismatch, there is also evidence that increased ambient temperatures during the brood rearing season may alleviate the effects of reduced food availability at least in the short term (McKinnon et al. 2013).

As generalist foragers, Semipalmated Plover adults consume food items that are available in abundance (Baker 1977; Skagen and Oman 1996; Smith and Nol 2000) with size selectivity for some prey items during the non-breeding season (Rose et al. 2016). This dietary flexibility allows them to forage in diverse habitats (Skagen and Oman 1996; Rose and Nol 2010). In this study, we defined our biomass peaks based on all available food items. However, our analyses could have been improved if we had site-specific diets of chicks, for example via DNA metabarcoding (McClenaghan et al. in press), and more accurately defined biomass peaks based on confirmed diet items only. In other studies detecting an effect of asynchrony in relation to seasonal peaks of insects, the study species exhibited more specialized foraging strategies, whereby they were reliant on a specific and/or smaller selection of invertebrate families [e.g., American Golden Plovers (*Pluvialis dominica*) (Pearce-Higgins et al. 2005) and Baird's Sandpipers (*Calidris bairdii*) on Tipulidae (McKinnon et al. 2012)]. This difference in foraging strategies between birds that do show signs of mismatch between timing of nesting and their prey, and those that do not is also born out in the literature on the impacts of mismatch on songbird demography (Dunn et al. 2011). Generalist bird species not only have more options for foraging, but peaks in invertebrate abundances are more difficult to document because total biomass encompasses a large range of invertebrate life histories. In the case of shorebirds nesting in the sub-Arctic, not only is there a greater abundance and diversity of invertebrates available for foraging shorebirds at lower latitude sites, but there are less consistent or pronounced peaks in food availability than there are at higher latitudes (Schekkerman et al. 2003; Tjorve et al. 2007; McKinnon et al. 2012; Bolduc et al. 2013).

The results here show an asynchrony between hatch and peaks in food resources for Semipalmated Plovers in Churchill, Manitoba but this asynchrony varied in direction between our two years of study. Further simultaneous sampling of food and nesting phenology over a much larger number of years, along with more detailed studies of chick diets, will allow determination of whether a shift in the seasonal abundance of invertebrates has occurred and whether there are negative consequences for plover demography.

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Compliance with ethical standards

Conflicts of interest There are no conflicts of interest to declare.

Ethical approval All protocols deployed during this study were approved by the animal care committee at Trent University.

References

Adams JB, Knoop WT, Bate GC (1992) The distribution of estuarine macrophytes in relation to freshwater. Bot Mar 35:215–226

Armstrong AR, Nol E (1993) Spacing behavior and reproductive ecology of the Semipalmated Plover at Churchill, Manitoba. Wilson Bull 105:455–464

Baker MC (1977) Shorebird food habits in the Eastern Canadian Arctic. Condor 79:56–62

Bolduc E, Casajus N, Laganeux P, McKinnon L, Gilchrist H, Leung M, Morrison RIG, Reid D, Smith PA, Bety Buddle CM, J, (2013) Terrestrial arthropod abundance and phenology in the Canadian Arctic: modelling resource availability for arctic-nesting insectivorous birds. Can Entomol 145:155–170

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298

Both C, Visser ME (2005) The effect of climate change on the correlation between avian life-history traits. Glob Chang Biol 11:1606–1613

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York

Danks HV (2004) Seasonal adaptations in Arctic insects. Integr Comp Biol 44:85–94

Drever MC, Clark RG, Derksen C, Slattery SM, Toose P, Nudds TD (2012) Population vulnerability to climate change linked to timing of breeding in boreal ducks. Global Change Biol 18:480–492

Dunn PO, Winker DW, Whittingham LA, Hannon SJ, Robertson RJ (2011) A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92:450–461

Environment Canada (2013) National climate data and information archive. https://www.climate.weatheroffice.gc.cahttps://www.climate.weatheroffice.gc.ca.

Hodkinson ID, Webb NR, Bale JS, Block W, Coulson SJ, Strathdee AT (1998) Global change and Arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. Arctic Alpine Res 30:306–313

Hoye TT, Forchhammer MC (2008a) Phenology of high-Arctic arthropods: effects of climate on spatial, seasonal, and inter-annual variation. Adv Ecol Res 40:299–324

Hoye TT, Forchhammer MC (2008b) The influence of weather conditions on the activity of high-Arctic arthropods inferred from long-term observations. BMC Ecol 8

Johansson J, Jonzen N (2012) Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. Ecol Lett 15:881–888

Liebezeit JR, Smith PA, Lanctot RB, Schekkerman H, Tulp I, Kendall J, Tracy DM, Rodrigues RJ, Meltofte H, Robinson J, Gratto-Trevor C, Mccaffery BJ, Morse J, Zack SW (2007) Assessing the development of shorebird eggs using the flotation method: species specific and generalized regression models. Condor 109:32–47

MacLean SF, Pitelka FA (1971) Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24:19–40

McClenaghan B, Nol E, Kerr K (in press) DNA metabarcoding reveals the broad and flexible diet of a declining aerial insectivore. Auk

McKinnon LM, Picotin M, Bolduc E, Juillet C, Bety J (2012) Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. Can J Zool 90:961–971

McKinnon L, Nol E, Juillet C (2013) Arctic-nesting birds find physiological relief in the face of trophic constraints. Sci Rep 3:1816

Meltofte H, Hoye TT, Schmidt NM (2008) Effects of food availability, snow and predation on breeding performance of waders at Zackenberg. Adv Ecol Res 40:325–343

Morrison RIG, Davidson NC, Wilson JR (2007) Survival of the fattest: body stores on migration and survival in red knots *Calidris islandica*. J Avian Biol 38:479–487

Nol E, Blanken MS (2014) Semipalmated Plover (*Charadrius semipalmatus*), In: Poole A (ed) The Birds of North America. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: https://bna.birds.cornell.edu/bna/species/444. https://doi.org/10.2173/bna.444

Pearce-Higgins JW, Yalden DW, Whittingham MJ (2005) Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). Oecologia 143:470–476

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria 3-900051-07-0 https://www.R-project.org/

Ritz C, Streibig JC (2005) Bioassay analysis using R. J Stat Softw 12:1–22

Rose M, Nol E (2010) Foraging behavior of non-breeding Semipalmated Plovers. Waterbirds 33:59–69

Rose M, Nol E, Pollock L (2016) Diet and prey size selectivity of Semipalmated Plovers in coastal Georgia. Can J Zool 94:727–732

SAS Institute (2014) JMP V. 11. SAS Institute Inc., Cary, NC, USA.

Schekkerman H, Tulp I, Piersma T, Visser GH (2003) Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134:332–342

Senner NR (2012) One species but two patterns: populations of the Hudsonian Godwit (*Limosa haemastica*) differ in spring migration timing. Auk 129:670–682

Skagen SK, Oman HD (1996) Dietary flexibility of shorebirds in the western hemisphere. Can Field Nat 110:419–444

Smith AC, Nol E (2000) Winter foraging behavior and prey selection of the Semipalmated Plover in coastal Venezuela. Wilson Bull 112: 467-472

Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. Proc Natl Acad Sci USA 99:13379–13381

Teather KL, Nol E (1997) Mixed sexual dimorphism in Semipalmated Plovers. Condor 99:803–806

Tjorve KMC, Schekkerman H, Tulp I, Underhill LG, de Leeuw JJ, Visser H (2007) Growth and energetics of a small shorebird species in a cold environment: the little stint *Calidris minuta* on the Taimyr Peninsula, Siberia. J Avian Biol 38:552–563

Tulp I, Schekkerman H (2008) Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61:48–60

Tulp I (2008) Correlates of growth rates in arctic shorebird chicks: daily weather and food abundance. In: Arctic pulse: timing of breeding in long-distance migrant shorebirds, pp 169–189. Ph.D. thesis, Rijksuniversitait, Groningen.

White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends Ecol Evol 22:323–330