

Terrestrial arthropod abundance and phenology in the Canadian Arctic: modelling resource availability for Arctic-nesting insectivorous birds

Elise Bolduc,¹ Nicolas Casajus, Pierre Legagneux, Laura McKinnon, H. Grant Gilchrist, Maria Leung, R.I. Guy Morrison, Don Reid, Paul A. Smith, Christopher M. Buddle, Joël Bêty

Abstract—Arctic arthropods are essential prey for many vertebrates, including birds, but arthropod populations and phenology are susceptible to climate change. The objective of this research was to model the relationship between seasonal changes in arthropod abundance and weather variables using data from a collaborative pan-Canadian (Southampton, Herschel, Bylot, and Ellesmere Islands) study on terrestrial arthropods. Arthropods were captured with passive traps that provided a combined measure of abundance and activity (a proxy for arthropod availability to foraging birds). We found that 70% of the deviance in daily arthropod availability was explained by three temperature covariates: mean daily temperature, thaw degree-day, and thaw degree-day². Models had an adjusted R^2 of 0.29–0.95 with an average among sites and arthropod families of 0.67. This indicates a moderate to strong fit to the raw data. The models for arthropod families with synchronous emergence, such as Tipulidae (Diptera), had a better fit (average adjusted R^2 of 0.80) than less synchronous taxa, such as Araneae ($R^2 = 0.60$). Arthropod abundance was typically higher in wet than in mesic habitats. Our models will serve as tools for researchers who want to correlate insectivorous bird breeding data to arthropod availability in the Canadian Arctic.

Résumé—Dans la toundra arctique, les arthropodes constituent des proies essentielles pour de nombreux vertébrés dont les oiseaux. Cependant, les populations d'arthropodes et leur phénologie sont susceptibles de subir des modifications face aux changements climatiques. Notre étude utilise des données sur les arthropodes terrestres provenant d'une initiative pancanadienne (Îles Southampton, Herschel, Bylot et Ellesmere), afin de modéliser la relation entre les changements saisonniers d'abondance d'arthropodes et les variables environnementales. Des pièges fournissant une mesure combinée de l'abondance et de l'activité des arthropodes ont été utilisés afin d'obtenir un indice de la disponibilité des arthropodes pour les oiseaux. Dans nos modèles, trois covariables liées à la température (température, degrés-jours et degrés-jours²) expliquent 70% de la déviance. Selon les sites et les familles d'arthropodes modélisés, les R^2 ajustés des modèles ont variés de 0.29–0.95 (moyenne de 0.67). Les modèles pour les familles d'arthropodes ayant une émergence synchronisée, comme les Tipulidae (Diptera), avaient de meilleurs R^2 ajustés (0.80 en moyenne) comparativement aux groupes dont la disponibilité est plus répartie dans le temps, comme les araignées (0.60). L'abondance d'arthropodes était généralement plus grande dans les milieux humides que dans les milieux plus secs. Nos modèles pourront servir d'outil aux chercheurs qui désireraient corrélés leurs données sur la reproduction des insectivores avec des données sur la disponibilité d'arthropodes dans l'Arctique Canadien.

Received 16 June 2012. Accepted 3 December 2012.

E. Bolduc,¹ N. Casajus, P. Legagneux, L. McKinnon, J. Bêty, Département de biologie & Centre d'études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Quebec, Canada G5L 3A1

H.G. Gilchrist, R.I.G. Morrison, National Wildlife Research Centre, Carleton University, 1125 Colonel By Drive (Raven Road), Ottawa, Ontario, Canada K1A 0H3

M. Leung, Wild Tracks Ecological Consulting, 39 Harbottle Road, Whitehorse, Yukon, Canada Y1A 5T2

D. Reid, Wildlife Conservation Society Canada, PO Box 31127, Whitehorse, Yukon, Canada Y1A 5T2

P.A. Smith, Smith and Associates Ecological Research Ltd, 772 – 7th Conc. South, Pakenham, Ontario, Canada K0A 2X0

C.M. Buddle, Department of Natural Resource Sciences, McGill University 21, 111 Lakeshore Road, Ste-Anne-de-Bellevue, Quebec, Canada H9X 3V9

¹Corresponding author (e-mail: elise_bolduc@uqar.ca).

doi:10.4039/tce.2013.4

Introduction

Climate change is a significant environmental disturbance that will alter the distribution and abundance of species (Thomas *et al.* 2004; Berteaux *et al.* 2006; Post *et al.* 2009). Changes in climate are not only associated with temperature changes but also with environmental stochasticity that directly affects life cycles of animals (Saether 1997; Thomas *et al.* 2004; Jenouvrier *et al.* 2009). As ectotherms, arthropods are particularly sensitive to climate variation since they are biochemically, physiologically, and behaviourally dependent on temperature (Huey and Berrigan 2001; Frazier *et al.* 2006) and their abundance is primarily driven by temperature (Deutsch *et al.* 2008; Tulp and Schekkerman 2008). Effects of climate change on arthropods may be most acute and significant in the Arctic since this region's climate is warming at a disproportionate rate relative to the rest of the planet (Arctic Climate Impact Assessment 2004) and rapid changes in arthropod phenology, abundance or species assemblage are expected (Deutsch *et al.* 2008).

Arctic food webs are relatively simple (Elton 1927; Gauthier *et al.* 2012) and many trophic interactions in the Arctic are linked to arthropods (Hodkinson and Coulson 2004). Millions of insectivorous birds breed in the Arctic (Committee for Holarctic Shorebird Monitoring 2004) and rely on terrestrial arthropods for their survival and reproduction (Pearce-Higgins and Yalden 2004; Schekkerman *et al.* 2004). On the Arctic tundra, surface-active arthropods are abundant only for a short period of time varying from a few days to a few weeks every year (MacLean and Pitelka 1971; Hodkinson *et al.* 1996; Schekkerman *et al.* 2004; Tulp 2007). In Arctic-nesting shorebirds, chick growth rates appear to be influenced strongly by the availability of arthropods (Tulp and Schekkerman 2001; Schekkerman *et al.* 2003; Schekkerman *et al.* 2004; McKinnon *et al.* 2012). The timing and duration of this period of high arthropod availability, however, can change rapidly because of global warming as recorded over the last 10–30 years in Siberia, Russia, and eastern Greenland (Høye *et al.* 2007; Tulp and Schekkerman 2008).

The relationship between climate change and the ecology of species is often assessed via

correlations within long-term data sets including climate, primary producers, and consumers (Both and Visser 2001; Root *et al.* 2003; Dickey *et al.* 2008; Visser 2008). Although long-term data sets on insectivorous birds exist, seasonal changes in Arctic arthropod abundance are poorly documented (but see Tulp and Schekkerman 2008) and this remains an obstacle in determining the effect of climate change on insectivorous bird populations.

Since climate (for which long-term data exist and are freely available; Hijmans *et al.* 2005) is directly related to the abundance of surface-active arthropods (Danks 1981; Hodkinson *et al.* 1998; Bale *et al.* 2002; Tulp and Schekkerman 2008), predicting or hindcasting Arctic arthropod abundance requires the selection of relevant climatic covariates to model arthropod abundance. This is the objective of our research. Here we report the results of a collaborative pan-Canadian study of surface-active Arctic arthropods and provide predictive models of daily arthropod availability for four sites that differ in terms of their climate and arthropod communities.

Methods

Arthropod sampling

Arthropods were sampled from June to August using a rectangular pitfall trap (38 cm × 5 cm and 7 cm deep). Above the pitfall trap, a 40 cm × 40 cm mesh screen was set vertically. Above the screen, a plastic cone funnelled flying insects into a collecting jar (Fig. 1). Traps were placed with the mesh perpendicular to prevailing winds, and their design was similar to traps used by Schekkerman *et al.* (2003). These passive traps provided a combined measure of abundance and activity levels of arthropods, and so a proxy for arthropod availability to foraging birds, and data from such methods have been correlated to chick growth rate (Schekkerman *et al.* 2003; McKinnon *et al.* 2012). Traps were used on four different Arctic islands across the Canadian Arctic: Southampton (63°59'N, 81°40'W; mean summer temperature = 7.1 °C) from 2006 to 2008, Herschel (69°35'N, 138°55'W; 10.6 °C) in 2007 and 2008, Bylot (73°8'N, 79°58'W; 5.8 °C) from 2005 to 2008, and Ellesmere (Alert)

Fig. 1. Arthropod trap in the field.

(82°29'N, 62°21'W; 3.8 °C) in 2007 and 2008. At each site, five traps located 20 m apart from each other on a straight line were set in both dry upland (mesic) or low wetland (wet) tundra, the main foraging habitats for the dominant insectivorous bird species (passerines and shorebirds) during their brood-rearing period. Site-specific habitat descriptions are available in Smith *et al.* (2007) (Southampton), Ale *et al.* (2011) (Herschel), Gauthier *et al.* (2011) (Bylot), and Morrison *et al.* (2005) (Ellesmere). Traps were emptied at approximately two-day intervals, and arthropods were stored in ethanol (70%) until sorting and identification in the laboratory. Insects were sorted into families, and spiders were grouped together. Springtails and mites were not included in the analyses because of their very low contribution to total arthropod biomass. Butterflies and bumblebees were also excluded because few individuals were collected due to the design of the traps and because these few heavy specimens had a strong influence on daily variation in biomass. Moreover, adults of these taxa are not key prey for shorebirds or passerines. Sorting and identification was conducted on a subsample of three to five traps for

each habitat and site. A standardised daily index of arthropod availability (mg/trap) was calculated by dividing the total arthropod biomass (dry mass) by the number of traps sorted and by the number of days between sampling event. To transform arthropod counts into dry mass, we used length to dry mass equations derived from our samples (Picotin 2008) or from the literature (Rogers *et al.* 1977; Sage 1982; Sample *et al.* 1993; Hodar 1996). For some of the dominant groups, we dried and weighed specimens and calculated a mean individual dry mass (Picotin 2008). When individual variation in size was high, individuals were grouped within size categories and mean dry mass was obtained for each category. A list of equations is provided in the supplementary materials of McKinnon *et al.* (2012).

Climate data

Mean hourly weather data (temperature in °C, precipitation in mm, relative humidity in %, radiation in W/m², and wind speed in km/h) from the closest automated weather stations were used to build predictive models of daily arthropod availability. Stations were located ~ 0.5 km (Southampton), 0.5–3.0 km (Herschel), 1 km (Bylot), and 2 km (Ellesmere) away from the trapping sites. Radiation data were unavailable for Ellesmere and Herschel Island.

Statistical analyses

Climatic variables known to influence the phenology of emergence, activity patterns, and/or abundance of arthropods (Wigglesworth 1972; Strathdee *et al.* 1993; Whittaker and Tribe 1998; Roy *et al.* 2001; Goulson *et al.* 2005; Høye and Forchhammer 2008; Tulp and Schekkerman 2008) were used to construct models of arthropod availability: daily temperature (T), relative humidity (H), precipitation (Rain), wind speed (Wi), thaw degree-days (D), and solar incidental radiation (R , log-transformed to improve normality). Correlations among meteorological variables ranged between 0.02 and 0.52 except between T and H (Pearson correlation = 0.70). High multicollinearity was coming from one study site: Ellesmere (Pearson correlation = 0.92). For this particular site, H and T were not entered simultaneously in the model. All variables were averaged over the number of days between trap

checks except for precipitation and thaw degree-days. The sum of precipitation between trapping sessions was used (95% of the trapping sessions lasted two days, 4% lasted one or three days and 1% lasted four days), and thaw degree-days represented the accumulated mean daily temperatures between the first spring day above 0 °C and the day of sampling (sub-zero temperatures being treated as zeros). The quadratic form of thaw degree-days (D^2) was included in the models in order to represent the curvilinear pattern of seasonal arthropod availability. We also included the interaction between T and D as a variable because (i) insect development is proportional to accumulation in degree-days (Wagner *et al.* 1991; Gullan and Cranston 2005) and (ii) temperature can affect insects differently depending on their developmental stage (Gullan and Cranston 2005).

We used generalised linear mixed models with a Poisson distribution (McCullagh and Nelder 1989) to analyse the relationships between weather variables and arthropod dry mass. To account for repeated data across years, year was treated as a random factor in the analyses. Since the purpose of our models was not to test hypotheses but rather to select the best predictors of arthropod availability, model selection was based on adjusted R^2 . When more than one model had the same adjusted R^2 (<1% variation), the model with the least number of parameters was preferred. For each of the four study sites, we created separate models for all of the dominant families. A family was considered dominant for a given site if its dry mass accounted for >10% of the total arthropod dry mass excluding spiders for at least one year (spiders had a high biomass contribution in early season and that could interfere with the contribution of other groups during the peak in arthropod abundance). Spiders were, by default, considered a dominant group at all sites. A threshold of 10% was set in order to select a limited number of dominant families while still accounting for most of the dry mass encountered. Dominant groups accounted for between 78% and 91% of total dry mass by site. Separate models were created for wet and mesic habitats.

For each model, the associated deviance for each selected variable (based on our model selection) was calculated. We then calculated the average deviance for each covariate based on the

37 models (each site/habitat/family) presented in Table 2. Proportions of deviance were calculated based on the partial R^2 and variables that were not included in a model were set to 0% except when data were unavailable (radiation in Ellesmere and Herschel).

Using the models described above, we calculated the estimated dry mass for each study site (sum of the predictions for the dominant groups). We then compared these predictions to the actual dry mass measured for all families (dominant and no-dominant altogether).

In order to validate the models, we developed a cross-validation technique to assess the fit of our models on an independent data set. For this sake, we used data from Bylot Island, the only site for which we had a relatively large data set available (*i.e.*, up to four years). We constructed models based on three years of data (except for Araneae and Ichneumonidae, where only three and two years were available) and confronted the predicted values from these models to the independent data of the fourth year. We repeated this procedure four times (for each three-year combination) for Chironomidae (Diptera), Carabidae (Coleoptera), Muscidae (Diptera), and Tipulidae (Diptera) and three or two times for Araneae and Ichneumonidae (Hymenoptera). We then calculated the adjusted R^2 and generated a figure for each year and taxon for the wet habitat. Such approach is ideal to assess the reliability of a predictive model (Efron and Tibshirani 1993).

We also performed a Linear Mixed Model to investigate both effects of habitat and study sites on arthropod availability (all families combined). In this model, we linked arthropod availability to site, habitat, and the interaction of both. We put days and years as random factors (days nested in year) in order to account for repeatability.

Results

Descriptive results

A total of 300 days of sampling over up to four years at four different sites yielded 342 451 arthropods identified to the family level, except for spiders. In total, representatives of 92 families were found. The most common groups were Araneae, Carabidae, Chironomidae,

Table 1. Total dry mass of the different families averaged over the number of years of sampling.

	Ellesmere (2007–2008)		Bylot (2005–2008)		Herschel (2007–2008)		Southampton (2006–2008)	
	mg/year	%	mg/year	%	mg/year	%	mg/year	%
Anthomyiidae	1	<1	25	1	46	1	116	3
Araneae	110	10	476	25	1367	21	2247	49
Carabidae			165	9	2179	33	366	8
Chironomidae	185	17	226	12	260	4	414	9
Dolichopodidae			61	3	17	<1	44	1
Empididae	<1	<1	38	2	59	1	58	1
Ichneumonidae	20	2	165	9	118	2	15	<1
Muscidae	445	41	321	17	110	2	259	6
Mycetophilidae	226	21	44	2	153	2	22	<1
Scatophagidae	1	<1	18	1	110	2	316	7
Sciaridae	49	5	18	1	57	1	38	1
Syrphidae	3	<1	32	2	9	<1	2	<1
Tipulidae	14	1	208	11	1600	24	563	12
Total								
Minimum	762		1133		6491		3321	
Maximum	1407		2160		6725		5504	
Average	1085		1870		6608		4583	

Only families representing more than 1% of total biomass for at least one year are presented in the table but all families are included in the totals.

Tipulidae, Muscidae (Diptera), Ichneumonidae, Mycetophilidae (Diptera), and Scatophagidae (Diptera) (Table 1). Diversity (expressed as the number of different families) was higher at Herschel ($n = 81$) than at Southampton, Bylot or Ellesmere ($n = 37, 38, 26$, respectively). At each site, only a few families (6–10) contributed significantly (more than 1%) to the total dry mass. There was considerable inter-annual variation in seasonal trends of arthropod availability in terms of timing, duration, and magnitude of peaks in total dry mass, both within and among sites (Fig. 2). Although variable among sites, arthropod availability was generally highest in early July (Fig. 2). On Bylot Island, for example, peaks were short-lived each year (two to seven days) and usually occurred within the same 17-day period (28 June to 14 July).

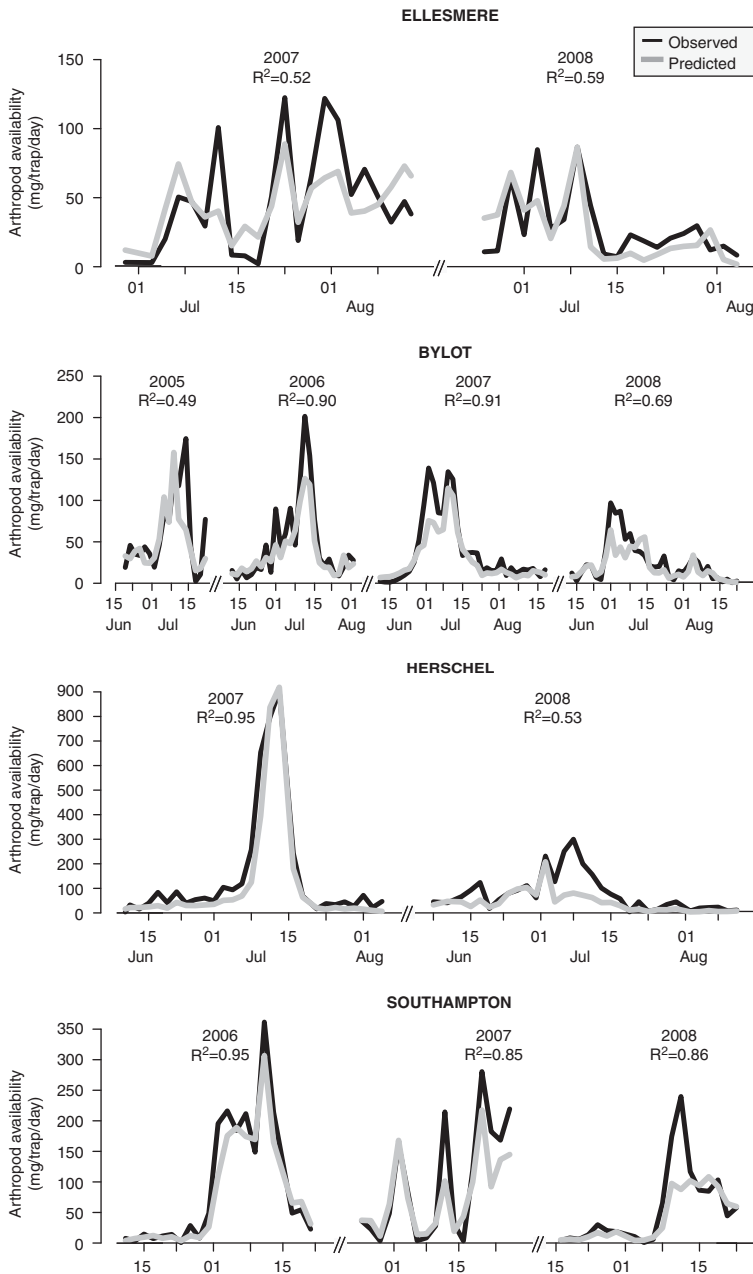
Modelling results

Our models had a relatively strong fit to the raw data for most arthropod families (adjusted R^2 up to 0.95; Table 2 and Fig. 3) across all sites. Seasonal change in daily availability of arthropods was determined primarily by the following environmental variables: cumulative temperatures

above 0°C (thaw degree-days) and its quadratic form (mean % deviance explained = $48.5\% \pm 4.7$ SE), and mean daily temperature (mean % deviance explained = $23.2\% \pm 4.6$ SE). The other climatic variables (mean daily wind speed, mean daily relative humidity, total daily precipitation, mean daily incidental radiation, and the interaction between daily temperature and thaw degree-day) each accounted for <10% of the deviance explained (Fig. 4).

Predicted and observed data are presented for each site, year, habitat, and family in Figure 3. Based on these models, we calculated an estimated dry mass for each study site (sum of the predictions for the dominant groups), which explained well the total dry mass of arthropods measured for all dominant and nondominant arthropods family pooled (R^2 varied from 0.30 to 0.95 depending on the site or year considered Fig. 2).

In the cross-validation, models generally performed slightly less than models with full data but overall the predictive power of the validation models was still good. Average adjusted R^2 of the validation models was 0.48 ± 0.042 SE and 0.35 ± 0.05 SE for the wet and mesic habitats, respectively. In all the validation models, the date

Fig. 2. Predicted and observed total daily arthropod availability in wet habitat in four Canadian Arctic sites.

of the peak of abundance could be assessed with great accuracy (Fig. 5 on wet habitat).

Arthropod availability differed according to habitat type. The mean dry mass was 63.37 ± 6.03 SE mg per trap per day and 40.84 ± 3.14 SE in wet and mesic habitats, respectively, all sites combined (Linear Mixed Models with days nested

in year: $F_{1,341} = 12.69$, $P < 0.001$). The interaction between habitat and study site was not significant ($F_{3,335} = 0.25$, $P = 0.86$) revealing that similar patterns of availability occurred in both habitats within a study site. The abundance also greatly differed according to study site ($F_{3,339} = 34.28$, $P < 0.001$).

Table 2. Parameter estimates for the generalized linear mixed models of weather variables on availability of the dominant arthropod groups (dry mass of arthropod expressed in mg/trap/day).

Site family	Habitat	Intercept	D (10^{-1} °C)	D^2 (10^{-4} °C ²)	T (10^{-2} °C)	Wi (10^{-1} km/h)	H (10^{-1} %)	R (10^{-2} ($\log(W/m^2)$))	Rain (10^{-1} mm)	$T \times D$ (10^{-3})	adj R^2
Ellesmere											
Araneae	Humid	0.24 (0.7)	0.13 (0.1)	-0.64 (0.38)	0.22 (0.04)	-0.60 (0.22)		NA	-0.43 (0.56)		0.70
Araneae	Mesic	7.29 (1.73)	-0.15 (0.1)	0.14 (0.41)		-0.52 (0.24)	-0.53 (0.18)	NA	-0.61 (0.56)		0.76
Chironomidae	Humid	-0.72 (0.72)	0.82 (0.12)	-5.36 (0.62)	-0.17 (0.07)	-0.84 (0.15)		NA		5.00 (0.8)	0.55
Chironomidae	Mesic	3.16 (1.25)	-0.12 (0.03)				-0.18 (0.14)	NA	-0.68 (0.52)		0.48
Muscidae	Humid	10.52 (0.76)				-1.08 (0.1)	-0.79 (0.07)	NA	-1.68 (0.38)		0.45
Muscidae	Mesic	-0.82 (0.71)	0.20 (0.03)			-0.45 (0.13)		NA	-1.11 (0.63)		0.47
Mycetophilidae	Humid	2.39 (1.22)	-0.14 (0.02)		0.30 (0.04)	-0.69 (0.17)		NA	-1.33 (0.29)		0.54
Mycetophilidae	Mesic	0.23 (1.97)	0.35 (0.29)	-2.30 (1.38)	0.51 (0.08)	-3.34 (0.53)		NA			0.78
Bylot											
Araneae	Humid	2.17 (1.63)	-0.01 (0.01)			-2.66 (0.61)	-0.55 (0.09)	0.99 (0.21)	-0.43 (0.25)		0.43
Araneae	Mesic	-12.65 (1.24)	0.03 (0.02)		0.53 (0.04)		0.46 (0.09)	1.74 (0.14)		-1.51 (0.26)	0.51
Carabidae	Humid	-6.63 (1.53)	-0.13 (0.01)		0.37 (0.04)		0.42 (0.12)	0.80 (0.13)			0.67
Carabidae	Mesic	1.1 (0.76)	-0.12 (0.02)		0.20 (0.05)	-3.15 (1.29)			-0.29 (0.18)		0.79
Chironomidae	Humid	-0.83 (0.53)	0.65 (0.04)	-2.67 (0.16)	0.09 (0.02)			-0.13 (0.1)			0.58
Chironomidae	Mesic	-7 (2)	0.12 (0.03)		0.78 (0.11)		0.38 (0.19)			-2.47 (0.57)	0.67
Ichneumonidae	Humid	-1.3 (0.73)	0.29 (0.04)	-0.73 (0.1)	0.06 (0.1)	-2.84 (1.12)			-0.32 (0.14)	0.56 (0.45)	0.69
Ichneumonidae	Mesic	-1.07 (4.14)	0.36 (0.07)	-0.76 (0.14)	0.23 (0.08)	-1.43 (1.82)	-0.18 (0.26)	-0.32 (0.41)	-0.43 (0.29)		0.72
Muscidae	Humid	-10.03 (1.51)	0.01 (0.01)		0.34 (0.03)	2.94 (0.55)	0.34 (0.11)	1.17 (0.15)	0.57 (0.1)		0.50
Muscidae	Mesic	-9.36 (1.47)	0.10 (0.01)			0.44 (0.8)		1.53 (0.2)	0.71 (0.13)		0.79
Tipulidae	Humid	-14.41 (0.95)	2.42 (0.14)	-8.85 (0.51)	0.04 (0.02)			0.24 (0.13)			0.87
Tipulidae	Mesic	-11.54 (6.11)	1.19 (0.24)	-4.23 (0.81)	0.59 (0.15)	-3.64 (2.55)	0.82 (0.48)	-1.01 (0.42)	-1.01 (0.31)		0.84
Herschel											
Araneae	Humid	3.47 (0.25)	0.05 (0.01)	-0.12 (0.02)		-0.77 (0.1)		NA	-0.36 (0.13)		0.38
Araneae	Mesic	9.61 (0.58)	-0.02 (0)			-0.28 (0.07)	-0.69 (0.07)	NA			0.29
Carabidae	Humid	2.33 (0.25)	0.03 (0.02)	-0.10 (0.03)	0.15 (0.02)	-0.42 (0.08)		NA			0.70
Carabidae	Mesic	11.69 (0.56)	0.00 (0.01)	-0.10 (0.02)	0.04 (0.01)	0.51 (0.04)	-1.00 (0.06)	NA			0.71
Tipulidae	Humid	-5.73 (0.42)	0.73 (0.04)	-1.80 (0.08)	0.30 (0.01)			NA			0.95
Tipulidae	Mesic	-5.16 (0.81)	0.10 (0.02)		0.79 (0.05)	1.34 (0.13)		NA		-2.25 (0.22)	0.55
Southampton											
Araneae	Humid	-7.05 (2.96)	-0.05 (0.01)		0.18 (0.03)		0.22 (0.19)	1.17 (0.3)			0.73
Araneae	Mesic	-6.19 (1.98)	-0.06 (0.02)		0.16 (0.02)	0.10 (0.11)		1.25 (0.32)			0.79
Carabidae	Humid	-7.18 (1.43)			0.19 (0.01)			1.32 (0.21)	-0.81 (0.41)		0.84

Table 2. Continued

Site family	Habitat	Intercept	D ($10^{-1} \text{ }^\circ\text{C}$)	D^2 ($10^{-4} \text{ }^\circ\text{C}^2$)	T ($10^{-2} \text{ }^\circ\text{C}$)	Wi (10^{-1} km/h)	H (10^{-1} %)	R (10^{-2} $\log(W/m^2)$)	Rain (10^{-1} mm)	$T \times D$ (10^{-3})	adj R^2
Carabidae	Mesic	-6.22 (1.61)	-0.10 (0.01)		0.15 (0.01)	-0.21 (0.06)		1.42 (0.19)			0.94
Chironomidae	Humid	-4.91 (1.84)	0.57 (0.05)	-1.34 (0.14)	0.37 (0.05)	-0.31 (0.06)	-0.23 (0.16)	0.83 (0.19)		-2.27 (0.47)	0.82
Chironomidae	Mesic	-2.3 (1.64)	0.45 (0.04)	-1.02 (0.13)	0.36 (0.04)	-0.27 (0.06)	-0.26 (0.14)	0.64 (0.18)		-2.40 (0.42)	0.80
Muscidae	Humid	-4.82 (1.05)	0.77 (0.06)	-1.84 (0.16)		-0.37 (0.07)		0.16 (0.15)	0.05 (0.21)		0.86
Muscidae	Mesic	12.74 (1.25)	0.17 (0.01)			-0.53 (0.07)	-1.50 (0.14)		0.90 (0.21)		0.60
Scatophagidae	Humid	6.77 (1.36)	0.11 (0.01)			-0.39 (0.05)	-1.05 (0.08)	0.68 (0.14)			0.39
Scatophagidae	Mesic	-11.97 (3.04)	0.90 (0.11)	-2.70 (0.33)	0.11 (0.06)		0.72 (0.29)		-0.30 (0.28)		0.53
Tipulidae	Humid	-9.81 (0.7)	1.67 (0.07)	-4.64 (0.21)	-0.01 (0.02)	-0.36 (0.04)			0.34 (0.09)		0.94
Tipulidae	Mesic	-11.4 (3.26)	1.05 (0.1)	-4.06 (0.35)	0.40 (0.12)	-0.34 (0.07)	0.95 (0.24)	-0.81 (0.21)	1.20 (0.26)	1.39 (0.97)	0.92

Coefficients in bold were significant and where coefficients are missing, the corresponding variable was absent from the model selected. Numbers in parentheses represent the standard errors associated with each coefficient. Certain variables were not measured (NA) at some sites. Weather variables are as follows: D is the accumulation of thaw degree-days ($10^{-1} \text{ }^\circ\text{C}$), D^2 is the square of the accumulation in thaw degree-days ($10^{-4} \text{ }^\circ\text{C}^2$), T is average daily temperature ($10^{-2} \text{ }^\circ\text{C}$), Wi is average daily wind speed (10^{-1} km/h), H is average daily relative humidity (10^{-1} %), R is average daily incidental radiation ($10^{-2} \log(W/m^2)$), Rain is total daily precipitation between two trapping sessions (10^{-1} mm), and $T \times D$ is the interaction between T and D (10^{-3}).

Discussion

The objective of our study was to generate predictive models of daily arthropod availability in the Canadian Arctic. Based on data collected at four different sites that varied in terms of their climate and arthropod communities, we found part of the variation to be dependent on climatic variables measured daily such as precipitation or wind. The other part of the variation was explained by daily temperature and a larger time scale measure of weather (thaw degree-day). Indeed, with mean daily temperature, thaw degree-day, and its quadratic form, more than 70% of the daily variation in arthropod availability was explained by our models. This is a substantial portion of the deviance, emphasising the overarching importance of both temperature and variables measured over larger time scales in determining seasonal change in arthropod availability. Our research results complement work conducted in other Arctic regions such as the Taymir Peninsula in Siberia, Russia, where cumulative degree-days was a better predictor of the number of arthropods caught than the combination of date and temperature (Schekkerman *et al.* 2004). Together with our results, this highlights the importance of including temperature, cumulative temperature, and its quadratic form in studies aimed at forecasting arthropod abundance rather than focusing mostly on daily temperature variation as is often the case (Deutsch *et al.* 2008).

As ectotherms, arthropods are highly sensitive to climate variation (Danks 1981; Hodkinson *et al.* 1998; Bale *et al.* 2002). Population growth rates and development of many arthropod species is linked to temperature (Huey and Berrigan 2001; Frazier *et al.* 2006). As expected, we found higher dry mass (and diversity) of arthropods for sites with a warmer summer. However, predicting the effect of global warming also requires further information on possible lagged effects (like density dependence and previous summer temperature).

There was considerable variation in seasonal trends of arthropod availability in terms of timing, duration, and magnitude of peaks in total biomass both between sites and between habitats within sites. Arthropod availability was higher in wet habitats than in mesic habitats and this was

Fig. 3. Predicted and observed arthropod availability split by sites, year, and habitat for the most abundant families.

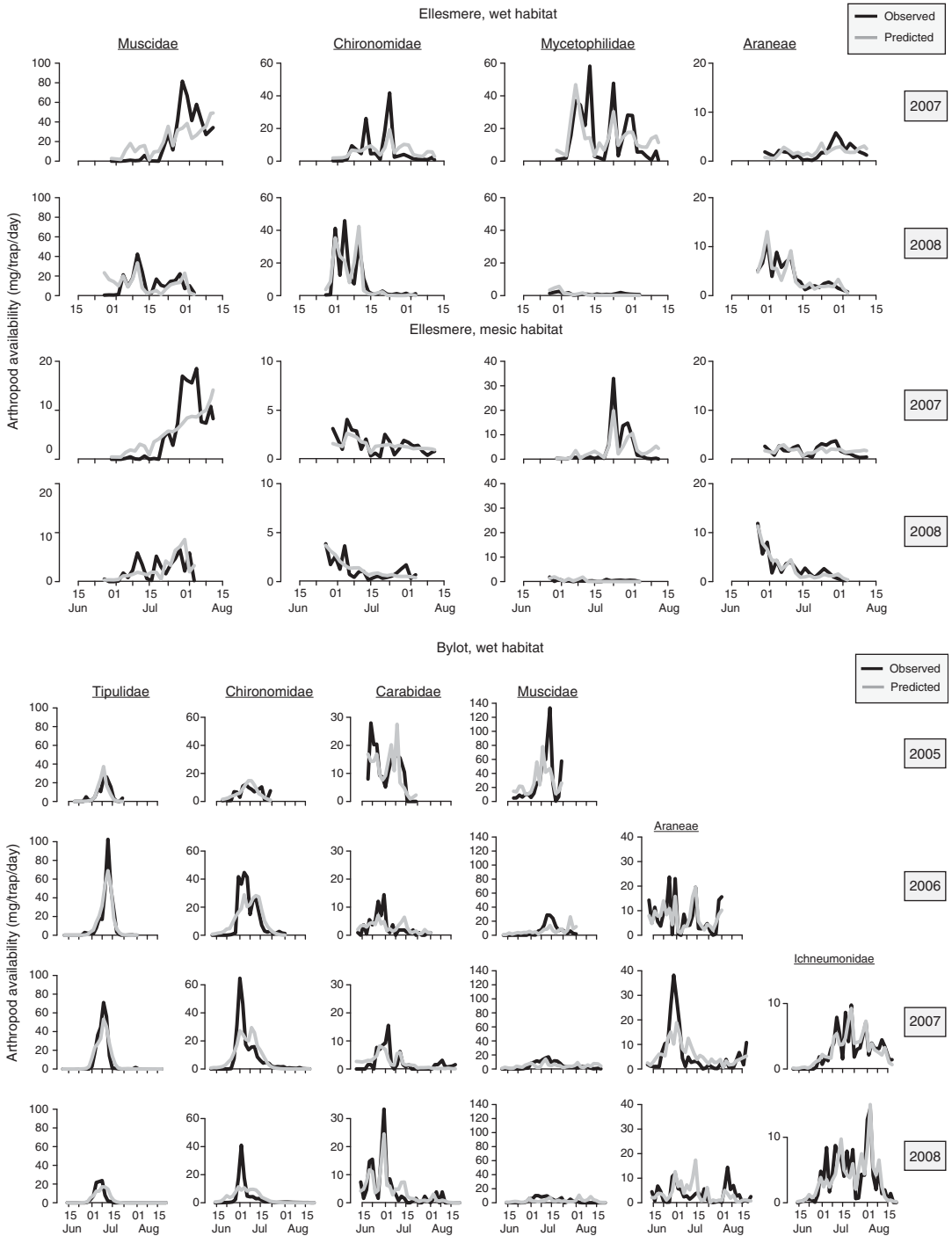


Fig. 3. Continued

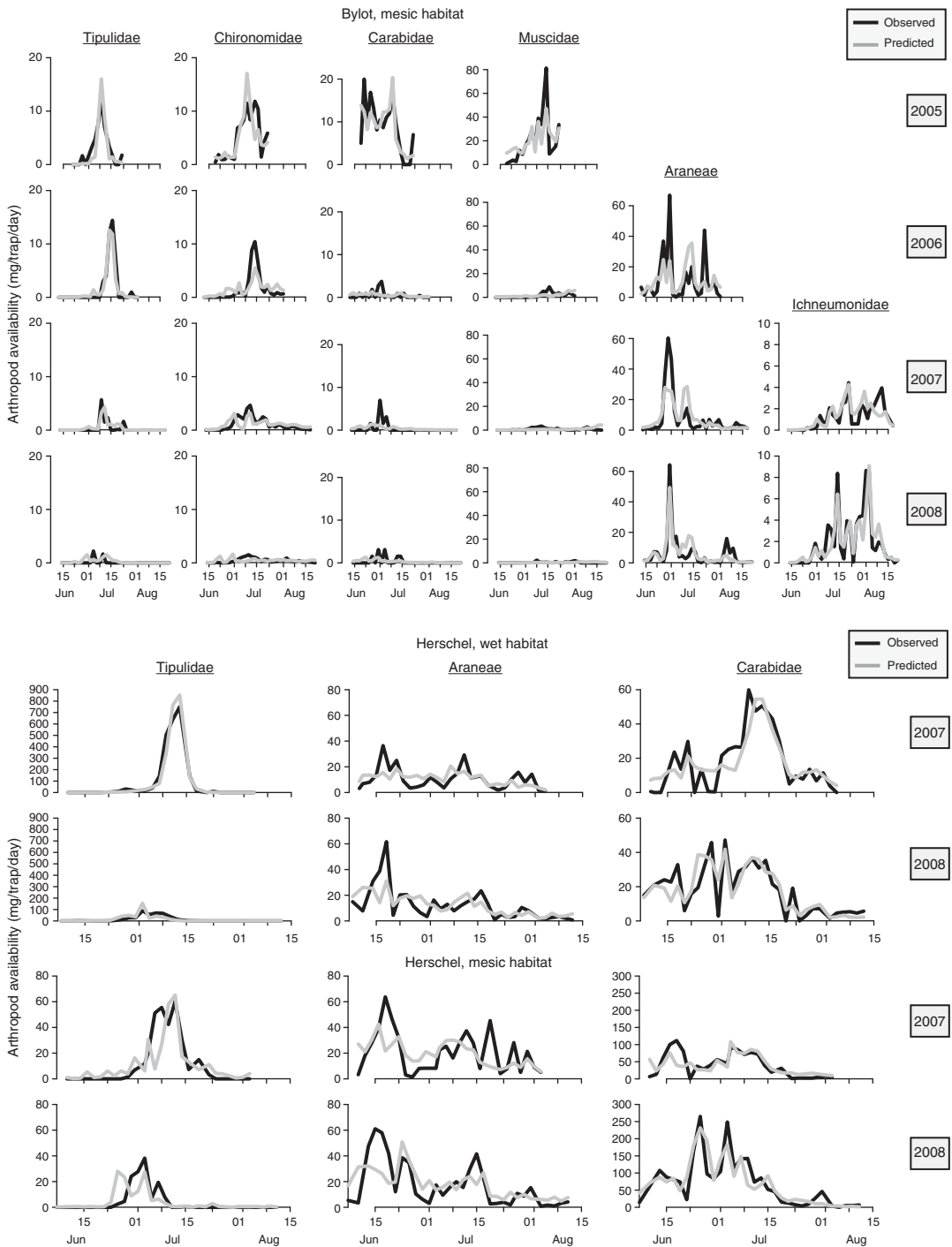
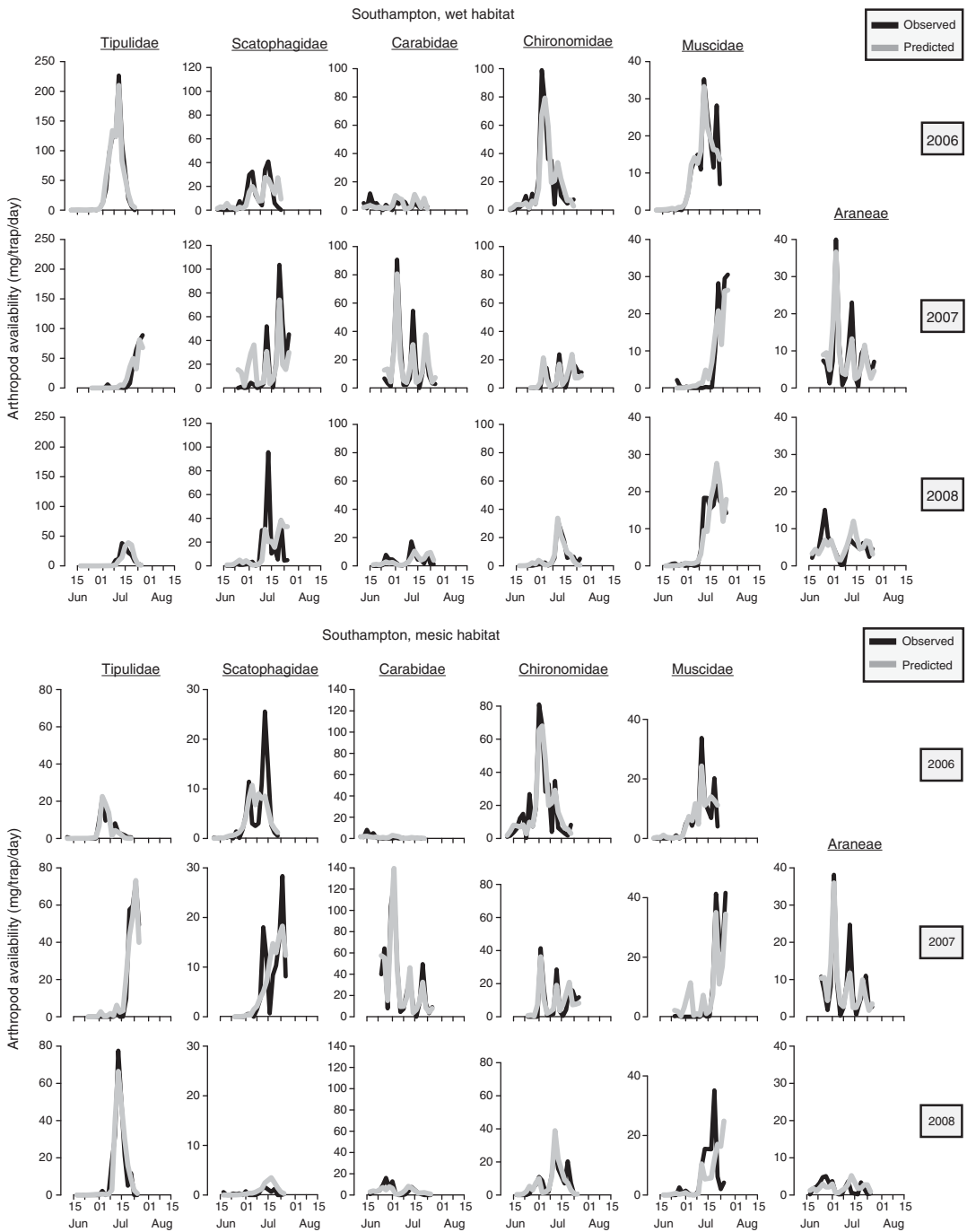


Fig. 3. Continued



consistent for all our study sites; we uncovered no significant interaction between habitat and site. Interestingly, for a specific site, climatic variables had similar effects on the abundance and pheno-

logy of a particular family for both habitats. Knowing the habitat characteristic of a site and its temperature thus appear to be an important covariate to model Arctic arthropod availability.

Across the sites, different patterns of abundance and phenology were evident among the different arthropod families that were sampled. For example, Tipulidae (Diptera; crane flies) showed very

synchronised peaks of abundance, whereas Araneae (spiders) were present throughout the study period. This is likely related to the natural history of the different families. In certain species of crane flies, for example, all adults that emerge in a given summer overwintered in the prepupal stage (MacLean 1973). As a result, there is no feeding requirement before their emergence as adults and a more synchronised emergence is therefore possible. Studies of crane flies in the Arctic, including ours (Fig. 3), have revealed well-defined peaks of abundance (MacLean and Pitelka 1971; Tulp and Schekkerman 2008) supporting the concept of a synchronised emergence. As a consequence, our climatic models for crane flies had a good fit to the data. This life-history strategy has also been observed in a number of Arctic Chironomidae (nonbiting midges) species (Danks and Oliver 1972). However, the timing of emergence of nonbiting midges is directly linked to the temperature of the pond in which the prepupal stage resides (Danks and Oliver 1972). Since ponds can warm up at different rates (based on depth, for example), emergence can be synchronised within ponds rather than across broad spatial scales. In

Fig. 4. Average (+SE) of the % of deviance explained by the different weather variables from models generated for each family and year. Weather variables are as follows: *D* is the accumulation of thaw degree-days, *D*² is the square of the accumulation in thaw degree-days, *T* is average daily temperature, *Wi* is average daily wind speed, *H* is average daily relative humidity, *R* is average daily incidental radiation, Rain is total daily precipitation between two trapping sessions, and *T* × *D* is the interaction between *T* and *D*.

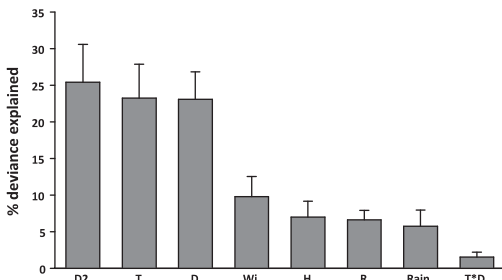
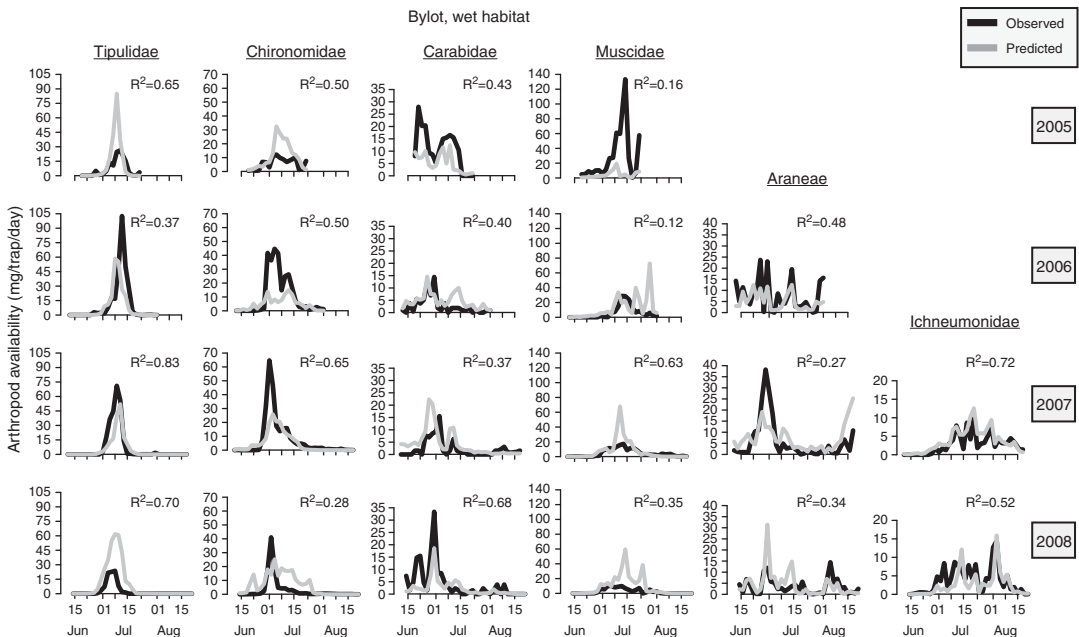


Fig. 5. Cross-validation models based on data from Bylot Island. We constructed models from all the data available minus one year. The observed values from the year left out (indicated on the left of the graphs) were then contrasted with the predictions from the cross-validation model.



our observations, there is more than one peak of nonbiting midges in any given year and the peaks are not as well defined as for crane flies (see Fig. 3). Numerous peaks may also be due to several species emerging at different times considering that nonbiting midges contributes a high proportion of species to the tundra insect fauna (MacLean and Pitelka 1971). In spiders, we did not observe a synchronised peak of abundance (see Fig. 3). They are present throughout the season and usually are active at the very beginning of snow melt (Meltofte and Høye 2007; this study).

These contrasting patterns of arthropod phenology may be important in their role as food for birds. Both spiders and crane flies are important to successful reproduction of insectivorous birds but they likely play different roles. Spiders are active at the very beginning of snow melt and are present throughout the season (Meltofte and Høye 2007; this study). It has been found that the abundance of wolf spider *Pardosa glacialis* (Thorell, 1872) (Araneae: Lycosidae) was probably the only variable influencing the timing of reproduction of jaegers *Stercorarius longicaudus* (Vieillot, 1819) (Aves: Stercoriidae) in Greenland (Meltofte and Høye 2007). Arthropods that are present early in the season may be especially important for the long-distant migrants that arrive at their Arctic breeding grounds with little to no stored energy and must rely upon early emerging arthropods in order to rebuild fat reserves and produce eggs (Danks 1971; Klaassen *et al.* 2001; Meltofte *et al.* 2008). On the other hand, arthropods such as crane flies, which exhibit peaks later in the season may be more important for the growth and survival of offspring (Pearce-Higgins and Yalden 2004).

Arthropods with an availability that is limited in time (synchronised emergence) can provide a great source of food for chicks if hatching is synchronised with emergence. But achieving this synchrony can be challenging, especially in the context of climate change (Both and Visser 2001; Thomas *et al.* 2001). For example, studies have now indicated that an asynchrony between hatch of shorebird chicks and peaks in crane flies can reduce chick growth rates (McKinnon *et al.* 2012) and even lead to potential population declines in some shorebird species (Pearce-Higgins *et al.* 2005). However, abundance of arthropods rather than asynchrony may better predict population

decline in different shorebirds species (Pearce-Higgins *et al.* 2009; Pearce-Higgins 2010).

Changes in climate are likely to induce changes in the patterns of arthropod availability with the potential to affect several trophic levels within the tundra food web. The unique data we have collected as part of this pan-Canadian effort, and the models we have tested will help us to forecast and/or hindcast arthropod availability over time, so that we can gain greater insight into the potential effects of changing arthropod availability for Arctic insectivores. Future research should continue to refine our understanding of seasonal variation in arthropod availability and attempt to study variation at lower taxonomic levels such as genus and, if possible, species. However, with over 2000 species of arthropods in arctic North America (Danks 1992), this could prove to be a very interesting, though rather challenging task.

Acknowledgements

Funding and logistic assistance for the collection of specimens was provided by grants from the Canadian federal government's International Polar Year program, the Natural Science and Engineering Research Council of Canada, and the Canadian Ministry of Environment to the Arctic Wildlife Observatories Linking Vulnerable EcoSystems International Polar Year project. Our study was also made possible due to funding by the Fonds Québécois de recherche sur la nature et les technologies (FQRNT), Wildlife Conservation Society Canada, the Garfield Weston Award for Northern Research, and the Northern Scientific Training Program. Logistical support was provided by Polar Continental Shelf Project and Parks Canada. Special thanks to Ludovic Jolicoeur, Benoit Laliberté, Émilie D'astous, Pierre-Yves l'Hérault, Maryse Cloutier, Jean-Rémi Julien, Scott Gilbert, Georges-Olivier Cimon, William Halliday, and Alice Kenney for field work. Thanks also to Valérie Delisle-Gagnon, Sarah Loboda, Hironelle Varady-Szabo, Annie Hibbert, Samuel Pinna, Maude Picotin, Ludovic Jolicoeur, and Karine Richer for identification of arthropods in the laboratory. Thank you to Alain Caron, Nicolas Lecomte, Arnaud Tarroux, Eeva Soininen, the members of the Bêty-Berteaux laboratory, and two anonymous referees for their helpful comments.

References

- Ale, S.B., Morris, D.W., Dupuch, A., and Moore, D.E. 2011. Habitat selection and the scale of ghostly coexistence among Arctic rodents. *Oikos*, **120**: 1191–1200. doi:10.1111/j.1600-0706.2010.18933.x.
- Arctic Climate Impact Assessment. 2004. Impacts of warming climate: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, United Kingdom.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., *et al.* 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**: 1–16. doi:10.1046/j.1365-2486.2002.00451.x.
- Berteaux, D., Humphries, M.M., Krebs, C.J., Lima, M., McAdam, A.G., Pettorelli, N., *et al.* 2006. Constraints to projecting the effects of climate change on mammals. *Climate Research*, **32**: 151–158.
- Both, C. and Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**: 296–298.
- Committee for Holarctic Shorebird Monitoring. 2004. Monitoring Arctic-nesting shorebirds: an international vision for the future. *Wader Study Group Bulletin*, **103**: 2–5.
- Danks, H.V. 1971. A note on the early season food of arctic migrants. *Canadian Field-Naturalist*, **85**: 71–72.
- Danks, H.V. 1981. Arctic arthropods: a review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada, Ottawa, Canada.
- Danks, H.V. 1992. Arctic insects as indicators of environmental change. *Arctic*, **45**: 159–166.
- Danks, H.V. and Oliver, D.R. 1972. Seasonal emergence of some high Arctic Chironomidae (Diptera). *The Canadian Entomologist*, **104**: 661–686.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., *et al.* 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, **105**: 6668–6672. doi:10.1073/pnas.0709472105.
- Dickey, M.-H., Gauthier, G., and Cadieux, M.-C. 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology*, **14**: 1973–1985. doi:10.1111/j.1365-2486.2008.01622.x.
- Efron, B. and Tibshirani, R.J. 1993. An introduction to the bootstrap. *In* *Monographs on statistics and applied probability*. Edited by B. Raton. Chapman & Hall, London, United Kingdom. Pp. 413–425.
- Elton, C.S. 1927. *Animal ecology*. Macmillan Company, New York, United States of America.
- Frazier, M.R., Huey, R.B., and Berrigan, D. 2006. Thermodynamics constrains the evolution of insect population growth rates: “Warmer is better”. *American Naturalist*, **168**: 512–520. doi:10.1086/506977.
- Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., *et al.* 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. *Ecoscience*, **18**: 223–235. doi:10.2980/18-3-3453.
- Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.F., McKinnon, L., *et al.* 2012. The Arctic tundra food web in a changing climate and the role of exchanges between ecosystems. *Ecoscience*, **18**: 223–235.
- Goulson, D., Derwent, L.C., Hanley, M.E., Dunn, D.W., and Abolins, S.R. 2005. Predicting calyptrate fly populations from the weather, and probable consequences of climate change. *Journal of Applied Ecology*, **42**: 795–804.
- Gullan, P.J. and Cranston, P.S. 2005. *The insects: an outline of entomology*. Blackwell Publishing, Oxford, United Kingdom.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**: 1965–1978. doi:10.1002/joc.1276.
- Hodar, J.A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica*, **17**: 421–433.
- Hodkinson, I.D. and Coulson, S.J. 2004. Are high Arctic terrestrial food chains really that simple? The Bear Island food web revisited. *Oikos*, **106**: 427–431.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R., Block, W., Strathdee, A.T., Bale, J.S., *et al.* 1996. Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos*, **75**: 241–248.
- Hodkinson, I.D., Webb, N.R., Bale, J.S., Block, W., Coulson, S.J., and Strathdee, A.T. 1998. Global change and Arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on spitsbergen. *Arctic and Alpine Research*, **30**: 306–313.
- Høye, T.T. and Forchhammer, M.C. 2008. The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations [online]. *BMC Ecology*, **8**. Available from <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2390509/pdf/1472-6785-8-8.pdf> [accessed 27 December 2012].
- Høye, T.T., Post, E., Møltøfte, H., Schmidt, N.M., and Forchhammer, M.C. 2007. Rapid advancement of spring in the High Arctic. *Current Biology*, **17**: R449–R451.
- Huey, R.B. and Berrigan, D. 2001. Temperature, demography, and ectotherm fitness. *The American Naturalist*, **158**: 204–210.
- Jenouvrier, S., Caswell, H., Barbraud, C., Holland, M., Stroeve, J., and Weimerskirch, H. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences of the United States of America*, **106**: 1844–1847.

- Klaassen, M., Lindstrom, A., Møtøfte, H., and Piersma, T. 2001. Ornithology – Arctic waders are not capital breeders. *Nature*, **413**: 794–794. doi:10.1038/35101654.
- MacLean, S.F. 1973. Life cycle and growth energetics of the Arctic Crane fly *Pedicia hannah antennata*. *Oikos*, **24**: 436–443.
- MacLean, S.F. and Pitelka, F.A. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. *Arctic*, **24**: 19–40.
- McCullagh, P. and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall, London, United Kingdom.
- McKinnon, L., Picotin, M., Bolduc, E., Juillet, C., and Bêty, J. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, **90**: 961–971. doi:10.1139/z2012-064.
- Møtøfte, H. and Høye, T.T. 2007. Reproductive response to fluctuating lemming density and climate of the long-tailed Skua *Stercorarius longicaudus* at Zackenberg, Northeast Greenland, 1996–2006. *Dansk Orn Foren Tidsskr*, **101**: 109–119.
- Møtøfte, H., Høye, T.T., and Schmidt, N.M. 2008. Effects of food availability, snow and predation on breeding performance of waders at Zackenberg. *In High-Arctic ecosystem dynamics in a changing climate. Edited by H. Møtøfte, T.R. Christensen, B. Elberling, M.C. Forchhammer, and M. Rasch.* Elsevier Academic Press Inc., San Diego, California, United States of America. Pp. 325–341.
- Morrison, R.I.G., Davidson, N.C., and Piersma, T. 2005. Transformations at high latitudes: why do red knots bring body stores to the breeding grounds? *Condor*, **107**: 449–457. doi:10.1650/7614.
- Pearce-Higgins, J.W. 2010. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, **45**: 119–130. doi:10.3354/cr00920.
- Pearce-Higgins, J.W. and Yalden, D.W. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover *Pluvialis apricaria* chicks. *Ibis*, **146**: 335–346.
- Pearce-Higgins, J.W., Yalden, D.W., Dougall, T., and Beale, C. 2009. Does climate change explain the decline of a trans-Saharan Afro-Palaearctic migrant? *Oecologia*, **159**: 649–659. doi:10.1007/s00442-008-1242-4.
- Pearce-Higgins, J.W., Yalden, D.W., and Whittingham, M.J. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia*, **143**: 470–476.
- Picotin, M. 2008. Variation climatique, abondance d'arthropodes et phénologie de la reproduction chez deux espèces de limicoles nichant dans le haut Arctique. Université du Québec à Rimouski, Rimouski, Québec, Canada.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., *et al.* 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science*, **325**: 1355–1358. doi:10.1126/science.1173113.
- Rogers, L.E., Buschbom, R.L., and Watson, C.R. 1977. Length–weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, **70**: 51–53.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature*, **421**: 57–60.
- Roy, D.B., Rothery, P., Moss, D., Pollard, E., and Thomas, J.A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**: 201–217.
- Saether, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution*, **12**: 143–149.
- Sage, R.D. 1982. Wet and dry-weight estimates of insects and spiders based on length. *American Midland Naturalist*, **108**: 407–411.
- Sample, B.E., Cooper, R.J., Greer, R.D., and Withmore, R.C. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist*, **129**: 234–240.
- Schekkerman, H., Tulp, I., Calf, K.M., and de Leeuw, J.J. 2004. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002 [online]. *In Alterra report 922.* Alterra, Wageningen, The Netherlands. Available from <http://edepot.wur.nl/23058> [accessed 30 December 2012].
- Schekkerman, H., Tulp, I., Piersma, T., and Visser, G.H. 2003. Mechanisms promoting higher growth rate in Arctic than in temperate shorebirds. *Oecologia*, **134**: 332–342.
- Smith, P.A., Gilchrist, G.H., and Smith, J.N.M. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. *The Condor*, **109**: 15–31. doi:10.1650/0010-5422(2007)109[15:eonhfa]2.0.co;2.
- Strathdee, A.T., Bale, J.S., Block, W.C., Coulson, S.J., Hodkinson, I.D., and Webb, N.R. 1993. Effects of temperature elevation on a field population of *Acyrtosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. *Oecologia*, **96**: 457–465.
- Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M., and Speakman, J.R. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, **291**: 2598–2600.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., *et al.* 2004. Extinction risk from climate change. *Nature*, **427**: 145–148. doi:10.1038/nature02121.
- Tulp, I. 2007. The Arctic pulse, timing of breeding in long-distance migrant shorebirds [online]. Ph.D. thesis, University of Groningen. Available from http://www.waddenacademie.nl/fileadmin/inhoud/pdf/06-wadweten/Proefschriften/Thesis_ITulp_verkl.pdf [accessed 30 December 2012].
- Tulp, I. and Schekkerman, H. 2001. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2001 [online]. *In Alterra report 451.* Alterra, Wageningen, The Netherlands. Available from <http://edepot.wur.nl/21801> [accessed 30 December 2012].

- Tulp, I. and 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.
- Visser, M.E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B – Biological Sciences*, **275**: 649–659. doi:10.1098/rspb.2007.0997.
- Wagner, T.L., Olson, R.L., and Willers, J.L. 1991. Modeling arthropod development time. *Journal of Agricultural Entomology*, **8**: 251–270.
- Whittaker, J.B. and Tribe, N.P. 1998. Predicting numbers of an insect (*Neophilaenus lineatus*: Homoptera) in a changing climate. *Journal of Animal Ecology*, **67**: 987–991.
- Wigglesworth, V.B. 1972. *The principles of insect physiology*. Chapman and Hall, London, United Kingdom.