Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic

L. McKinnon, M. Picotin, E. Bolduc, C. Juillet, and J. Bêty

Abstract: In seasonal environments, breeding events must be synchronized with resource peaks to ensure production and growth of offspring. As changes in climate may affect trophic levels differentially, we hypothesized that a lack of synchrony between chick hatch and resource peaks could decrease growth rates in chicks of shorebirds nesting in the High Arctic. To test this hypothesis, we compared growth curves of chicks hatching in synchrony with peak periods of food abundance to those hatching outside of these peak periods. We also tested for changes in lay dates of shorebirds in the Canadian Arctic using recent and historical data. Mean daily temperatures during the laying period increased since the 1950s by up to 1.5 °C, and changes in lay dates were apparent for three shorebird species, yet differences in median lay dates between 1954 and 2005–2008 were only significant for White-rumped Sandpiper (*Calidris fuscicollis* (Viellot, 1819)). During 2005–2008, there was only 1 year of relatively high synchrony between hatch and resource peaks. Asynchrony between hatch and peaks in Tipulidae biomass reduced growth rates in chicks of Baird's Sandpiper (*Calidris bairdii* (Coues, 1861)). As anticipated changes in climate may decouple phenological events, the effects of asynchrony on growth rates of arctic-nesting birds warrant further investigation.

Key words: phenology, mismatch, shorebirds, arthropods, Tipulidae.

Résumé : Dans les milieux saisonniers, les évènements de reproduction doivent être synchronisés avec les pointes de ressources pour assurer la production et la croissance de la progéniture. Comme l'incidence des changements climatiques peut varier selon les niveaux trophiques, nous avons postulé que l'absence de synchronisme entre l'éclosion des oisillons et les pointes de ressources pourrait entraîner une réduction des taux de croissance des oisillons d'oiseaux de rivage qui nichent dans l'Extrême Arctique. Pour vérifier cette hypothèse, nous avons comparé les courbes de croissance d'oisillons éclos durant des périodes de pointe d'abondance de nourriture à celles d'oisillons éclos en dehors de ces périodes. Nous avons également vérifié la présence d'éventuels changements aux dates de ponte d'oiseaux de rivage de l'Arctique canadien à l'aide de données récentes et historiques. Si les températures moyennes quotidiennes durant la période de ponte ont connu une augmentation allant jusqu'à 1,5 °C depuis les années 1950 et que des changements apparents aux dates de ponte ont été notés pour trois espèces d'oiseaux de rivage, les variations des dates de ponte médianes de 1954 à 2005–2008 n'étaient significatives que pour le bécasseau à croupion blanc (*Calidris fuscicollis* (Viellot, 1819)). De 2005 à 2008, il n'y a eu qu'une seule année où le synchronisme entre l'éclosion et les pointes de ressources était relativement élevé. L'asynchronisme entre l'éclosion et les pointes de biomasse de tipulidés s'est traduit par une diminution des taux de croissance d'oisillons de bécasseaux de Baird (*Calidris bairdii* (Coues, 1861)). Comme les changements climatiques prévus pourraient causer le découplage d'évènements phénologiques, un examen plus approfondi des effets de l'asynchronisme sur les taux de croissance des oiseaux qui nichent dans l'Arctique serait opportun.

Mots-clés : phénologie, décalage, oiseaux de rivage, arthropodes, tipulidés.

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Introduction

In seasonal environments, it is critical for birds to synchronize breeding events with peaks in resource availability to ensure adequate resources for the production and growth of offspring. In general, optimal hatching dates occur a few days prior to seasonal peaks in food resources (Visser et al. 2006) permitting chicks to access food resources over a lon-

ger time period (Lepage et al. 1998), thus providing the greatest abundance of food at the time of highest energetic requirements (Visser et al. 2006). In temperate-breeding insectivores, a lack of synchrony between hatch and peaks in resources (mismatch), mostly attributed to recent climate changes, has led to negative fitness effects and population declines in some species (Both and Visser 2001, 2005; Both et al. 2005). In arctic-nesting insectivores, the mismatch phe-

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nomenon has been less well studied (Pearce-Higgins et al. 2005, 2009) despite the increased potential for a mismatch owing to a highly compressed breeding season for birds and the sharp, short-lived peaks in resource availability (Tulp and Schekkerman 2008; Høye and Forchhammer 2008).

With approximately 50 species nesting in the Arctic, shorebirds represent the most diverse group of arctic-nesting insectivores (Meltofte et al. 2007). Most arctic-nesting shorebirds are income breeders, meaning they are highly dependent upon energy acquired on the breeding grounds for egg production and subsequent breeding stages (Klaassen et al. 2001). Shorebird eggs are large relative to adult body size so as to maximize the size of young at hatch (Moskoff and Montgomerie 2002) and growth rates of young are rapid (Schekkerman et al. 2003). Abundant resources are thus crucial for both egg production and the growth and survival of chicks during the short arctic summer. Variation in food resources has been shown to influence interannual variation in the breeding phenology of arctic-nesting shorebirds in High-Arctic Greenland and Russia (Meltofte et al. 2007; Schekkerman et al. 2004). The seasonal abundance and availability of arctic arthropods (their main food resource) is highly correlated with temperature, resulting in sharp and short-lived peaks in resource availability (Hodkinson et al. 1996; Holmes and Pitelka 1968; Schekkerman et al. 2004).

The combination of high energetic requirements upon arrival, large egg size, rapid chick growth rates, and short-lived peaks in resource availability leave arctic-nesting shorebirds particularly vulnerable to climate-induced changes in the seasonal phenology of food resources. Therefore, we hypothesized that variation in growth rates of arctic-nesting shorebirds would be influenced by synchrony between chick hatch and food resource peaks. More specifically, we predicted that chicks hatching in synchrony with peak periods of arthropod abundance would experience higher growth rates than chicks hatching outside of these peak periods. Given that advances in the timing of breeding have been documented in other populations of arctic-nesting shorebirds (Høye et al. 2007), we also predicted that median lay dates observed during the period of this study (2005–2008) would be significantly earlier than median lay dates observed during the 1950s.

Materials and methods

Study area and shorebird species

The study was conducted within Sirmilik National Park of Canada on Bylot Island (73°N, 80°W). The study area, located on the south plain of Bylot Island, is characterized by a polygon tundra wetland (Ellis and Rochefort 2004) with vegetation dominated mainly by sedges (primarily water sedge (*Carex aquatilis* var. *minor* Boott), white cottonsedge (*Eriophorum scheuchzeri* Hoppe), and narrowleaf cottonsedge (*Eriophorum angustifolium* Honck.)), grasses (mostly Fisher's tundragrass (*Dupontia fisheri* R.Br.), wideleaf polargrass (*Arctagrostis latifolia* (R.Br.) Griseb.), and false semaphoregrass (*Pleuropogon sabinei* R.Br.)), and fen mosses (drepanocladus moss (genus *Drepanocladus* (Müll. Hal.) G. Roth) and aulacomnium moss (genus *Aulacomnium* Schwägr.)), as well as upland mesic tundra dominated mainly by shrubs (willow (genus *Salix* L.), bog blueberry (*Vacci-*

nium uliginosum L.)), forbs (white arctic heather (*Cassiope tetragona* (L.) D. Don), Maydell's oxytrope (*Oxytropis maydelliana* Trautv.), alpine milkvetch (*Astragalus alpinus* L.), mountainsorrel (*Oxyria digyna* (L.) Hill), alpine bistort (*Polygonum viviparum* L.)), grasses (wideleaf polargrass, arctic bluegrass (*Poa arctica* R.Br.), woodrush (genus *Luzula* DC)), and some mosses (for details see Gauthier et al. 2011). The three shorebird species most commonly nesting in the area during the period of study were White-rumped Sandpiper (*Calidris fuscicollis* (Vieillot, 1816)), Baird's Sandpiper (*Calidris bairdii* (Coues, 1861)), and American Golden Plover (*Pluvialis dominica* (Statius Müller, 1776)).

### Shorebird breeding phenology

Active nest searching and subsequent nest monitoring was conducted for all shorebirds between 5 June and 15 July within an 8 km² study site located in the Qarlikturvik Valley (73°9′N, 79°58′W). Nests found opportunistically outside this study site were also monitored when possible. For each nest found, information on egg measurements, number of eggs and (or) young upon hatch, and incubation stage was collected. When nests were not found during laying, first egg lay dates were estimated based on egg flotation (Liebezeit et al. 2007), or on back calculations from known or actual hatching dates. Hatching dates were estimated based on either (*i*) known laying dates (adding 21 days incubation + number of eggs laid for sandpipers or 25 days incubation + number of eggs laid for plovers), (*ii*) egg flotation (Liebezeit et al. 2007), or (*iii*) signs of hatch in the nest (starred or pipped eggs). Actual hatching dates were based on confirmed sightings of newly hatched chicks in the nest. Estimated laying and (or) hatch dates were used only when actual dates were not available. On a subsample of nests for which both estimated and actual hatch were recorded, no significant difference in median lay dates were detected between the two methods (Fisher's exact test; Baird's Sandpiper: $p = 0.23$, $n = 47$; White-rumped Sandpiper: $p = 0.35$, $n = 19$; American Golden Plover: $p = 0.31$, $n = 22$). Estimated hatch dates were thus considered nonbiased.

To investigate changes in the timing of breeding, we compared the data collected from 2005 to 2008 with historical data collected in 1954 (Drury 1961) and 1977 (Kempf et al. 1978) at the Aktinek Glacier Valley (72°48′N, 78°49′W) on Bylot Island. Data on laying dates for White-rumped Sandpiper, Baird's Sandpiper, and American Golden Plover were extracted from published papers and reports from these two expeditions on Bylot Island (Drury 1961; Kempf et al. 1978). In 1954 and 1977, fieldwork was conducted from 12 June to 19 July and from 8 to 26 July, respectively.

Climate

Mean daily air temperature was collected on Bylot Island by an automated weather station located in the Qarlikturvik Valley from 1994 to 2008. We calculated the mean daily air temperatures from 1 to 30 June, hereafter the laying period, as these dates included all lay dates recorded across all years and species on Bylot Island. To provide an index of temperature on Bylot Island in the 1950s and the 1970s, mean daily air temperature data for Pond Inlet (72°40′N, 77°58′W; the closest weather station to Bylot Island approximately 90 km away) from 1950 to 2008 was obtained from the National

Fig. 1. Boxplots of laying dates for American Golden Plover (*Pluvialis dominica*) (A), Baird's Sandpiper (*Calidris bairdii*) (B), and White-rumped Sandpiper (*Calidris fuscicollis*) (C), and mean daily temperatures during the laying period (1–30 June; D). Lay dates are presented for all birds found both within and outside the 8 km² study site in the Qarlikturvik Valley. Boxplots present the median, 10th, 25th, 75th, 90th percentiles, and all outliers. Mean daily temperatures for 1954 and 1977 are predicted temperatures based on the relationship between daily temperatures on Pond Inlet and Bylot Island (see Materials and methods).
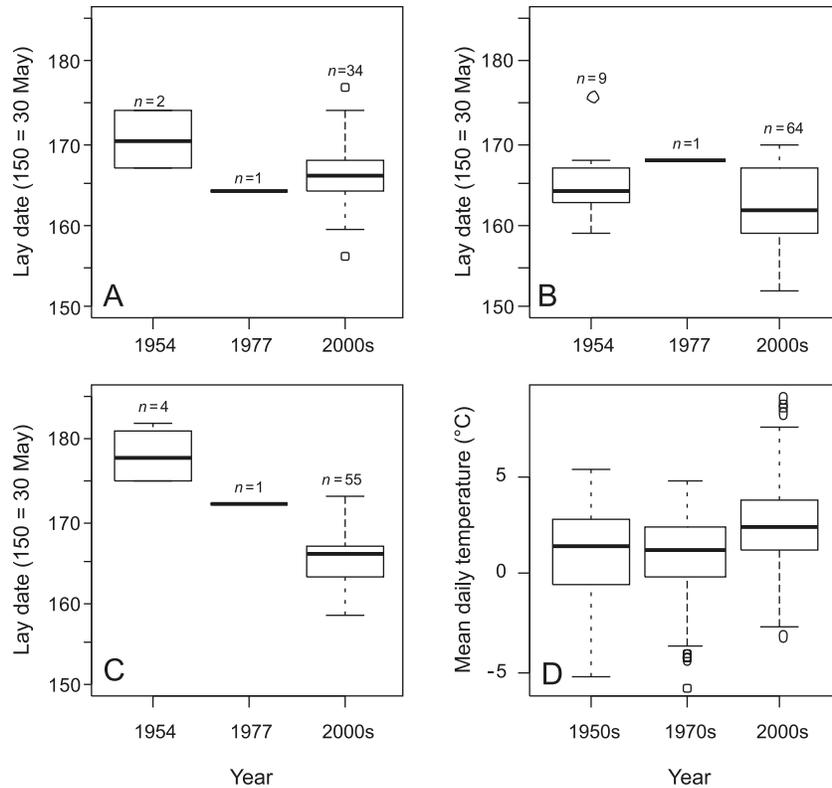
Climate Data and Information Archive, Environment Canada (available from http://climate.weatheroffice.gc.ca/Welcome_e.html, accessed May 2009). Mean daily temperatures during the laying period for a 4-year period in the 1950s (1954–1957) and the 1970s were then predicted based on a linear regression equation of mean daily temperatures using Pond Inlet data and Bylot Island data from 1993 to 2008 (Bylot Island = 0.555 + 0.744(Pond Inlet), $R^2 = 0.75$, $p < 0.001$, $n = 333$ days). Though we only had shorebird breeding data available for 1 year in each of these periods, mean daily temperatures were calculated for 4 years during each time period to provide a more comprehensive comparison with the current 4-year sampling period.

Seasonal availability of food resources

To observe seasonal changes in the availability of arthropods, pitfall traps with modified Malaise traps were used to capture surface active and low-flying arthropods. Traps were composed of a 38 cm × 5 cm × 7 cm plastic pitfall trap from which extended a 40 cm × 40 cm vertical mesh screen topped with a white plastic cone funnelling into a bottle trap to capture flying insects (Fig. S1).[1] Traps were distributed equally between wetland and mesic tundra, the two dominant foraging habitats used by the study species during the brood-rearing period in the Qarlikturvik Valley. In 2005, eight traps

were distributed throughout the study area, four in wetland and four in mesic tundra habitats. In subsequent years, two transects of 5 traps, each placed 20 m apart, were set in both habitats for a total of 10 traps. Traps were sampled every 2 days throughout the summer from approximately 12 June to 15 August. The contents of 6–10 traps per year (3–5 per habitat) were sorted and identified to family. To account for variable sampling effort, total arthropod biomass was divided by the number of traps sampled and sorted, and is presented as arthropod biomass (mg·trap⁻¹·day⁻¹). Biomass per trap was calculated for each arthropod family using one of the following three methods: (1) when individual variation in size was low, mean individual mass was measured and used for calculation; (2) when individual variation in size was high, individuals were grouped within size categories and a mean was obtained for each category; or (3) when individual variation was too high to make size categories or specimens were too rare to obtain a mean, length to biomass equations were used. Equations were either constructed based on our samples or from the literature (Hódar 1996; Picotin 2008; Rogers et al. 1977; Sage 1982; Sample et al. 1993; for a complete list of equations and references thereof see Table S1[1]).

Arthropods previously confirmed in the diet of White-rumped Sandpiper and Baird's Sandpiper at the study site include Aranea (spiders), Anthomyiidae, Carabidae, Chirono-

Fig. 2. Timing of hatch for American Golden Plover (*Pluvialis dominica*) (AMGP), Baird's Sandpiper (*Calidris bairdii*) (BASA), and White-rumped Sandpiper (*Calidris fuscicollis*) (WRSA) from 2005 to 2008 in relation to seasonal variation in arthropod biomass (mg·trap^{-1}·day^{-1}) each year for Aranea (except 2005), Carabidae, Chironomidae, Muscidae, Mycetophilidae, Tipulidae, and all families combined. For each year, the vertical broken gray lines link the hatch date graphs with the biomass graphs by indicating the full range of hatch dates for the three shorebird species illustrating when peaks in arthropod biomass fall within documented hatch date ranges. Ideal shorebird hatching dates (dates within which the 10-day running biomass totals are maximized, top 10th percentile) are indicated in boldface type on the line graphs for each insect group.

midae, Muscidae, Mycetophilidae, and Tipulidae adults and larvae (stomach content analysis; Drury 1961). The same groups have been confirmed in the diet of a close congener of American Golden Plover, the European Golden Plover (*Pluvialis apricaria* (L., 1758)), from other sites (Pearce-Higgins and Yalden 2004). When evaluating synchrony of hatch dates with abundance of arthropods, only nests found within the 8 km^2 study site in the Qarlikturvik Valley were included because all of these nests were at a maximum distance of 3 km from the arthropod trapping areas.

Chick growth

During the summers of 2006–2008, we visited nests of Baird's Sandpiper at hatch so that chicks could be banded at age 0 in the nest. All four eggs generally hatch within 24 h and chicks often leave the nest within 24 h after hatch. Chicks that were completely out of the egg and dry were banded with a metal band and an individual combination of four colour bands and then weighed to the nearest 0.25 g with a 30 g pesola scale. Banders returned to the previous banding site approximately every 2 days and searched for marked broods within a few hundred metres. Chicks were relocated by following banded adults performing distraction displays. Nest trapping and banding of adults occurred throughout the incubation period. When relocated, we recaptured chicks by hand and reweighed them.

Data analysis

Shorebird breeding phenology and climate

Differences in median laying dates between 1954 and the 2000s (2005–2008 combined) were tested with pairwise Mann–Whitney–Wilcoxon tests. Data on laying dates from 1977 are presented graphically but are not included in the statistical analyses because only one estimated data point was available for each species. To test for differences in mean daily air temperature during the laying period between the three time periods, we used a linear mixed effects model with period (1950s, 1970s, 2000s) as a fixed effect and year as a random effect to account for the hierarchical structure of the data.

Seasonal availability of food resources

Variation in arthropod biomass was described graphically for all families combined, and separately for the confirmed prey groups: Aranea (spiders), Anthomyiidae, Carabidae, Chironomidae, Muscidae, Mycetophilidae, and Tipulidae. As shorebird broods are found throughout both wetland and mesic habitats during the brood-rearing period (J. Bêty and L. McKinnon, unpublished data), biomass data were pooled for both habitats to provide a general index of seasonal abundance for the entire study area.

Synchrony between hatch and food resource peaks

To evaluate synchrony between hatch dates and peaks in arthropod biomass, we defined an ideal shorebird hatch period (hereafter ideal hatch period) per prey group and presented the proportion of hatch dates (per species, per year) falling inside this peak period. The ideal hatch period was defined as a period within which each day was followed by 10 days where the cumulative arthropod biomass (10-day running biomass total) was in the top 10th percentile of all 10-day running biomass totals. A 10-day period was chosen, as it has been shown that shorebird chicks may be most vulnerable to starvation and exposure during the first 9 days of the prefledging period (Pearce-Higgins and Yalden 2003). Though energy expenditure and thus energetic requirements may be greater in older chicks (Tjørve et al. 2007), capture of chicks past the age of 12 days becomes impossible because they are capable of short flights at this time (L. McKinnon, personal observations). Analyses were also run using running biomass totals calculated over an 8- and 12-day period to ensure that the analyses were not sensitive to the chosen 10-day period. Each year we also calculated the mean biomass available during the 10-day period following all observed hatch dates for each species and compared this with the mean biomass available during the ideal hatch period for each arthropod group using pairwise two-sided Student's t tests with Bonferroni correction for multiple comparisons ($p = 0.05/3 = 0.017$).

Chick growth

To assess the importance of asynchrony on chick growth, we generated growth curves for chicks of Baird's Sandpiper hatching in synchrony (within the ideal hatch period, see above) and chicks hatching out of synchrony (hatching outside the ideal hatch period) for each prey group separately, and compared these to growth modeled on age alone using the package "drc" in R (Ritz and Streibig 2005). To model growth, we applied a four parameter type 2 Weibull model (Ritz and Streibig 2005):

$$f(x) = c + (d - c) \cdot [1 - \exp^{-\exp^{b(\log x - \log e)}}]$$

where b is the slope, c is the intercept, d is the upper limit, and e is the inflection point. The type 2 Weibull was the best fitting growth model based on preliminary model selection (using Akaike's information criterion, AIC) among a series of growth models applied to the combined data set. As sample sizes were low each year, data were pooled across all 3 years.

The model with the lowest AIC score was considered the best fitting model, and models with <2 ΔAIC from the top model were considered competitive (Burnham and Anderson 2002). Unless otherwise specified, all statistical tests are one-sided and statistical significance is based on a type 1 error of <0.05.
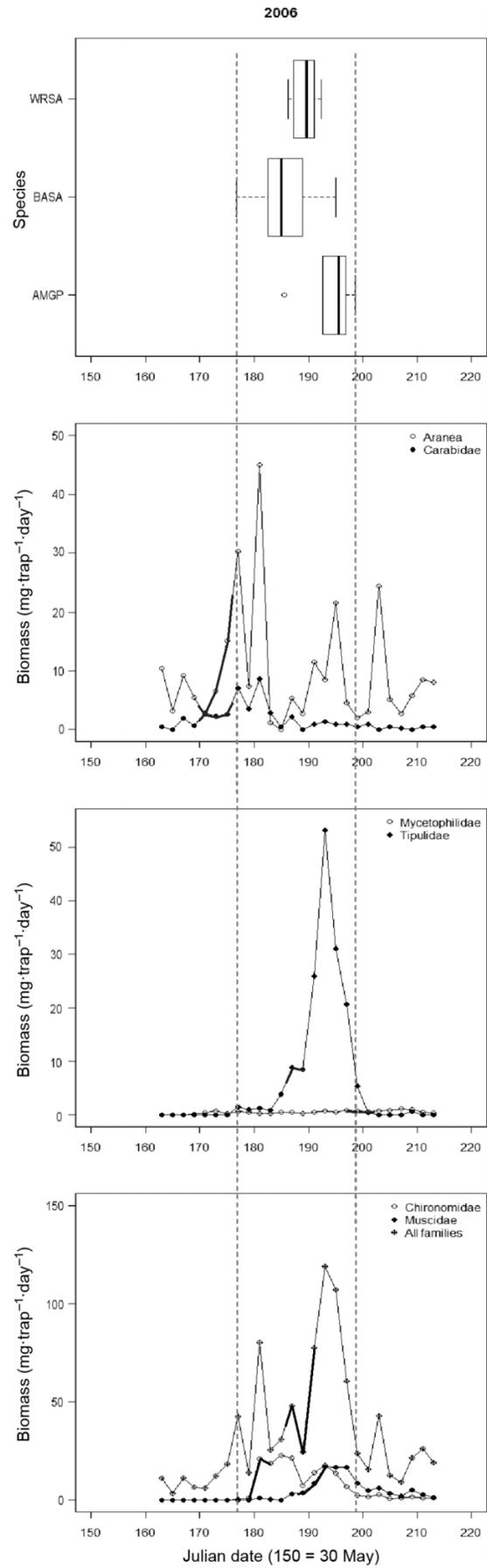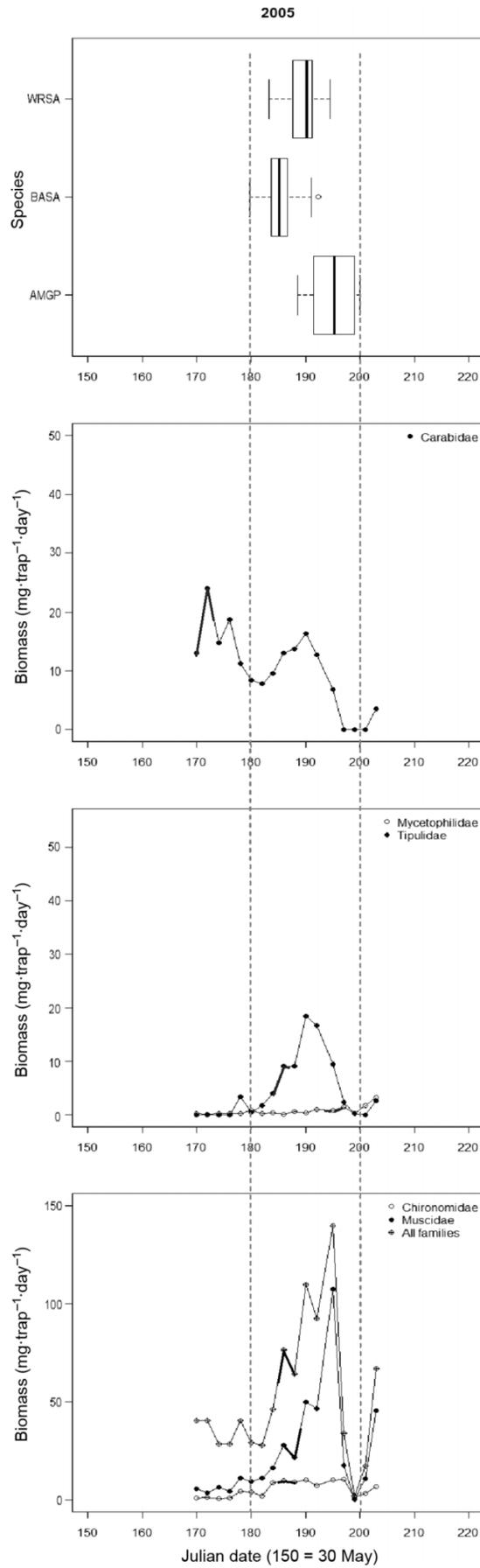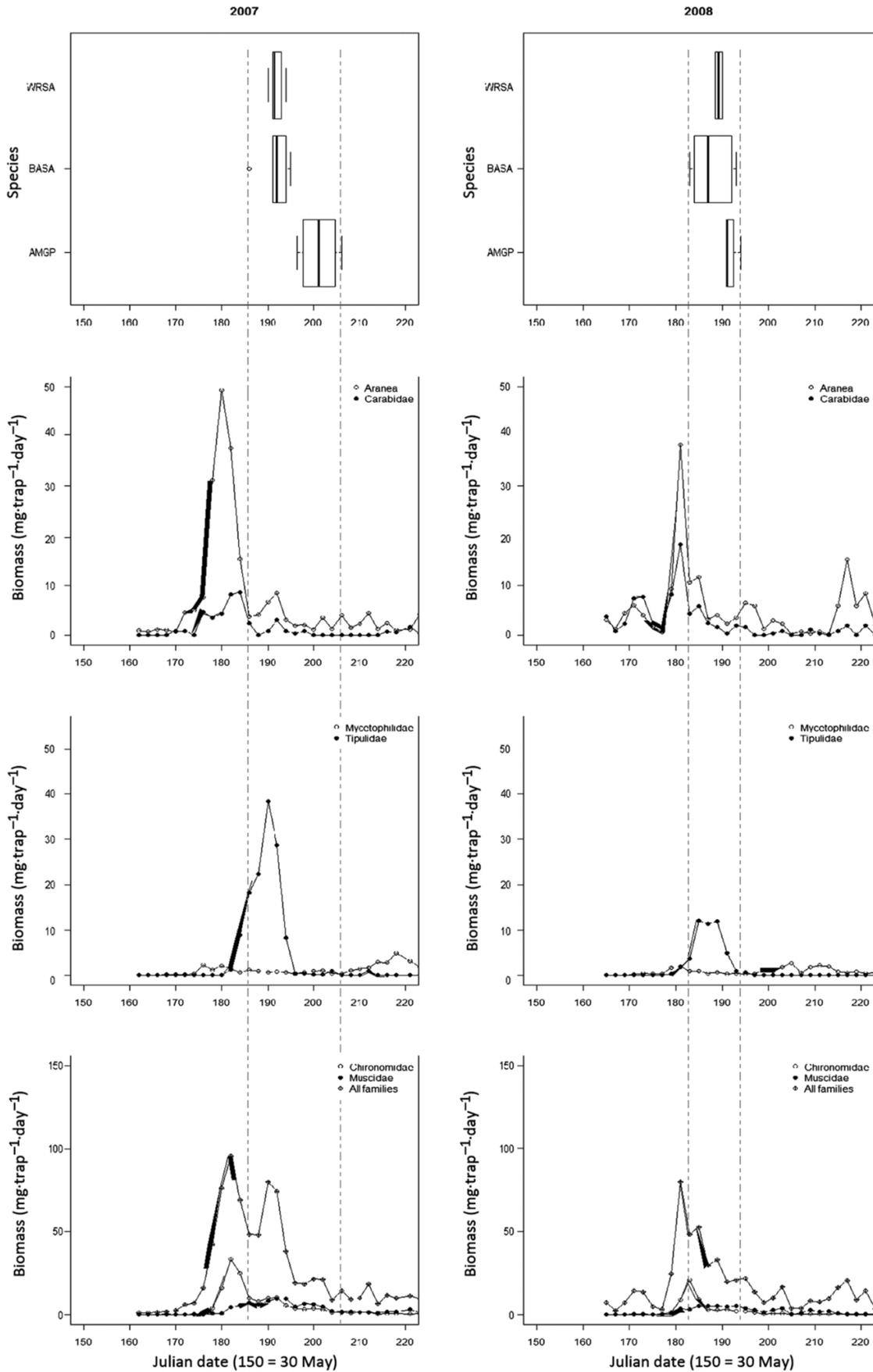
Fig. 2. (*concluded*).

Table 1. Proportion of individuals for which hatch dates fall within the defined ideal shorebird hatch period[a] per species, year, and arthropod group.

Year	N	Anthomyiidae	Chironomidae	Mycetophilidae	Muscidae	Tipulidae	All families
American Golden Plover (*Pluvialis dominica*)							
2005	6	0	0	0	0.17	0	0.17
2006	5	0.20	0	0.40	0.20	0.20	0.20
2007	4	0	0	0	0	0	0
2008	3	0	0	0	0	0	0
Baird's Sandpiper (*Calidris bairdii*)							
2005	13	0	0.08	0	0.31	0	0.54
2006	29	0.21	0.54	0	0.21	0.92	0.92
2007	9	0	0.11	0	0.11	0.11	0
2008	9	0	0	0	0.56	0.44	0
White-rumped Sandpiper (*Calidris fuscicollis*)							
2005	24	0	0	0	0.29	0	0.25
2006	14	0.64	0	0	0.64	0.86	0.86
2007	7	0	0	0	0.14	0	0
2008	2	0	0	0	0	0	0

[a]The ideal hatch period was defined as a period within which each day was followed by 10 days where the cumulative arthropod biomass (10-day running biomass total) was in the top 10th percentile of all 10-day running biomass totals.

All methods in this study were reviewed and accepted by the Animal Care Committee of the Université du Québec à Rimouski.

Results

Current versus historical shorebird breeding phenology and climate

For all three species, lay dates occurred earlier in the 2000s than in 1954 (Figs. 1A, 1B, 1C), yet differences in median lay dates were only statistically significant for the White-rumped Sandpiper. The median lay date for White-rumped Sandpiper was 8 days earlier in the 2000s compared with 1954 ($W_{[1]} = 230$, $Z = 3.3$, $p = 0.0005$; Fig. 1C). Mean daily temperatures during laying differed between the three time periods ($\beta \pm SE = 0.76 \pm 0.32$, $p = 0.036$) with a mean value of 1.2 °C in the 1950s, 1 °C in the 1970s, and a much higher mean value of 2.7 °C in the 2000s (Fig. 1D).

Seasonal availability of food resources 2005–2008

A total of 138 212 individual arthropods belonging to 30 different families were identified. Confirmed shorebird prey groups (i.e., Aranea (spiders), Anthomyiidae, Carabidae, Chironomidae, Muscidae, Mycetophilidae, and Tipulidae combined) accounted for 93%, 84%, 83%, and 83% of the total biomass captured in the traps in 2005, 2006, 2007, and 2008, respectively (Table S2).[1] Each year, ideal shorebird hatch periods for Aranea and Carbidae occurred earliest in the season (18–29 June), followed by Chironomidae (24 June to 7 July), Tipulidae (28 June to 10 July), Muscidae (30 June to 12 July), Mycetophilidae (12 July to 4 August), and finally all families combined (24 June to 10 July) (Fig. 2).

Synchrony between hatch dates and ideal hatch periods for food resources 2005–2008

For each species, the proportion of individuals with hatch dates falling within the ideal hatch period was low across years with the exception of 2006 (Table 1). In 2006, hatch dates were best synchronized with peaks in Tipulidae abundance with 86% of hatch dates of White-rumped Sandpiper and 92% of hatch dates of Baird's Sandpiper falling within the ideal hatch period (Table 1). In 2006, the hatch dates of American Golden Plover were best synchronized with Mycetophilidae (40% of hatch dates within the ideal period; Table 1). For observed hatch dates of Baird's Sandpiper and White-rumped Sandpiper, the mean biomass available during the 10-day period following hatch in 2005 and 2006 was comparable (up to 90%) with that available during the ideal hatch period for Mycetophilidae, Chironomidae, and Tipulidae, and all families combined (Table 2). In 2007 and 2008, however, the mean biomass available during the 10-day period following hatch was lower (<60%) than that available during the ideal hatch period for each arthropod family except Muscidae (80%–90%; Table 2). For the American Golden Plover, biomass available during the observed hatch dates (10-day period) compared with that available during the ideal period was generally low (<60%) with the exception of Mycetophilidae in 2005 and 2006 (80%–90%; Table 2). Across all years and all species, the biomass available during actual hatching periods was usually significantly lower than that available during the ideal period (Table 2).

Chick growth

A total of 41 chicks of Baird's Sandpiper of known age, from 14 families were captured and weighed up to five times throughout the brood-rearing period over the three summers providing a total of 61 mass measurements. The ratio of captured chicks falling within versus outside the ideal hatch period was well balanced for Tipulidae. The model including Tipulidae synchrony fit the data better than the model of age alone (Table 3). Chicks hatching within the ideal hatch period for Tipulidae had greater mass (29.4 ± 2.0 g) after day 8 than those chicks hatching outside of the ideal period (24.5 ± 0.7 g; Fig. 3, Table S3[1]). Results were the same re-

Table 2. Mean arthropod biomass (mg·trap^{-1}·10 days^{-1}) during the ideal shorebird hatch period dates (IDEAL) for each arthropod family and mean arthropod biomass following observed hatch dates for each species (AMGP, American Golden Plover (*Pluvialis dominica*); BASA, Baird's Sandpiper (*Calidris bairdii*); WRSA, White-rumped Sandpiper (*Calidris fuscicollis*)).

Year	Species	Anthomyiidae	Aranea	Carabidae	Chironomidae	Mycetophilidae	Muscidae	Tipulidae	All families
2005	IDEAL	31.6	31.8	153.4	94.9	13.8	583.1	122.6	983.9
	AMGP	**3.6**	**1.7**	**25.5**	**49.2**	11.0	**283.2**	**33.7**	**429.3**
	BASA	18.5	**10.6**	99.4	84.5	**7.0**	434.8	96.7	805.6
	WRSA	**10.3**	**5.7**	**71.4**	80.5	9.3	451.3	82.8	755.4
2006	IDEAL	6.5	187.4	46.5	173.0	8.4	126.5	266.1	759.6
	AMGP	3.8	**85.2**	**6.6**	**56.7**	7.3	80.3	**115.8**	**420.0**
	BASA	**3.9**	**89.3**	**15.1**	138.9	**5.0**	73.5	168.0	584.2
	WRSA	6.1	**93.4**	**9.1**	108.9	6.1	119.2	244.8	715.5
2007	IDEAL	6.7	263.2	53.3	172.7	30.6	77.4	212.7	665.5
	AMGP	0.3	**24.4**	**0.6**	**16.6**	9.7	26.5	**2.6**	**137.9**
	BASA	**1.0**	**29.3**	**6.4**	46.3	**6.4**	64.6	**61.5**	299.2
	WRSA	1.0	**27.4**	**6.2**	42.6	6.2	64.0	44.9	274.6
2008	IDEAL	9.9	136.9	74.6	84.0	16.3	47.8	79.7	441.8
	AMGP	**1.4**	**38.6**	6.6	**12.7**	**7.0**	**30.6**	**4.6**	**146.8**
	BASA	**0.8**	**44.4**	15.2	**28.4**	**5.1**	42.1	44.8	**234.7**
	WRSA	**1.0**	**40.1**	8.5	**18.6**	**4.4**	37.1	**18.6**	178.6

Note: Measures that are significantly different from the IDEAL ($p < 0.017$) are in boldface type.

Table 3. Comparison of growth models for chicks of Baird's Sandpiper (*Calidris bairdii*).

| Model	Number of parameters	AIC	ΔAIC
Age + Tipulidae[a]	3	257.77	0
Age	2	268.67	10.9

[a]The factor Tipulidae indicates whether chicks hatched within or outside the ideal hatch period relative to Tipulidae availability. AIC, Akaike's information criterion.

gardless of whether a shorter (8 days) or longer (12 days) running biomass total was used to calculate the peak period for Tipulidae. Regarding ideal periods for Chironomidae and Mycetophilidae, all chicks that were captured hatched outside the ideal hatch period, thus similar comparisons could not be made. Similarly, for Anthomyiidae, Muscidae, and all insect groups combined, too few mass measurements were from chicks hatching within the ideal hatch period, so comparisons could not be made.

Discussion

In seasonal environments such as the Arctic, reproduction of birds must be synchronized with peaks in resource availability to ensure adequate resources for egg production and the subsequent growth and survival of offspring. In this study, we hypothesized that variation in growth rates of arctic-nesting shorebirds would be influenced by synchrony between chick hatch and food resource peaks. As predicted, our results indicated that chicks hatching in synchrony with peak periods of arthropod abundance experienced higher growth rates than chicks hatching outside of these peak periods. Chick mass after day 8 was higher for those chicks hatching within the ideal hatch period for Tipulidae than those chicks hatching outside of the ideal period. Tipulidae are known to be an important component of the diet in many arctic-nesting calidrids (Baker 1977; Holmes and Pitelka 1968) and growth rates of other shorebird species have

Fig. 3. Plot of the two type 2 Weibull growth curves for chicks of Baird's Sandpiper (*Calidris bairdii*) with hatch dates falling within the defined peak period for Tipulidae (solid line) and chicks with hatch dates outside the defined peak period for Tipulidae (broken line). Raw data points are provided for chicks hatching within the ideal period (△) and chicks hatching outside the ideal period (○).
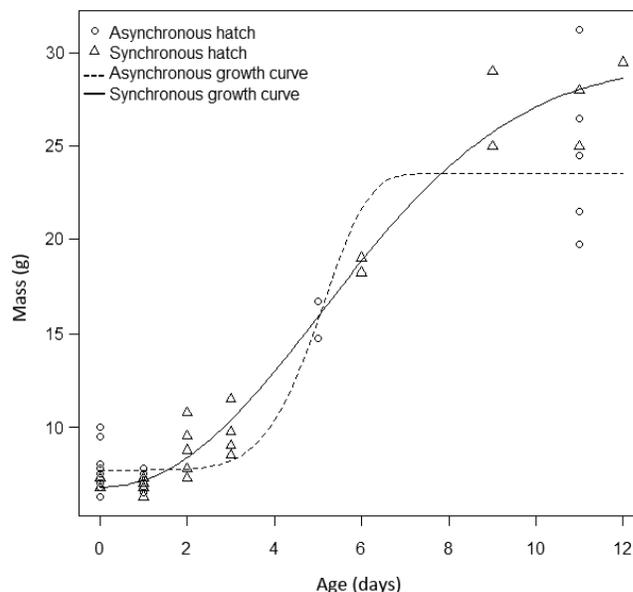
been shown to be correlated with Tipulidae biomass (Pearce-Higgins and Yalden 2004; Pearce-Higgins et al. 2005). Our results thus provide additional evidence that shorebirds may indeed be sensitive to climate-induced changes in the phenology of food resource peaks.

Given that advances in the timing of breeding have been documented in other arctic-nesting shorebird populations (Høye et al. 2007), we also predicted that median lay dates observed during the period of this study (2005–2008) would be significantly earlier than median lay dates observed during the 1950s. As predicted, we found that for all three species,

median lay dates occurred earlier in the 2000s than in 1954, yet differences were only statistically significant for the White-rumped Sandpiper. The median lay date for White-rumped Sandpiper was 8 days earlier in the 2000s than in 1954. Despite the small sample sizes for 1954, these results are consistent with data from other high-arctic sites that have indicated advancements in lay dates by as much as 2–10 days over a considerably shorter period of 8–10 years (Høye et al. 2007). Comparisons of mean daily temperature during the laying period indicated a significant increase between the 1950s and the 2000s, with the mean daily temperature during the laying period in later years of the study up to 1.5 °C higher than in 1954. That a significant difference in lay dates was not detected in all study species could be partly attributable to limitations in sample size.

Despite any potential advances in lay dates, synchrony between hatch and peaks in food resources between 2005 and 2008 was low for all three study species. Between 2005 and 2008, seasonal biomass of shorebird food resources varied in terms of the timing and magnitude of peaks, yet within years most insect families exhibited a typical pattern of seasonal variation, with a slow increase in biomass at the beginning of the season, a sharp increase to a peak lasting from 2 days to 2 weeks in July, followed by an equally sharp decline. Seasonal trends for Aranea and Carabidae differed in that the short-lived peaks occurred earlier in the season, coinciding with the tail end of the laying date range, suggesting that these two groups may be more important resources for laying adults as opposed to hatching chicks. Each year, with the exception of 2007, peaks in biomass of Chironomidae, Muscidae, Tipulidae, and all arthropod families combined occurred within the observed range of shorebird hatch dates (all shorebird species combined), indicating some synchrony between hatch dates and peaks in food resources. However, when ideal hatch periods for each arthropod family were redefined in terms of periods within which 10-day running biomass totals were maximized (top 10th percentile), 2006 was the only year in which hatch dates and peak periods in resources were relatively synchronized for all three species.

In 2006, hatch dates were best synchronized with peaks in Tipulidae abundance. Also, in both 2005 and 2006, mean 10-day running biomass totals for observed hatch dates of Baird's Sandpiper and White-rumped Sandpiper were similar to that available during the ideal hatch period for most arthropod families. An apparent asynchrony between hatch and peaks in food resources was most striking in 2007 where very few observed hatch dates fell within the ideal period. In addition, in 2007, the 10-day running biomass totals for observed hatch dates were generally 10%–30% of that available during the ideal period for most arthropod families (the exception being Muscidae at 80%). The striking asynchrony in 2007 was due to an earlier peak in arthropod abundance combined with later laying dates for both Baird's and White-rumped sandpipers.

At other arctic-breeding sites, interannual variation in egg laying has been explained best by food availability, though early season snow cover has a strong effect in years of late snow melt (Meltofte et al. 2008). However, variation in lay dates is not simply a result of ecological conditions experienced upon arrival to the breeding grounds, but can also result from carry over effects of conditions experienced during spring migration (Mainguy et al. 2002, Norris 2005). In 2007, temperatures during the laying period were similar to that in 2005 and 2006, and snow cover was low on Bylot Island, providing ample available nesting habitat, yet all three study species nested later than usual for the 2005–2008 period. During spring 2007, many bird species arrived at Bylot Island approximately 1 week later than usual (J. Bêty, unpublished data), potentially attributable to storms in the low eastern Arctic. Delays to arrival times caused by inclement weather during migration can be particularly critical for shorebirds, especially if the inclement weather leads to a reduction of body stores upon arrival, reducing the already limited window between arrival and laying (Ganter and Boyd 2000). On Bylot Island, the later arrival of shorebirds in 2007 (J. Bêty, unpublished data) translated into later laying dates for both Baird's and White-rumped sandpipers. In 2008, laying dates returned to normal for the 4-year period; however, asynchrony occurred again, this time attributable to even earlier peaks in arthropod abundance.

Inevitably, the definition of peaks in food resources will influence our evaluation of synchrony between hatch dates and peaks in food resources. Here we assessed intra-annual synchrony based on the proportion of birds hatching within an ideal period as defined by the top 10th percentile of the 10-day running biomass totals. This approach has some drawbacks. First, by comparing growth relative to a defined peak within each year, we do not account for the interannual variation in the magnitude of the peaks, which could be important. Second, it is difficult to assess whether the biomass calculated from the trap samples represents the food resources actually available to and selected by foraging birds. The best way to determine the representativeness of our traps is to measure some component of fitness (i.e., chick growth, survival, or recruitment) in relation to trap biomass as in Tjørve et al. (2007), while controlling for other potentially important confounding environmental factors such as wind, temperature, and precipitation (Bakken et al. 2002). One advantage of our definition of the peak period is that the asynchronous group of birds included those hatching both before and after the defined peak period, which means that both early and late nesters could be asynchronous. As early nesters are often assumed to be higher quality birds (Parsons 1975), this definition provides a means of controlling, at least in part, for this confounding factor. This was the case for at least 1 year in our study, and indeed, across all the years we found that asynchronous chicks exhibited hatch dates both before and after the median hatch dates for their respective years.

Though we did find evidence that asynchrony between hatch dates and defined peaks in Tipulidae biomass may reduce growth rates for chicks of Baird's Sandpiper as predicted, we did not have the sample sizes required to test these other potentially important factors. We were able to generate and compare growth curves based on the latest methodological recommendations for growth curve analysis using nonlinear models (Tjørve and Tjørve 2010a, 2010b; Paine et al. 2012); however, we were unable to find a statistically valid method to incorporate random effects such as brood, thus our results should be interpreted with caution. Despite these caveats, our results of higher growth rates in the presence of higher Tipulidae biomass are consistent with

previous studies (Pearce-Higgins and Yalden 2004; Pearce-Higgins et al. 2005). Taken together, these studies and ours suggest that synchrony with insect groups such as Tipulidae are important factors affecting chick growth in arctic-nesting shorebirds and require further investigation.

Understanding the causes and consequences of variation in timing of breeding in shorebirds is essential in the context of current and future changes in arctic climate. Our study indicates that temperatures during the laying period on Bylot Island have increased since the 1950s, and differences in lay dates have occurred but were only significant for one of three shorebird species studied. Also, synchrony between hatch dates and defined peaks in food resources varied considerably between 2005 and 2008. Only 1 out of 4 years (2006) exhibited relatively high synchrony and here, as in other studies (Pearce-Higgins and Yalden 2004; Tulp 2007), we show that asynchrony can negatively affect chick growth. Unfortunately, the best apparent year for chicks in terms of synchrony with food resources (2006) was also a year of very high predation with only 0%–20% of nests hatching (McKinnon and Bêty 2009), thus measures of chick growth in relatively synchronous years were lacking in our study. As anticipated changes in climate risk to further alter the synchrony of hatch and peak food resources in arctic-nesting shorebirds (Pearce-Higgins et al. 2009), future ecological studies on shorebirds should continue to investigate potential fitness effects of asynchrony on shorebird reproduction, especially chick growth, survival, and recruitment. Effort should also be directed towards a better understanding of both intrinsic (hormonal, genetic, etc.) and extrinsic (temperature, snow melt, etc.) cues for timing of breeding in arctic-nesting birds (see also Love et al. 2010), how these cues relate to peaks in food abundance, and how this latter relationship may be altered in the face of a changing arctic climate.

Acknowledgements

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