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ARTICLE

Phenology of hatching and food in low Arctic passerines and shorebirds: is there a mismatch?

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Abstract: The warming climate is driving earlier spring snow melt and longer growing seasons in tundra regions of northwestern North America, thereby changing the timing of ecological processes. On Herschel Island, Yukon, Canada, we investigated changes in the migratory bird community, and the potential for phenological mismatch of egg hatching with the pulses in abundance of arthropod prey on which young birds depend for growth. We found an apparent reduction in abundance or loss of some species dependent on freshwater ponds or sparsely vegetated upland tundra. Tracking hatch dates of passerines and shorebirds along with the changes in biomass of mobile life history stages of arthropods (principally Araneae, Tipulidae, Carabidae, Muscidae, Chironomidae, Mycetophilidae, and Ichneumonidae), we found no evidence for phenological mismatch in the 2007–2009 time period. Most nests hatched, and the period of most rapid chick growth occurred, in advance of the highest availability of arthropod biomass. Shorebirds hatched significantly later than passerines, less in advance of the peak abundances of arthropods. They are most at risk of future mismatch, given likely trend to earlier onset of arthropod availability and longer migration routes. Herschel Island is a well-studied site warranting further monitoring to assess changes in the Arctic tundra ecosystem.

Key words: arthropod, bird, nesting, phenology, Herschel Island.

Résumé : Le réchauffement climatique provoque la fonte précoce des neiges et des saisons de croissance plus longues, dans les régions de la toundra du nord-ouest de l'Amérique du Nord, changeant ainsi la synchronisation des processus écologiques. Sur l'île Herschel (Yukon, Canada), nous avons étudié les changements chez les oiseaux migrateurs et le potentiel d'écart phénologique entre l'éclosion des œufs et les pics d'abondance des proies arthropodes desquelles les oisillons dépendent pour leur croissance. Nous avons constaté une diminution d'abondance apparente ou même la perte de quelques espèces dépendant des étangs d'eau douce ou de la toundra de haute terre à végétation clairsemée. En faisant le suivi des dates d'éclosion des passereaux et des oiseaux de rivage, ainsi que des changements du stade mobile du cycle biologique des arthropodes (principalement Araneae, Tipulidae, Carabidae, Muscidae, Chironomidae, Mycetophilidae et Ichneumonidae), nous n'avons pas trouvé de preuves d'écart

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phénologique sur la période de temps 2007–2009. La plupart des œufs ont éclos et la période de croissance la plus rapide des oisillons est survenue en avance par rapport à la plus haute disponibilité de biomasse d'arthropodes. Les oiseaux de rivage ont éclos significativement plus tard que les passereaux et moins en avance par rapport à la période de pointe d'abondance des arthropodes. Ils sont plus exposés à un risque d'écart à l'avenir, compte tenu de la tendance probable d'une disponibilité plus précoce des arthropodes et de routes migratoires plus longues. L'île Herschel est un site bien étudié, justifiant plus de suivi pour évaluer les changements de l'écosystème de la toundra arctique. [Traduit par la Rédaction]

Mots-clés : arthropode, oiseau, nidification, phénologie, île Herschel.

Introduction

Arctic regions, especially in northwestern North America, have experienced and are expected to experience among the fastest rates of climate change, with dramatic impacts on the cryosphere (IPCC 2013). Change is evident on tundra of northwestern North America, with increasing mean annual temperature, increasing spring temperature associated with earlier snow melt, increasing duration of snow-free period, and increasing precipitation (Stone et al. 2002; Brown and Robinson 2011; Burn 2012*a*; Candlish et al. 2015). Such changes are now having pervasive influences on Arctic biodiversity (Meltofte et al. 2013).

Changes in the abiotic environment potentially lead to changing phenologies of key ecosystem processes that are directly influenced by ambient temperature and the distributions of snow (Parmesan and Yohe 2003; Gilg et al. 2012). Spring is a season of particularly fast phenological change in Arctic ecosystems because the rapidly lengthening daylight results in a major increase in energy input to the ecosystem, quickly melting snow, and decreasing tundra albedo (Serreze and Barry 2005). Among the ecosystem processes potentially affected by temperature are the timing of arrival and egg-laying in migratory birds which nest on snow-free ground (Ganter et al. 2013), and the emergence and hatch of diverse arthropod taxa which are crucial prey for many nesting birds (Meltofte et al. 2007*a*, 2007*b*).

Being largely quiescent in winter, the life cycles of Arctic arthropods (araneids, collembolans, and insects) are stimulated by spring temperatures and the warming of the ground and upper soil layers (Bale et al. 1997). Groups that over-winter as adults (e.g., araneids) may quickly become active above ground in spring. Most taxa have an above-ground and/or aerial life history stage that is particularly mobile, and therefore available, for relatively short periods or pulses, sometime during spring or summer (Danks 1981; Bale et al. 1997). The timing of emergence for these mobile life history stages has been best explained by timing of snow melt in one high Arctic study (Høye and Forchhammer 2008). The daily abundance of the arthropods during the course of the growing season is strongly influenced by a combination of mean daily temperature and cumulative thaw degree-days during the growing season (Bolduc et al. 2013). Assuming no major increases in winter snow accumulation, earlier warming in spring, driving earlier snow-melt, is likely to lead to advancing phenology of the pulses of arthropods active above-ground (Høye and Forchhammer 2008; Bolduc et al. 2013) and, therefore, available to birds.

Lack (1954) hypothesized that reproductive timing in birds would have evolved such that the period of highest energy demand (chick growth) would coincide with highest availability of food. Subsequent work on Arctic nesting passerines and shorebirds has shown that they rely on arthropod prey for two periods of relatively high energy demand, — egg production, and growth of chicks to fledging (Holmes and Pitelka 1968; Custer and Pitelka 1978; Meltofte et al. 2007*a*, 2007*b*). One possibility of phenological mismatch between timing of reproduction and food availability occurs with timing of arrival on the nesting grounds. When onset of migration is relatively inflexible, and/or onset of spring is slower along the migration route compared with the nesting grounds, then arrival may be relatively late compared with the availability of food (Jones and Cresswell 2009; Clausen and Clausen 2013). Whether or not this has reproductive consequences then depends on any flexibility the birds have in quickly developing and laying eggs to start a relatively inflexible incubation period (Visser et al. 2004). A second possibility for phenological mismatch occurs with the timing of hatch dates compared with dates of summer pulses in arthropod abundance supporting chick growth (Meltofte et al. 2007*a*; Tulp and Schekkerman 2008). Arrival and hatch would ideally occur shortly prior to pulses in high food availability such that egg production and chick growth would coincide with high food availability (Visser et al. 2004).

Arctic nesting shorebirds and passerines do show substantial flexibility in the timing of egg-laying which is strongly influenced by timing of snow melt (Meltofte et al. 2007*a*, 2007*b*; Grabowski et al. 2013; Liebezeit et al. 2014; Ward et al. 2016), but not so much in the timing of their arrival (Smith et al. 2010). Such behavioural flexibility would be adaptive because of interannual variability in spring temperature and snow regimes, independent of any directional climate change (Smith et al. 2010). However, with a trend of advancing snow melt driven by warming spring temperatures across years, there is some evidence that the birds are not advancing their arrival dates or lay dates as quickly as the snow melt is advancing (Smith et al. 2010; Grabowski et al. 2013), suggesting the possibility of an emerging mismatch. This has been investigated on Bylot Island in the Canadian high Arctic where most nests in only one out of three shorebird species hatched just before or within the period of highest prey availability, suggesting a developing mismatch for some species (McKinnon et al. 2012).

In this study, part of a broader International Polar Year project (Gauthier and Berteaux 2011), we investigate the risk of mismatch between hatch and food availability for chicks in a low Arctic bird community in north Yukon, Canada. In relation to this risk, we have three objectives (*i*) to describe changes in composition of the arthropod-feeding bird community for comparison to historical information; (*ii*) to compare the timing of egg hatch with the timing of the pulse in biomass of arthropod prey for the major arthropod groups in the system; and (*iii*) to compare passerine and shorebird reproductive timing.

Materials and methods

Study area

Herschel Island (69°34.2′N; 138°54.1′W), Qikiqtaruk in the Inuvialuit language, is a 110 km^2 island in the Beaufort Sea about 1 km off the north coast of Yukon. It consists of sea floor and coastal sediments pushed into a terminal moraine by a lobe of the Laurentide ice sheet (Burn 2012*b*). Most of the island is upland plateau (30–170 m above sea level) with well-incised drainage channels and coastal cliffs comprised of permafrost-laden sediments. Some streams form fairly extensive alluvial fans where they reach the coast, often in association with sea-shore spits of sands and gravels (Burn 2012*b*).

Herschel Island is a low Arctic site, in bioclimatic subzone D (primarily erect dwarf shrub tundra) of the circum-arctic vegetation map (Walker et al. 2005). We did our work on the eastern 20 km^2 of the island, accessible from Pauline Cove. This area has two distinct habitats, — upland plateau, and lowland alluvial fan and beach, — differentiated by landscape position and proximity to water drainage. Most of the study area is on the relatively well-drained upland area, dominated by three vegetation communities: (*i*) a tussock meadow of cottongrass (*Eriophorum vaginatum*) and moss; (*ii*) a dwarf shrub heath of Arctic willow (*Salix arctica*), mountain avens (*Dryas integrifolia*) along with various graminoids (notably *Arctagrostis latifolia*), Arctic lupine (*Lupinus arcticus*), and other forbs; (iii) sparser cover of Arctic willow, wormwood (*Artemisia* spp.), legumes (Leguminosae), and grasses on steeper, eroding slopes. The second extensive habitat is the alluvial fan and associated sea-shore beach spit at Pauline Cove. The fan is covered with patches of erect willow shrub (*Salix richardsonii*) and moss, interspersed with meadows of grasses (e.g., *Alopecurus alpinus*), sedges (e.g., *Carex aquatilis*), and forbs. The spit has a sparse vegetation cover dominated by wild rye grass (*Elymus arenarius*) and *Stellaria humifusa*, along with some brackish ponds. Smith et al. (1989) provide more detail on these vegetation communities.

Herschel Island is experiencing a number of changes associated with a warming climate including more extensive retrogressive thaw slumps (Lantuit and Pollard 2008), a deeper active layer accompanying permafrost thaw (Burn and Zhang 2009), and a trend to earlier snow melt (Grabowski et al. 2013).

Bird community, abundance, and nesting phenology

To quantify the composition of the nesting bird community and the timing of hatch, we collected bird nesting data in three summers: 2007–2009. Comparative data from the 1980s were obtained from Talarico and Mossop (1986) and are presented in the “Results”.

In all years, we found nests during repeated ($n = 3$) searches during June of gridded (stakes with 20 m × 20 m spacing) small mammal live trapping plots of 9 ha ($n = 2$, both in upland habitat) and 1.8 ha ($n = 1$, in fan habitat) (Krebs et al. 2011). In 2008, we found nests in repeated ($n = 3$) foot surveys during June of two additional 12 ha plots in the upland habitats (gridded with 50 m × 50 m spacing). We surveyed these by generally following the Program for Regional and International Shorebird Monitoring (PRISM) protocol, but at reduced intensity (Bart and Earnst 2005).

In addition, we located other nests as we walked through the study area to access sites for a wide variety of ecological measurements (Gauthier and Berteaux 2011). These nests were added to the sample used in phenological assessment, being ascribed to either the mesic (upland) or hygric (alluvial fan and beach) habitats.

Nests in the beach component of the hygric habitat were limited to common eider (*Somateria mollissima)* (all in each year), semipalmated plover (*Charadrius semipalmatus*) (all in each year), semipalmated sandpiper (*Calidris pusilla*) (six in 2007, one in 2008, and two in 2009), savannah sparrow (*Passerculus sandwichensis*) (one in 2009), common redpoll (*Acanthis flammea*) (one in 2007, one in 2008, and four in 2009), Lapland longspur (LALO) (*Calcarius lapponicus*) (three in 2009), and snow bunting (SNBU) (*Plectrophenax nivalis*) (all in each year, in buildings). All were within 450 m of the arthropod traps in the alluvial fan.

In all cases, we back-tracked a flushed bird to try to find an existing nest. If successful, we took a handheld GPS location with which to re-locate the nest. Each nest was re-visited, at two-day intervals. We assigned successful hatch only to those nests (*i*) for which our period of observation fell within the published duration of incubation (Ehrlich et al. 1988; Rodewald 2015) and the nest (shorebirds) was empty, and (*ii*) with at least one pipped egg or chick seen in or within about 10 m of the nest. We considered the date on which the first egg in the clutch hatched as the nest’s hatch date. We calculated lay date by backdating from hatch date based on published incubation periods (details in Grabowski et al. 2013).

To assess relative success in food provisioning to chicks, in 2007, we continued to monitor survival of passerine chicks to fledging. Nests were considered to have failed after hatch when hatchlings were no longer present and are unlikely to have fledged based on published duration of nest dependence and the stage of development of their feathers. We excluded any nest for which lay date and fledging date could not be determined.

Arthropod availability

We sampled arthropods in 2007 (June 10 to August 4), 2008 (June 3 to July 31), and 2009 (June 19 to July 13) using modified Malaise traps (Bolduc et al. 2013; more detail in

Supplementary Material).[1] Traps were placed with the mesh perpendicular to prevailing winds. These passive traps caught arthropods in proportion to their abundance and level of activity, so can be considered as providing a proxy of arthropod availability to foraging birds (McKinnon et al. 2012; Bolduc et al. 2013).

We trapped in the upland habitat (dwarf shrub heath), hereafter termed mesic, in 2007 and 2008, and the fan habitat (graminoid meadow), hereafter termed hygric, in all three years. In each habitat, we placed five traps located 20 m from each other along a straight line. These trap lines were within or immediately adjacent to the small mammal live trapping grids, within 800 m of nests in the hygric habitat, and within 3 km of nests in the mesic habitat. Although traps cannot accurately record food availability at each nesting territory, a recent study of the most abundant species in our work (Lapland longspur) indicates high synchrony in timing of nesting over distances up to 2.5 km (Doucet 2014).

Traps were emptied at approximately two-day intervals, and arthropods were stored in ethanol (70%) until sorting and identification in the laboratory. We sorted and identified collections from the same three traps, located at the normal upwind end of the sequence during clear (warmer) weather, in both habitats each year. Insects were sorted into families, and spiders were grouped together. Springtails (Collembola) and mites (Acari) were not included in the analyses because of their very low contribution to total arthropod biomass. Lepidopterans and bumble bees (Bombidae) were also excluded because few individuals were collected due to the strong flight control of adults and low mobility of larvae, and because these few heavy specimens had a strong influence on daily variation in biomass.

Bolduc et al. (2013) provide details on how daily arthropod counts were transformed to dry mass (mg/trap/day) using length to dry mass equations and/or mean individual dry mass of specimens collected. A list of equations is also provided in the Supplementary Material[1] of McKinnon et al. (2012). We use the dry mass data from Bolduc et al. (2013) for this study.

Assessment of synchrony between hatch and food availability

To assess the temporal relationship between hatching and the summer pulses of arthropod biomass, we followed the procedure of McKinnon et al. (2012). This is based on the assumption that an ideal hatch period (i.e., a good match between hatching and food for chicks) occurs when hatch is followed by a pulse of arthropod food availability lasting at least the period during which chicks are most vulnerable to starvation. This period is about the first 9–11 days of life in precocial shorebirds (Grant et al. 1999; Pearce-Higgins and Yalden 2003; McKinnon et al. 2013). Such a period compares well to the periods of time that altricial passerine chicks remain in the nest [mean = 11 days, range = 9–14 days for seven species in this study, data from species accounts in Rodewald (2015)].

Specifically, we define the ideal hatch period as the period within which each day is followed by 10 days where the cumulative arthropod biomass (10-day running biomass total) is in the top 10th percentile of all 10-day running biomass totals. We made these assessments of ideal hatch period individually for each of seven arthropod taxonomic groups (Araneae and insect families such as Carabidae, Chironomidae, Ichneumonidae, Muscidae, Mycetophilidae, and Tipulidae) that contributed the most biomass in our samples, and, perhaps most importantly, based on the biomass of all the diverse arthropod taxa combined.

We lacked information on prey selection by the birds in our study area, so we refer to other studies on nesting grounds, choosing those from Arctic tundra whenever possible (summarized in Table 1). Shorebirds show remarkable overlap in foods dominated heavily by arthropod prey (Holmes and Pitelka 1968; Baker 1977; Lanctot and Laredo 1994)

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[1] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2017-0054.

Table 1. Summary of the principal foods in spring and summer breeding period for each bird species assessed for mismatch.

Species	Principal foods in spring and summer	Site and reference
Shorebirds		
American golden-plover *Pluvialis dominica*	Seeds, molluscs, Chironomidae, Tipulidae, Dolichopodidae, Chrysomelidae	Arctic tundra, MB (Baker 1977)
Baird's sandpiper *Calidris bairdii*	Tipulidae, Chironomidae, Muscidae, Anthomyidae, Araneae	Arctic tundra, AK (Holmes and Pitelka 1968)
Buff-breasted sandpiper *Calidris subruficollis*	Tipulidae, Muscidae, Chironomidae, Chrysomelidae, Carabidae	Arctic tundra, Wrangel Island, Russia (Lanctot and Laredo 1994)
Least sandpiper *Calidris minutilla*	Chironomidae, Psychodidae, Ceratopogonidae, Tipulidae, Dolichopodidae	Arctic tundra, MB (Baker 1977)
Semipalmated plover *Charadrius semipalmatus*	Tipulidae, Chironomidae, Dolichopodidae, Muscidae, Ceratopogonidae, Araneae	Arctic tundra, MB (Baker 1977)
Semipalmated sandpiper *Calidris pusilla*	Chironomidae, Tipulidae, Araneae, Staphylinidae, Carabidae	Arctic tundra, AK (Holmes and Pitelka 1968)
Wilson's snipe *Gallinago delicata*	Tipulidae, Tabanidae, other insects (orders: Diptera, Coleoptera, Odonata)	Boreal, NL (Mueller 1999)
Passerines		
American pipit *Anthus rubescens*	Araneae, Chironomidae, Tipulidae, Lepidoptera (Nymphalidae, Geometridae), Acrididae	Alpine tundra, WY (Verbeek 1970)
Common redpoll *Acanthis flammea*	*Collembola, Culicidae, Chironomidae, Tipulidae, Mycetophilidae, seeds*	Subalpine, Scandinavia (Knox and Lowther 2000)
Horned lark *Eremophila alpestris*	Seeds, molluscs, Chironomidae, Tipulidae, Dolichopodidae, Chrysomelidae	Arctic tundra, MB (Baker 1977)
Lapland longspur *Calcarius lapponicus*	*Tipulidae, Chironomidae, Empididae, Muscidae, Tenthredinidae, Araneae*	Arctic tundra, AK & NU (Hussell and Montgomerie 2002)
Savannah sparrow *Passerculus sandwichensis*	*Araneae, insects (orders: Diptera, Coleoptera, Hymenoptera, Homoptera, Lepidoptera)*	Arctic tundra — various (Wheelwright and Rising 2008)
Snow bunting *Plectrophenax nivalis*	*Tipulidae, Chironomidae, Empididae, Muscidae, Araneae, Lepidoptera*	Arctic tundra — various (Montgomerie and Lyon 2011)
White-crowned sparrow *Zonotrichia leucophrys*	Seeds, grains, insects (orders: Lepidoptera, Hymenoptera, Coleoptera)	Temperate — various (Chilton et al. 1995)
Others		
Long-tailed jaeger *Stercorarius longicaudus*	Arvicoline rodents, young birds, Araneae, Tipulidae, Lepidoptera	Nearctic tundra — various (Wiley and Lee 1998)
Sandhill Crane *Antigone canadensis*	Plants, seeds, arvicoline rodents, Araneae, bird eggs and nestlings, various insects	Nearctic tundra — various (Reed 1988)

Note: Birds are listed alphabetically by taxonomic group. Arthropod foods are listed to family or order for comparison to arthropod data presented in this study, and also in apparent order of abundance in the diet according to the references. Information is for adult birds, unless in italics, when it shows diet of young birds.

(Table 1). However, they respond strongly to the availability of different arthropods, feeding heavily on the most available taxa and switching when availability changes (Holmes and Pitelka 1968; Baker 1977). Although some species eat seeds and berries, especially early and late in the season, the precocial hatchlings generally feed on arthropods (Holmes and Pitelka 1968; Lanctot and Laredo 1994; Moskoff and Montgomerie 2002; Nebel and Cooper 2008; Johnson and Connors 2010). Although adults of some species (semipalmated sandpiper, semipalmated plover, and least sandpiper) feed primarily on aquatic invertebrates, notably larval insects, young chicks tend to concentrate more on terrestrial prey (Holmes and Pitelka 1968; Baker 1977; Lanctot and Laredo 1994). We assume that the shorebirds, especially the young chicks, feed mostly on terrestrial arthropods and that a suite of arthropod groups (Table 1) could be primary prey for chick growth.

Similarly, Arctic passerine chicks, in their first few weeks of life, mainly get fed, or feed on, terrestrial arthropods (Table 1), with choice changing as availability changes

Table 2. Summary of numbers of nests reaching hatch by species, listed alphabetically, in each of the two habitat types by year.

	2007		2008		2009	
Species	Hygric	Mesic	Hygric	Mesic	Hygric	Mesic
American golden-plover (AMGP)	0	1	0	1	0	1
American pipit (AMPI)	0	3	0	4	1	3
Baird's sandpiper (BASA)	0	3	0	11	1	1
Buff-breasted sandpiper (BBSA)	0	0	0	2	0	0
Common eider (COEI)	3	0	3	0	5	0
Common redpoll[a] (CORE)	1	0	4	4	7	3
Horned lark (HOLA)	0	1	0	1	0	0
Lapland longspur (LALO)	7	9	11	25	5	10
Least sandpiper (LESA)	1	0	0	0	1	0
Long-tailed jaeger (LTJA)	0	4	0	2	0	2
Rock ptarmigan (ROPT)	0	0	0	0	0	3
Sandhill crane (SACR)	0	0	0	1	0	1
Savannah sparrow (SAVS)	7	3	9	6	2	1
Semipalmated plover (SEPL)	2	0	1	0	3	0
Semipalmated sandpiper (SESA)	8	0	8	0	5	0
Snow bunting (SNBU)	2	0	2	0	1	0
White-crowned sparrow (WCSP)	0	0	1	0	0	1
Wilson's snipe (WISN)	0	0	1	0	1	0
Totals	31	24	40	57	32	26
Totals by year	55		97		58	

Note: Four-letter species codes are from IBP (2017), and are used subsequently in the text.
[a] Might have included some Hoary Redpoll (*Acanthis hornemanni*).

(Custer and Pitelka 1978). Although many species are strongly granivorous much of the year, they focus on arthropods during the nesting season and in feeding chicks (Custer and Pitelka 1978; Montgomerie and Lyon 2011). We assume that adult passerines also choose arthropods in general proportion to availability when feeding chicks. The principal food types known from other studies (Table 1) closely match those we address for ideal hatch periods, and, in the "Discussion", we address potential biases in our assessment of food availability for chicks.

Statistical tests were run in NCSS (Hintze 2012). The field work methods were reviewed and endorsed by the University of British Columbia Animal Care Committee with Certificates A05-1695 and A06-0132. The field work was also permitted by Government of Yukon Wildlife Research Permits 2007-0002, 2008-0028, and 2009-0044, by Yukon Scientists and Explorers Act Licences (07-22S&E, 08-27S&E, and 09-21S&E), and by Research Permits from Yukon Parks Branch.

Results

Bird community composition, abundance, and nesting phenology

Across years, we found nests of 18 species (excluding raptors and alcids), — 13 species in 2007, 16 in 2008, and 16 in 2009 (Table 2). Lapland longspurs and savannah sparrows were the most abundant breeders, totalling 67 and 28 nests, respectively.

The species composition of the terrestrial arthropod-feeding bird community was somewhat different than that documented during three years in the mid-1980s over the same portion of the island. We found no evidence of nesting in the 2000s for two species nesting in the 1980s: red-necked phalarope (*Phalaropus lobatus*) and ruddy turnstone (*Arenaria interpres*). In the 2000s, we found nests of four species for which nests were not found in the 1980s: sandhill crane (*Antigone canadensis*); buff-breasted sandpiper (BBSA) (*Calidris subruficollis*); least sandpiper; and white-crowned sparrow (*Zonotrichia leucophrys*). In addition, American golden-plover (AMGP) (*Pluvialis dominica*) were considered common nesters (up to eight nests per year in the study area) in the mid-1980s, but they were uncommon in our study (Table 2). Conversely, savannah sparrows were considered rare though successful nesters in the mid-1980s, but had become the second most common nesting species by the time of our work (Table 2). In Table 2, we introduce the four-letter codes for each species (IBP 2007) and use these codes in the text when the species has already been introduced with Latin name.

Of the nests we discovered, a total of 210 successfully hatched: 55 in 2007, 97 in 2008, and 58 in 2009 (Table 2). Of these, 107 were in the mesic (upland) habitats and 103 were in the hygric (alluvial fan and beach) habitats. The higher number in 2008 reflects more field staff focussing on nest searches and inclusion of PRISM sampling. Two species were not considered in further analysis, because their young do not feed on terrestrial arthropods [common eider (COEI)] or arthropod data were not available for the occupied mesic habitat in 2009 (rock ptarmigan, *Lagopus muta*). Similarly, none of the other nests in mesic habitat in 2009 was analysed for mismatch because arthropod data were not collected in that habitat. Consequently, 173 nests were assessed for phenological match with arthropod prey.

The earliest observed hatch date was 11 June for a LALO nest in 2008, and the latest was 14 July for a Baird's sandpiper (*Calidris bairdii*) nest in 2007 (Figs. 1 and 2). Hatching started earlier in 2008 (11 June) than in 2007 (20 June) and 2009 (19 June). However, the dates of last hatch were very consistent across years (2007: 14 July; 2008: 13 July; and 2009: 13 July), being determined by two species [common redpoll (CORE) and Baird's sandpiper (BASA)]. Consequently, the duration of the hatch period across all species varied substantially among year and habitat combinations, ranging from 18 to 33 days. The longest hatch periods, for both habitats, were in 2008, a year of relatively early snow melt and warm temperatures that may have allowed early nesting by the particular species that arrive relatively early on the nesting grounds.

Figures 1–3 give the median dates of hatch by species for the three years of study. Sample sizes of successful nests were often small, making interspecific comparisons of timing tentative. However, SNBU and LALO consistently produced the earlier hatching nests, whereas least sandpiper (LESA), Wilson's snipe (*Gallinago delicata*), and AMGP were regularly late hatchers. When a species hatched at least five nests in a specific habitat in a year, its range of hatch dates tended to span most of the full hatching period (between dashed lines in Figs. 1–3), so there was quite a high degree of synchrony in hatch periods among species.

Arthropod availability

Arthropods collected in traps belonged to 81 families, of which few contributed >1.0% of the total biomass for the habitat by year [details in Bolduc et al. (2013), Table 1]. Seven groups — Araneae (spiders) plus the insect families Tipulidae (crane flies), Carabidae (ground beetles), Muscidae (house flies), Mycetophilidae (fungus gnats), Chironomidae (midges), and Ichneumonidae (parasitoid wasps) — contributed the most to biomass. Their changes in biomass (our measure of food availability for birds), as well as the biomass of all groups combined (including the numerous other families that contributed much less to the total), are depicted in Figs. 1–3, and more detail is provided in Supplementary Material.[1] Each group showed a summer pulse of heightened biomass, indicated by the "ideal hatch periods" in Figs. 1–3.

Arthropod biomass varied substantially when considering all groups combined, as well as groups individually, among habitats and years (Figs. 1–3). Considering total biomass of all groups, the hygric habitat in 2007 produced by far the highest peak biomass (902 mg/trap/day) of any year by habitat combination, driven largely by Tipulidae. By contrast, peak biomass was 300 mg/trap/day in 2008 and 133 mg/trap/day in 2009. The mesic habitat produced two peaks in biomass for all groups combined in both years sampled, comprised largely of Carabidae and Araneae (Figs. 1 and 2). The magnitudes of these peaks

Fig. 1. The timing of hatch aligned with arthropod abundance in 2007. The temporal distributions of hatch dates by species are shown in box plots at the top of each column of the figure, where each column is a separate habitat (mesic and hygric). Each box plot includes the full range of hatch dates, and a box encompassing the middle 50% of the dates and including the median date. The four-letter species codes are as in Table 2. The temporal distributions of arthropod biomass are shown in sets of line graphs arrayed below the plots of hatch dates, and aligned to show correspondence across Julian dates (160 = June 9 in 2007 and 2009, and June 8 in 2008). Arthropod biomass is shown for all groups combined, and for the seven most abundant taxonomic groups (Note that *y*-axis scales vary among graphs). The dark horizontal rectangles are the ideal hatch periods (defined in the text) for each taxonomic group of arthropods, but their positions with respect to the *y*-axes do not have any meaning. The vertical dashed lines joining graphs within a column lay out the temporal extent of the hatch periods (drawn from box plots) for visual reference to the arthropod data.

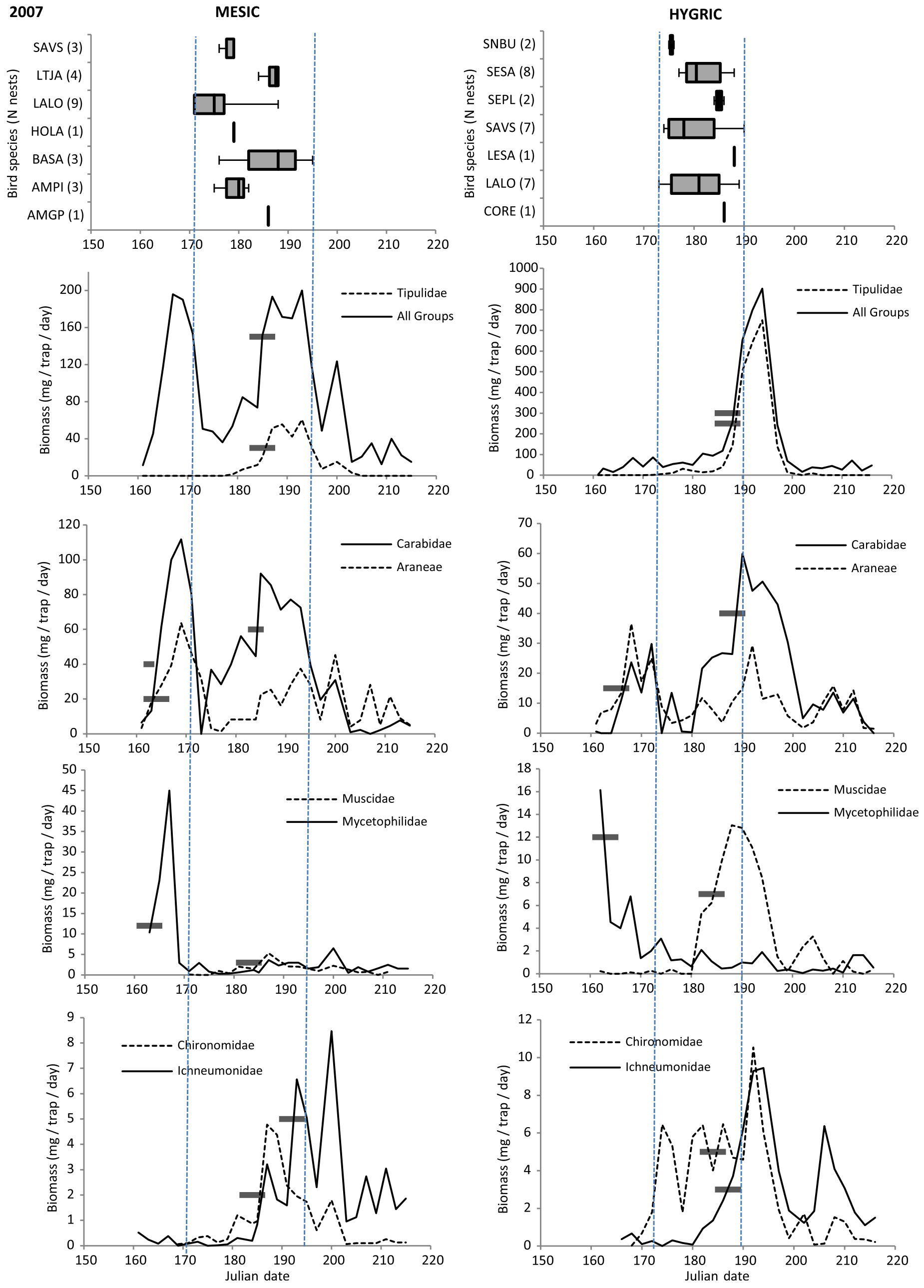


Fig. 2. The timing of hatch aligned with arthropod abundance in 2008. Explanations of layout and symbols are provided in caption to Fig. 1.

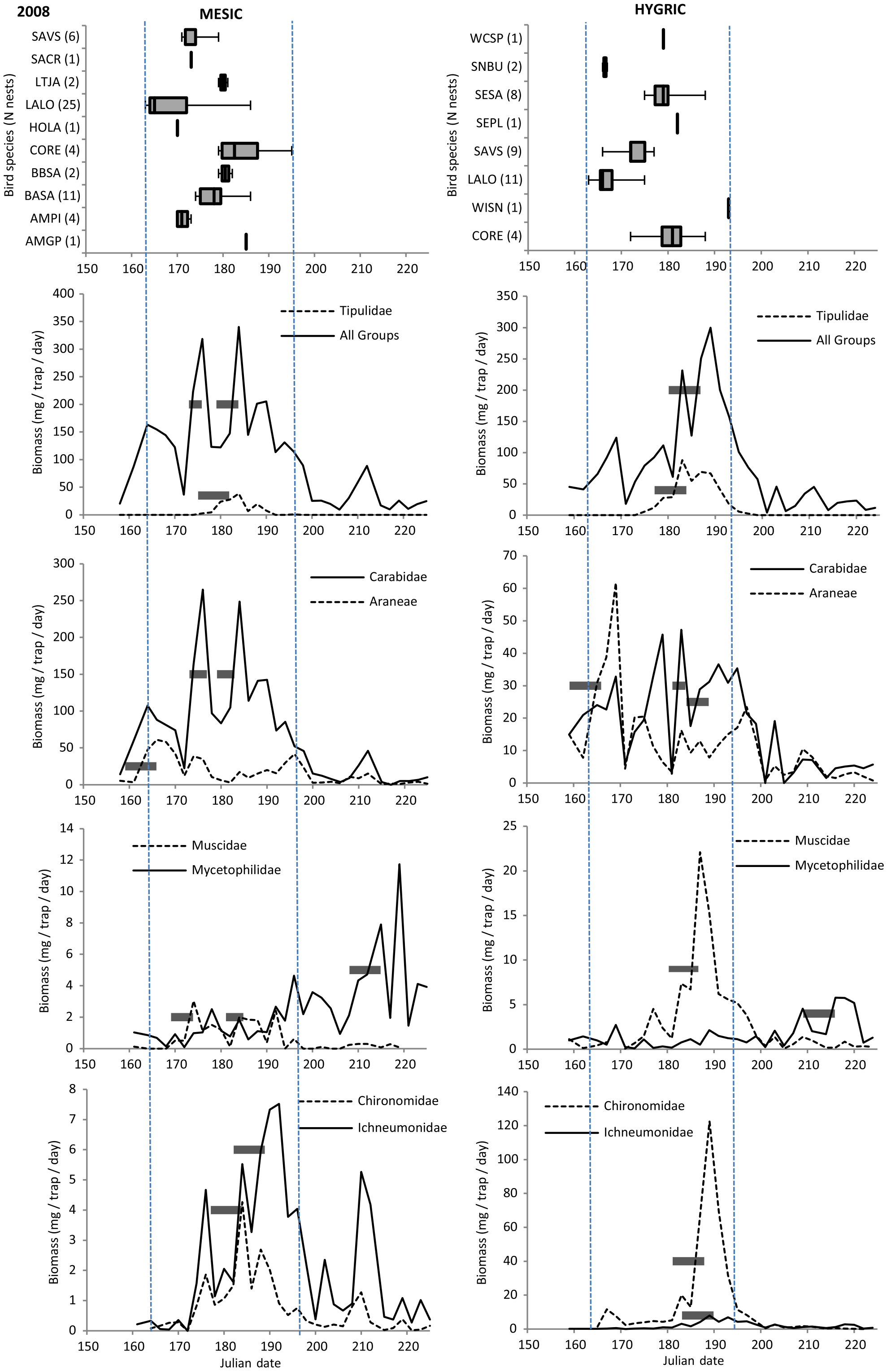
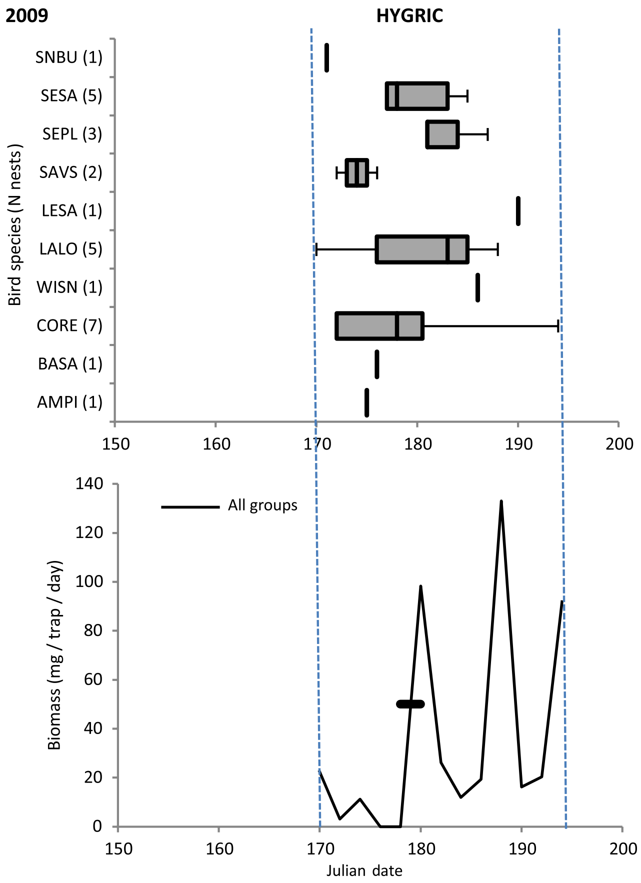


Fig. 3. The timing of hatch aligned with arthropod abundance in 2009. Explanations of layout and symbols are provided in caption to Fig. 1. LALO, Lapland longspur (LALO); SAVS, Savannah sparrow; SESA, Semipalmated sandpiper; BASA, Baird's sandpiper; AMPI, American pipit; SNBU, snow bunting; WISN, Wilson's snipe, CORE, common redpoll; SEPL, semipalmated plover.



were fairly similar to those in the hygric habitat in 2008. In 2007, biomass in the mesic habitat peaked at 196 mg/trap/day and 200 mg/trap/day. In 2008, it peaked at 319 mg/trap/day and 340 mg/trap/day. However, total biomass amounts collected were not consistently higher in either of the two habitats in the two years with full sampling (hygric: 2007 — 4046 mg, 2008 — 2531 mg; mesic: 2007 — 2392 mg, 2008 — 3368 mg).

Relationship of hatch dates to arthropod biomass

Ideal hatch periods coincided with the leading edge of pulses in arthropod biomass for individual arthropod groups and all groups combined (Figs. 1–3). Our tracking of seven arthropod groups plus all arthropod groups combined, allowed us to calculate 39 ideal hatch periods (horizontal bars in Figs. 1–3). Thirty of these 39 coincided with the observed hatch periods for all birds (time between the vertical lines in Figs. 1–3), indicating a good correspondence overall between the timing of high food availability and bird hatching. The exceptions were seven ideal hatch periods (with Araneae, Carabidae, and Mycetophilidae) in spring and preceding the range of observed hatch dates, plus 2 ideal hatch periods (with Mycetophilidae in 2008) occurring after the end of all bird hatching (Figs. 1–3). When an ideal hatch period associated with either Araneae or Carabidae

Table 3. Tests of the hypothesis that the mean arthropod biomass (mg/trap/day) available to hatchlings in the first 10 days after hatching (of all nests by species, habitat, and year) was equal to the mean arthropod biomass in the 10 days periods following each day in the ideal hatch period (IHP) associated with all arthropod groups.

				10 days biomass statistics			Test statistics	
Year	Habitat	Subject of the 10 days biomass sequences	Number of 10 days biomass sequences	Mean (mg/trap/d)	SD	SE	*T*	*P*
2007	Mesic	IHP	5	1650.5	83.0	37.1		
		LALO	9	824.4	351.7	117.2	−5.09	0.000
2007	Hygric	IHP	5	5588.4	110.7	49.5		
		SESA	8	2999.2	2199.4	777.6	−3.32	0.006
		SAVS	7	2234.2	2148.2	812.0	−4.12	0.003
		LALO	7	2705.5	2196.4	830.2	−3.47	0.008
2008	Mesic	IHP	6	2035.4	47.3	19.3		
		BASA	11	1889.1	136.6	41.2	−3.22	0.003
		SAVS	6	1859.8	167.8	68.5	−2.47	0.025
		LALO	25	1501.4	258.4	51.7	−9.68	0.000
2008	Hygric	IHP	6	2095.4	73.7	30.1		
		SESA	8	1587.4	327.1	115.6	−4.25	0.001
		SAVS	9	991.4	264.9	88.3	−11.83	0.000
		LALO	11	770.6	142.4	42.9	−25.27	0.000

Note: The statistical test is the Aspin–Welch unequal variance test (one-tailed). The hypothesis is rejected in all cases, so the alternative hypothesis is accepted. Species codes are the same as those in Table 2. LALO, Lapland longspur; SAVS, Savannah sparrow; SESA, semipalmated sandpiper; BASA, Baird's sandpiper.

occurred in spring, that arthropod group also had a later pulse in biomass during or just after the observed bird hatching period.

Only 33 of 173 nests (19%) hatched directly within ideal hatch periods associated with biomass of all arthropod groups combined (Figs. 1–3): 12 of 52 in 2007, 16 of 94 in 2008, and 5 of 27 in 2009. The null hypothesis that the proportion of nests hatching during the ideal hatch period was no greater than the proportion hatching at other times through the entire hatch period could not be rejected for any year by habitat combination (Fisher's exact tests, *P* ranging from 0.28 to 1.00). This indicates that the ideal hatch period did not have a strong concentration of hatching events.

Most nests [i.e., 122 of 173 nests (71%)] hatched in advance of the ideal hatch periods associated with all arthropod groups combined, indicating that most of the "mismatched" hatching was because birds nested relatively early compared with the time at which the aggregate pulse of total food became available. On average, the arthropod biomass was significantly lower in the 10-day periods following bird hatching compared with the 10 days following ideal hatch periods (associated with all groups) in all year by habitat combinations and for species with >5 nests (Table 3). We also assessed, for each bird species, the numbers and proportions of nests hatching within the specific ideal hatch periods associated with Araneae, Carabidae, Tipulidae, or all arthropod groups combined (Table S1 in Supplementary Material).[1]

Relatively few nests [18 of 173 (10%)] hatched after the end of the ideal hatch period associated with all arthropod groups combined (Figs. 1–3): 5 of 52 (9.6%) in 2007, 8 of 94 (8.5%) in 2008, and 5 of 27 (18.5%) in 2009. Ten of those 18 nests hatched within 2 days of the end of the associated ideal hatch periods, so were barely mismatch. The bird species with individual nests hatching long after the ideal hatch periods were low Arctic nesters [CORE, LESA, and Wilson's snipe (WISN)] and one nest of BASA. All these species, except WISN, had other nests that hatched early enough to coincide with ideal hatch periods, so were not consistently late nesters.

The null hypothesis that shorebirds and passerines did not differ in median hatch dates, for species ranked individually and habitats combined, was rejected in one-tailed

Mann–Whitney *U* tests (2007: $U^1 = 27.5$, $P < 0.025$, $n_1 = 5$, $n_2 = 6$; 2008: $U^1 = 37.5$, $P < 0.025$, $n_1 = 6$, $n_2 = 7$). Thus, the alternative hypothesis, that shorebird hatching was significantly later than passerine hatching, was supported.

Of 21 passerine nests followed through the nestling period in 2007, 16 hatched before the ideal hatch period associated with all arthropod groups, 4 during, and 1 after. The proportion of eggs resulting in fledged chicks was not significantly different between those hatched before the ideal hatch period (54 of 79 eggs) compared with those hatched during the ideal hatch period (12 of 17 eggs) (Fisher's exact test $P = 1.00$).

Discussion

Breeding bird community

Since the 1980s there have been a few changes in the composition of the nesting bird community on the east end of Herschel Island, characterised by a loss of two species currently facing population declines (Zöckler et al. 2013) and particularly associated with brackish and freshwater ponds (RNPH and RUTU), and a gain of some species more typically associated, at least west of the Mackenzie River, with boreal and subarctic habitats [sandhill crane (SACR), LESA, and white-crowned sparrow (WCSP)] (Chilton et al. 1995; Nebel and Cooper 2008; Eckert 2012; Gerber et al. 2014). Increasing sea level, coupled with greater variability associated with more frequent and intense storm surges, have resulted in increased flooding of significant portions of the beach and alluvial fan habitats each summer (Pollard et al. 2012). Flooding may have impacted nesting success of phalaropes and turnstones directly or through disruptions in availability of aquatic prey. Species gains appear to be small range expansions.

A longer growing season has stimulated the expansion and increased stature of willow (*Salix* spp.) (Myers-Smith et al. 2011), plus increased cover of some grasses and forbs in upland tundra habitats on Herschel Island (Kennedy et al. 2001). Savannah sparrows (SAVS) are probably benefitting from increased shrub growth which is typical of their northern nesting areas (Wheelwright and Rising 2008). AMGP prefers sparsely vegetated open tundra habitat (Johnson and Connors 2010), the disappearance of which may be influencing AMGP abundance. All the losses or declines have been with shorebird species, the group that seems to be most at risk of phenological mismatch (see "Discussion" below). Although habitat changes may be causing the changes in species abundance, we lack historical data on arthropod community composition and abundance so cannot assess any influence of prey. In addition, abundance of these birds may be strongly influenced by sources of mortality in migration and wintering habitats (Ganter et al. 2013). Long-term monitoring is required to determine whether these changes in the bird community continue, and the extent to which changes in habitat and/or prey drive them.

Phenological mismatch

Overall our results provide no evidence of phenological mismatch of low Arctic passerine and shorebird reproduction and the availability of arthropod prey for chick growth, where mismatch is defined as reproduction happening too late in the growing season to take advantage of the summer pulse in arthropod biomass. During our particular study period, the large majority of nests hatched earlier than or during the various ideal hatch periods for those arthropod groups that contributed strongly to the summer pulses in arthropod biomass. The relatively few nests hatching after the pulses in arthropod prey may have been re-nesters, given that conspecifics successfully hatched much earlier in the season (e.g., BASA and CORE). Alternatively, they may be species (e.g., LESA and WISN) relatively recently establishing themselves as nesters in north Yukon, which is at the northern limit of their documented distributions (Salter et al. 1980; Mueller 1999; Nebel and Cooper 2008). Talarico and Mossop (1986) report no LESA and one WISN nest from the same study area in the mid-1980s. Neither species was reported during 2002 and 2004 shorebird breeding surveys of the Arctic National Wildlife Refuge, about 150 km to the west (Brown et al. 2007).

Our measure of food availability has some potential biases. Four of the seven arthropod groups contributing heavily to our biomass measures (Araneae, Tipulidae, Chironomidae, and Muscidae) are known to be prominent foods for most of the birds studied (Table 1). The remaining three groups (Carabidae, Mycetophildae, and Ichneumonidae) are documented less frequently as foods (Table 1), leading to a possible overestimation of food availability by our traps. Contrastingly, several fairly prominent known foods [Lepidoptera (butterflies and moths), Dolichopodidae (long-legged flies), Ceratopogonidae (biting midges), and Empididae (dance flies)] (Table 1) were present but not very prominent in our trap samples (Bolduc et al. 2013), leading to a possible underestimation of food availability. Birds might avoid eating the hard-shelled carabids (ground beetles), and, if our study represents seasonal availability of mycetophilids (fungus gnats) more generally, their peaks in abundance rarely overlap the chick-rearing period (Figs. 1 and 2). The potentially underestimated foods are relatively immobile as larvae, and often associated with semi-aquatic sites, so our traps might not have been a useful means of sampling them. The three groups potentially over-estimating food availability contributed about 37% of our total trapped arthropod biomass in 2007 and 2008 (Bolduc et al. 2013), but their inclusion does not significantly alter the timing of pulses in total biomass during the hatch period because of the high degree of synchrony with other groups (Figs. 1 and 2).

Other factors, such as weather and foods other than arthropods, might influence chick survival more than phenological mismatch. Regarding weather, arthropods tend to be less mobile during relatively cold days (Bolduc et al. 2013). If their mobility influences bird foraging success, or adult birds must spend extra time sheltering chicks from cold, intense heat, or precipitation [as indicated, for example, by Lanctot and Laredo (1994) and Hussell and Montgomerie (2002)], then poor weather coincident with nestling (passerines) or early fledgling (shorebirds) periods might strongly influence chick survival independent of background arthropod abundances (Meltofte et al. 2007*b*). Regarding other foods, long-tailed jaeger (LTJA) rely more on small rodents to satisfy growth requirements of chicks (Wiley and Lee 1998), and SACR on Arctic nesting grounds consume many foods other than invertebrates (Reed 1988) (Table 1). The importance of matching hatch with arthropod prey is likely quite limited in these two species.

Comparison with other study

Our results differ from those of McKinnon et al. (2012) who assessed three shorebird species, using the same protocols and time period, on Bylot Island, a high Arctic site. They found relatively high coincidence of hatching with ideal hatch periods in only one of four years. In the other three years, most hatching occurred well after the ideal hatch periods for Araneae, Carabidae, Tipulidae, and all groups combined. Differences between study areas may be related to differences in snow melt, primary productivity, and associated arthropod abundance, and also to the suite of species studied and their patterns of travel during migration.

Regarding snow, late-winter maximum accumulations are substantially higher in the eastern Canadian Arctic (including Bylot Island, 100–199 cm) than in the more arid west (Herschel Island, 30–49 cm) (1979–1997 data in Natural Resources Canada 2010). Although the Arctic snow pack has been melting earlier since the 1980s and especially since 2005 (Derksen et al. 2016), under the same amount of spring heating, deeper snow will take longer to melt, so birds in the western Arctic likely experience earlier exposure of bare ground relative to cumulative heating and perhaps a more prolonged nesting season and period of arthropod availability.

Regarding primary productivity, our low Arctic site in bioclimatic subzone D (S1: erect dwarf-shrub tundra), is considerably more productive than Bylot Island, a high Arctic site in subzone C (G2: graminoid, prostrate dwarf-shrub, and forb tundra) reflecting a warmer climate and longer growing season on Herschel Island (Walker et al. 2005). These lead to higher species diversity, and mean biomass of trapped arthropods at Herschel (6608 mg/season) compared with Bylot (1870 mg/season) (Bolduc et al. 2013). The pulse of trapped arthropods reached significantly higher peaks ($t_s = 3.4$, $P = 0.014$, $df = 4$) in mesic habitat on Herschel (240–300 mg/trap/day) compared with the similar habitat on Bylot (80–140 mg/trap/day; McKinnon et al. 2012). In addition, the duration of high availability of prey lasted longer on Herschel. Based on a threshold biomass of all arthropods of 70 mg/trap/day [the minimum observed level at which successful fledging of shorebirds occurred on Bylot (McKinnon et al. 2012), Fig. 2], Herschel exceeded this threshold in the mesic habitat most similar to Bylot for significantly longer periods [Herschel: 21–38 days ($n = 2$); Bylot: 3–10 days ($n = 4$); $t_s = 3.9$; $P = 0.009$; $df = 4$]. Higher diversity and productivity of prey, spread over longer time spans, probably enhance the ability of chicks to grow. Evidence for improved chick growth in years with longer time span of prey availability is provided by Reneerkens et al. (2016) for sanderling (*Calidris alba*) in high Arctic Greenland. Herschel Island may be so productive that food availability is rarely limiting during the period up to the sharp decline in biomass of all arthropod groups combined at about Julian date 200 (c. 19 July).

Regarding specific species, all three shorebirds studied by McKinnon et al. (2012) winter in middle to extreme southern South America: white-rumped sandpiper (Parmalee 1992), BASA (Moskoff and Montgomerie 2002), and AMGP (Johnson and Connors 2010). Two of those (AMGP and BASA) also nested on Herschel. AMGP was the latest hatching species on Bylot, and also tended to hatch later than others on Herschel. Of the four other shorebird species we followed on Herschel, the BBSA also winters in southern South America (Lanctot and Laredo 1994), the SESA and SEPL winter in coastal northern South America and the Caribbean (Hicklin and Gratto-Trevor 2010; Nol and Blanken 2014), and the LESA in the Caribbean and even further north through southern North America and the temperate Pacific Coast (Nebel and Cooper 2008).

By contrast, the passerines on Herschel had generally shorter migratory distances than shorebirds, having wintered in Central America plus south temperate North America [American pipit (AMPI) (Hendricks and Verbeek 2012) and SAVS (Wheelwright and Rising 2008)], entirely in temperate North America [LALO (Hussell and Montgomerie 2002), SNBU (Montgomerie and Lyon 2011), and horned lark (HOLA) (Beason 1995)], or north temperate and boreal North America [CORE (Knox and Lowther 2000)].

Birds with shorter migrations, often including shorter travel bouts, appear able to better respond to changes in spring phenology than birds travelling longer distances including long-distance travel bouts (Miller-Rushing et al. 2008; Both et al. 2010). The shorebirds migrating long distances from the tropics and southern temperate latitudes may be less flexible in tracking spring phenology during migration, and therefore less able to fine-tune arrival on the breeding grounds and most at risk of mismatch (Both et al. 2010). The Bylot Island shorebirds (McKinnon et al. 2012), and the AMGP and SESA on Herschel, are examples. Although we found no clear evidence of mismatch on Herschel during our study period, a projected ongoing advancement of spring phenology (Candlish et al. 2015) probably means the risk is increasing. Re-evaluation would be warranted in the not too distant future, with special focus on the full sequence of reproduction in shorebirds.

Conflict of interest

The authors have no conflicts of interest to report.

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