

**EFFECTS OF SPATIAL AND TEMPORAL VARIATION IN RESOURCE
AVAILABILITY ON THE GROWTH RATES AND SURVIVAL OF
DUNLIN (*CALIDRIS ALPINA HUDSONIA*) CHICKS**

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ABSTRACT

Long-distant migrants nesting in the Arctic experience condensed breeding seasons and shorter periods of high arthropod availability due to climate change. Shorebirds have precocial chicks which may compensate for food shortages by responding to spatial and temporal variation in arthropod availability. I hypothesize that shorebirds capitalize on this mobility to select quality foraging habitats to maximize chick growth and survival. I monitored arthropod biomass during chick rearing in Churchill, Manitoba and East Bay, Nunavut to document variation in habitat use, growth and survival in relation to variation in arthropod biomass. Movements of Dunlin (*Calidris alpina hudsonia*) chicks were observed from hatch until fledging to investigate whether chicks responded to resource hotspots. Dunlin chicks, however, did not significantly respond to hotspots of arthropod biomass. Despite potential asynchronies between chick rearing and food resources from climate change, flexibility of foraging behaviour among Arctic-breeding shorebirds may contribute to reducing vulnerabilities for other species.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS.....	iv
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION	1
MATERIALS & METHODS	6
RESULTS	13
DISCUSSION	16
LITERATURE CITED	23

LIST OF TABLES

Table 1. Number of Dunlin nests, broods, and resights/recaptures summarized by site, Churchill, MB or East Bay, NU, and by year.	33
Table 2. Summary of shorebirds which are regularly recorded to nest at both the Churchill, MB and East Bay Migratory Bird Sanctuary, NU sites.	34
Table 3. Linear regression models describing distance travelled by broods between detections compared using Bayesian Information Criterion (BIC scores). Models with $\Delta\text{BIC} < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC and difference between highest ranked model BIC value are included.....	35
Table 4. Generalized Linear Models describing presence/absence of broods at a site compared using Bayesian Information Criterion (BIC). Models with $\Delta\text{BIC} < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC, difference between highest ranked model BIC value and loglikelihood are included.....	36
Table 5. Linear regression models describing chick growth residuals compared using Bayesian Information Criterion (BIC). Models with $\Delta\text{BIC} < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC and difference between highest ranked model BIC value are included.....	37
Table 6. Survival models rate from best fitting to least with delta AIC, AIC weight, number of parameters, and deviance.	38
Table 7. Home range reported in hectares calculated using minimum convex polygons on six Dunlin broods with five or more detections, sampled in Churchill, MB 2011.....	39
Table 8. Proportion of home range overlap for six Dunlin broods from Churchill, MB in 2011 using utilization distribution (UD) calculations.....	40

LIST OF FIGURES

Figure 1. Variation in average arthropod biomass (mg/trap) at Churchill, MB from June 28, 2011 to July 16, 2011 across nine transects designated by letter.....	41
Figure 2. Variation in average arthropod biomass (mg/trap) at Churchill, MB from July 4, 2014 to July 16, 2014 across six transects designated by letter.....	42
Figure 3. Variation in average arthropod biomass (mg/trap) at East Bay Migratory Bird Sanctuary, NU from July 13, 2018 to July 25, 2018 across six transects designated by letter.....	43
Figure 4. Variation in average temperature (degrees Celsius) at Churchill, MB from July 4, 2014 to July 16, 2014 across six transects designated by letter.....	44
Figure 5. Variation in average temperature (degrees Celsius) at East Bay Migratory Bird Sanctuary, NU from July 13, 2018 to July 25, 2018 across six transects designated by letter.....	45
Figure 6. Scatter plot showing the relationship between age (days) of Dunlin chicks after hatching and distance travelled (m) by broods between subsequent detections. Brood identification is indicated by a unique colour and shape.	46
Figure 7. Home ranges and overlap of six Dunlin broods sampled in Churchill, MB in 2011 using Minimum Convex Polygons. Points indicate detections of broods identified by a unique colour with the corresponding polygons identifying home ranges.	47

INTRODUCTION

How animals occupy and use a given environment in order to increase survival and reproductive success is a key ecological question. The distribution of species across landscapes is influenced by a variety of factors including, but not limited to, climate, available habitat types, interspecific interactions or anthropogenic covariates (Virkkala et al. 2005, Folmer et al. 2010, Glisson et al. 2017). Individuals within a population will often inhabit various habitat types based on specific site characteristics, which once selected, will uniquely impact their growth, life span, and overall fitness (Pulliam & Danielson 1991, MacKenzie et al. 2003). Understanding how species exploit and respond to variations in their surrounding environment may provide important insight as to whether species are likely to adapt under rapidly changing environments.

The availability of food resources is one of the most universal factors influencing habitat use across taxa (Harrold & Reed 1985). The ability to find and exploit food resources greatly influences the development of organisms. For example, Eurasian Perch (*Perca fluviatilis*), exhibit varying morphologies depending on whether they inhabit pelagic or littoral lake zones due to changes in food types available in each habitat (Svanback & Eklov 2002). Littoral perch feed on macroinvertebrates and other fish resulting in larger adult bodies whereas pelagic perch feed mainly on zooplankton and develop more streamlined adult bodies; each developed body type seemingly best suited to their specific habitat. In small rodents, winter food availability is determined in part by adequate subnivean space in winter (i.e. navigable areas under the snow). Changes in weather conditions, such as warm days and cool nights can cause snow to melt and subsequently freeze, locking available food in ice, preventing rodents from foraging effectively and negatively impact their survival (Korslund & Steen 2006). This change in subnivean space then, forces rodents to select habitat based on available space as opposed to food resources, since

areas of high food availability maybe locked in ice. In many cases, selecting or migrating to preferred habitats for many species is largely driven by seasonal changes in food availability or by predator avoidance (Fryxell & Sinclair 1988, Alexander 1998).

The phenology of available resources in an environment can have significant consequences for fitness (Visser et al. 2006). Phenology specifically refers to the timing of annually reoccurring biological events such as reproduction, migration, leaf-out, and insect emergence. These events are sensitive to, and can be significantly shaped by, climate change (Edwards & Richardson 2004). In many organisms, timing of breeding must be synchronized with the phenology of food resources so that offspring can achieve levels of growth that favour survival and eventual recruitment into a breeding population. Many larval fish for instance rely on a synchronization between hatch and peak food resources. Fish species such as Atlantic Cod (*Gadus morhua*) on the east coast of Canada or Arctic Cod (*Boreogadus saida*) and Sand Lance (*Ammodytidae sp.*) in Hudson Bay rely heavily upon the synchronized phenology of their preferred food resources, phytoplankton and copepods respectively (Fortier et al. 1995, Edwards & Richardson 2004). Reproductive success of Fork-marked Lemurs (*Phaner furcifer*) is closely linked to tree exudates (resins, gums, and saps). These exudates are available year-round; however, they do exhibit cycles from rapid depletion to renewal. Female lemurs that are most familiar with these cycles and gain access to this key, short-term food resource may experience higher fertility compared to females that miss or are unable to compete for these exudates (Schulke 2003). When organisms are unable to track changes in the phenology of key food resources, the resulting phenological mismatch, or trophic asynchrony, often negatively affects survival and fitness (Durant et al. 2005).

In recent years, an increasing frequency of phenological mismatches have been documented globally (Cotton 2003, Jones & Cresswell 2010) and have been linked to population

declines in multiple taxa. Temporal shifts in plant phenology for instance, can have negative impacts on a range of species. For example, due to warming temperatures, flowering plants are now emerging earlier. One study examining pollinator communities surrounding the Mediterranean Sea found that pollinator abundance was out of sync with flowering plants, not only resulting in decreased pollinators over the long-term but fewer wildflowers as well (Petanidou et al. 2014). Migratory Caribou (*Rangifer tarandus*) in western Greenland, have also been impacted by similar shifts in food availability. Caribou historically arrive to their calving grounds in sync with peaks in vegetation; however, due to increasing temperatures on the breeding grounds there has been a temporal shift in plant emergence to which the Caribou have yet to synchronize with (Post et al. 2008). In Pied Flycatchers (*Ficedula hypoleuca*), Both et al. (2006) reported a 90% decline in populations in habitats that experienced an earlier peak in insect abundance than historically recorded, likely due to insufficient food for provisioning nestlings. Links between climate change and phenological mismatch have been mounting as shifts in the timing of resource availability, migration, and reproduction, and have become better documented in the literature (Cotton 2003, Both et al. 2006, McKinnon et al. 2012).

Recent changes in climate, specifically warming global temperatures, have already had significant negative impacts on many species worldwide (Foden et al 2013, Thomas et al. 2004). Species exhibiting a greater range of phenotypic plasticity, defined as a genotypes' ability to express a range of phenotypes when exposed to different environments, may be more likely to adapt to rapid environmental change (Jonsson & Jonsson 2019, Pigliucci et al. 2006). Phenotypic plasticity can impact development in juveniles on behavioural, physiological, or biochemical levels (DeWitt et al. 1998, Pigliucci et al. 2006). For example, wood frog (*Rana sylvatica*) tadpoles have been shown to alter their morphology in response to changes in local predator populations;

tadpoles in predator rich environments are more mobile with longer tails (Maher et al. 2013). Individual female Great Tits (*Parus major*) advance lay dates in response to increasing temperatures and earlier food peaks, indicating a population response to the environment with a possible degree of phenotypic plasticity which allows them to remain in the same environment despite rapid short-term changes (Charmantier et al. 2008). Some Arctic-breeding shorebirds also exhibit variation in egg-laying using behavioural responses to the environment with individuals delaying nest initiation to increase nest survival and ultimately fledging success (Kwon et al. 2017, Saalfeld et al. 2018). Overall, phenotypic plasticity of individuals may permit some populations to persist even in the face of climate change (Charmantier et al. 2008, Przybylo et al. 2000, Reed et al. 2010).

Arctic ecosystems have experienced some of the most dramatic environmental changes due to climate change with temperatures increasing by 2 degrees Celsius above the average temperature from 1951-1990 (Przybylak 2007). This increase has caused a cascading effect on sea ice structure and breakup, permafrost depth, and consequently animal abundance and behaviour (Hobbie et al. 1999, Johannessen et al. 2004, Post et al. 2009, Bolduc et al. 2013). How exactly these changes will alter arctic phenology is still being investigated. However, since the Arctic is a strongly seasonal environment where organisms rely heavily on the timing of biotic and abiotic processes, changes in phenology are likely to have significant ecological consequences in Arctic communities (Ji et al. 2013, Zeng et al. 2013).

Long distance migrants such as Arctic-nesting shorebirds rely upon a finely tuned synchrony between hatch and peaks in arthropod abundance in order to capitalize on food resources to ensure growth and survival of their broods (Both et al. 2006, Kathleen et al. 2007, McKinnon et al. 2012). Arthropods are one of the key drivers of community structure and

composition in Arctic food webs, providing a resource for many species; however, many arthropods are emerging earlier due to warming temperatures (Tulp & Schekkerman 2008). A phenological mismatch between shorebird hatch and peak insect abundance has been one of the most commonly hypothesized impacts of climate change in the Arctic (Bolduc et al. 2013, McKinnon et al. 2012). Shorebird chicks are precocial and capable of moving soon after hatch to forage for themselves without aid from their parents (Bolduc et al. 2013). For broods that hatch out of synch with resource peaks, this mobility may permit adults to take advantage of fine scale spatial and temporal variation in arthropod abundance to compensate for the poor timing of hatch. Understanding the range of behavioural responses available to shorebirds to mitigate the effects of climate induced mismatch, will provide us with a better understanding of the future impacts of climate change.

The purpose of this study is to investigate whether shorebirds respond behaviourally to small scale spatial and temporal variation the phenology of food resources in order to reduce the negative effects of reduced food availability on chick growth and survival. I hypothesize that adult shorebirds respond to spatial and temporal micro-variation in food resources in order to select the highest quality brood rearing areas to maximize chick growth and survival. Specifically, I predict:

- 1) higher rates of brood occupancy in foraging areas of higher arthropod biomass at small spatial scales
- 2) parents and their broods will actively select foraging areas of high arthropod biomass
- 3) broods foraging in areas of high arthropod biomass will have higher growth rates
- 4) brood foraging in areas of high arthropod biomass will have higher survival over the brood rearing period (approximately 15 days from hatch)

MATERIALS & METHODS

Study Sites:

This study was conducted during the summers of 2011, 2014 and 2018 at two sub-arctic sites located in 1) Churchill, MB and 2) Southampton Island, NU. Data from Churchill was collected as part of my supervisor's (Dr. Laura McKinnon) postdoctoral research whereas I collected data at the Southampton Island site. Complete methods are provided here for both study sites, however, due to drastic weather and limited sample sizes at East Bay in 2018 and Churchill in 2014 (Table 1), the bulk of the results are based on Churchill 2011 data.

The Churchill study site is located approximately 20 km southeast of the town of Churchill, at the Twin Lakes fen ($58^{\circ} 44' 34''$ N, $93^{\circ} 57' 59''$ W). The Twin Lakes fen is representative of Hudson Bay lowland habitat dominated by sedge meadow and wetlands with interspersed spruce and willow stands (Brook 2001). As part of the largest peatland and wetland complex in North America (Glaser et al. 2004) Hudson Bay provides significant habitat for shorebirds along its coastal stretches. The Southampton Island site is located within the East Bay Migratory Bird Sanctuary (Hereafter East Bay site), NU ($63^{\circ} 59' 14.1''$ N, $81^{\circ} 41' 43.9''$ W). The East Bay site is dominated by sedge meadows, gravel ridges, and extensive shallow ponds. While still part of the subarctic, the East Bay site is representative of high arctic tundra in terms of plant community and landscape.

Study Species:

Shorebirds are a highly diverse group encompassing 215 species across 14 families of the order Charadriiformes, which includes gulls, plovers, sandpipers, and their allies (Colwell 2010).

Baker et al. 2007). The origin of today's three shorebird sub-orders: Lari, Scolopaci, and Charadrii arose during the late Cretaceous 79 to 102 million years ago (Baker et al. 2007). Across these shorebird communities there is a great diversity in morphology, behavior, and general ecology (Baker et al. 2007. Thomas et al. 2004. Thomas et al. 2004). Of the 215 species of shorebird distributed across the globe, upwards of 75 species occur in North America with the majority of these being Arctic breeders (Donaldson et al. 2000). All of these Arctic breeding shorebirds are highly migratory, with the majority of these, approximately 47 species, returning to the Canadian Arctic each year where they take advantage of the relatively resource rich tundra (Pielou 1994. Donaldson et al. 2000. Bart et al. 2012).

Both study sites are home to breeding populations of up to 7 shorebirds species (Table 2). Shorebirds arrive in the Arctic in May and June to select ground nest sites based on unique habitat characteristics; once a nest site is selected, four eggs are typically laid and incubated for approximately 3 weeks (Smith & Wilson 2010). The breeding season is only two months long. Shorebirds have precocial chicks which leave the nest soon after hatch and proceed to forage unaided by their parents. Chicks only need adults during early development mainly for thermoregulation, with parents brooding chicks to keep them warm and adults possibly leading chicks to areas of good forage for at least the first five days after hatch (Hill 2012). Predator detection and avoidance is also provided by parents, with adult's alarm calling and distracting predators often using a 'broken wing' display. After the first five days chicks stay with their brood but begin to better regulate their body temperature and become more mobile, exploring new areas for resources and being able to avoid predators by escaping or relying on their cryptic colouration.

Dunlin (*Calidris alpina*) are long distance migratory shorebirds, comprised of 11 different subspecies (Fernández et al. 2010) with 3 subspecies breeding in North America (Andres et al.

2012). On the wintering grounds and during migration Dunlin form mixed flocks with other shorebirds as they forage in shallow waters along coastlines (Sibley 2014). Dunlin eventually migrate to breeding grounds in the low and high Arctic, where they form monogamous pair bonds, sharing in incubation efforts, and laying 4 egg nests located in inland low lying tundra habitats composed of sedge meadows and shallow ponds (Borowik & McLennan 1999, Sibley 2014, Doll et al. 2015). Incubation lasts over twenty days, at which point precocial chicks emerge and leave the nest approximately 24-hours after hatch and to forage independently on terrestrial arthropods, with parents brooding chicks for thermoregulation and predator avoidance (Ricklefs and Williams 2003, Doll et al. 2015). For the purpose of this study I focused on the *Calidris alpina hudsonia* subspecies which breeds in the central and eastern Canadian Arctic (Andres et al. 2012).

Monitoring Broods

Intensive nest searching was conducted between June and July each summer at both sites. Study area size varied by site and year due to differences in nest density. At the Churchill site, the study plot measured 1 km x 1.5 km in 2011 and 1 km x 1km in 2014. At the East Bay site (2018), the plot measured 1 km x 2 km. Nest searching involved walking the plot in preferred nesting habitat to flush birds off the nest or watching for nest defense behaviour, such as alarm calling, and observing birds until they returned to the nest. Once located, GPS coordinates were recorded for each nest, and nests were re-visited on a five-day schedule until four days before hatch when nests were checked every day until hatch or nest failure occurred. Upon finding a nest, hatch date was estimated using the ‘egg flotation’ method as described by Liebezeit et al. (2007) which involves submerging eggs in the water and recording the angle and depth of the egg in the water

column. As eggs develop, the inner air pocket grows and changes position systematically permitting a reliable estimation of incubation stage and hatch date ± 4 days.

Upon hatch, chicks were banded in the nest with U.S. Geological Survey metal bands with unique number codes and a unique colour band combination on the opposite leg to ease individual identification in the field. Culmen and tarsus were also measured to the nearest decimal using digital calipers, and mass was taken using a digital or 50-gram pesola scale. All chicks within one brood were released together so brooding or foraging could continue in family groups. Prior to hatch, adults were also captured on the nest using a bownet and received unique colour band combinations and/or alphanumeric bands, and U.S. Geological Survey metal bands. This additional adult banding aided in efforts when relocating broods. All animal capture and handling protocols were reviewed and approved by the York University animal care and use committee

Growth and Survival of Chicks

Brood surveys were conducted over a 3-week period beginning when the first of the monitored nests hatched. Surveys were conducted every other day by 2-3 people actively searching for broods along pre-determined transects. Study plots were placed in habitats of high shorebird nest density, with each plot being comprised of six to nine transects (nine in 2011 and 6 in 2014 and 2018). At Churchill, transects were 1 – 1.5 km long and spaced 100 m apart, while at East Bay, transects were 2 km long and spaced 150 m apart. Once a brood was re-sighted, either by spotting chicks or noting alarm behaviour by an adult, chicks were recaptured by hand, coordinates were recorded, and morphometric measurements taken. All chicks within one brood were released together so brooding or foraging could continue as a family.

Arthropod Biomass and Microclimate:

Data on arthropod biomass and microclimate were collected at 150 m intervals along the transects at the Churchill site (54 stations in 2011, 36 in 2014) and at 200 m intervals at the East Bay site (36 stations in 2018). Pitfall traps using plastic cups were buried at designated stations and filled with a mixture of dish soap and water to provide an estimate of relative arthropod biomass. Pitfall traps were sampled every two days. Samples were stored in pre-dried and pre-weighed paper envelopes. Upon return from the field, samples were re-dried using a Fisher Scientific oven (Fisher Sci 60L Ovn Grvty) set at 50 degrees Celsius for at least 48 hours to provide a measure of dry biomass for each sample. To record microclimate, ibutton temperature loggers (Model: DS1920, hourly recordings) were placed within 50 cm of each pitfall trap in 2014 and 2018 recording at each station until the last survey, at which time they were collected, and the data was downloaded. Arthropod data are reported in milligrams per trap (mg/trap).

ANALYSIS:

Movements and Home Range of Broods

To describe general movements and habitat use of broods, the average distance between subsequent detections of known age broods was calculated for 11 broods from Churchill, MB using the 2011 data. Given that older chicks are likely to move larger distances than younger chicks, I tested for an effect of brood age on distance moved using mixed effects linear regression models. Four models were constructed based on a combination of age and brood as fixed effects and brood as random (Table 3). Models were compared using Bayesian information criterion (BIC) which is a more conservative information criterion for mixed models (Zuur et al. 2009).

The model with the lowest BIC score was selected as the top model with any models within 2 BIC of the top being considered competitive.

Brood home ranges were calculated using a 100% minimum convex polygon (MCP) under the `adeHabitatHR` package (Calenge 2006) in Program R (R Core Team 2017) for each brood with five or more detections during the study period ($n = 6$). Home ranges were calculated for broods from hatch up to 15 days old, thus they represent the home range of a brood within the first few weeks of life. Home range overlap between broods during the same period was calculated using the “`kerneloverlap`” command under the `adeHabitatHR` package. Specifically, I used the home range (“HR”) method to calculate the proportion of one brood’s home range overlapping another brood’s home range (Fieberg & Kochanny 2005).

Habitat use in relation to arthropod biomass

To test whether insect biomass influenced the presence/absence of Dunlin broods I used generalized linear mixed effects models (GLM, binomial family) with presence/absence as the dependent variable, arthropod biomass as a fixed effect, and site and Julian date as random effects to account for spatial and temporal variation. Five models were constructed (Table 4) and compared using Bayesian information criterion (BIC). The model with the lowest BIC score was selected as the top model with any models within 2 BIC of the top being considered competitive.

Brood movements in relation to arthropod biomass

To determine if broods were actively moving towards areas of increased arthropod biomass, I compared average arthropod biomass levels where broods were detected to average arthropod biomass levels where broods could have traveled based on the average age specific

distances between brood detections calculated above; that is the potential versus observed values for arthropod biomass. Brood detection data was imported into Google Earth Pro and the distance was measured between detections. Average arthropod biomass was calculated for the four stations closest to a given brood detection. This was also completed for all the possible areas a brood could have travelled to within the same time frame and the same maximum distance traveled by a specific brood. That is, if a brood moved 100 m northwest from its last detection, then the observed biomass would be the average biomass for the closest four stations, with the expected biomass being the average biomass for stations 100 m away from the original detection excluding the actual brood location chosen.

Differences between average biomass of the observed versus potential sites were compared using a two-sample t-test.

Chick Growth

To test whether insect biomass influenced the growth of Dunlin chicks (n=25 chicks from 7 broods), I used linear mixed effects models with growth residuals as our dependent variable and arthropod biomass as our fixed effect. I also tested for random effects of brood, site and Julian date. Ten models were constructed (Table 5) and compared Bayesian information criterion (BIC). The model with the lowest BIC score was selected as the top model.

Growth residuals were extracted from a growth model based on known-age chicks. Four different 4-parameter growth models (logistic, Log-logistic, Weibull Type 1, & Weibull Type 2) were generated using the ‘drc’ package in R (R Core Team 2017) and compared using Akaike’s Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). The

model with the lowest AICc score was selected as the top model and residuals were extracted from this top model for analysis.

Chick Survival

I estimated survival of 53 Dunlin chicks by fitting a Cormack-Jolly-Seber (CJS) capture-mark-recapture model using program MARK (White & Burnham 1999). To test for an effect of arthropod biomass on survival I ran five different models (Table 6) and compared them using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). The model with the lowest AICc score was selected as the top model.

RESULTS

Arthropod Biomass and Microclimate:

As expected, I found considerable temporal and spatial variation in arthropod biomass at both sites. The average daily arthropod biomass value for Churchill in 2011 was 52.64 ± 42.64 mg/trap (range 0 – 349.7 mg/trap). The daily average varied from a low of 33.09 ± 26.06 (June 28th) to a high of 76.96 ± 49.48 mg/trap (June 30th; Figure 1). Spatial variation across sites on a given day was considerable with some sites exhibiting a coefficient of variation (CV = 1.04) of up to 104% on the most variable days (July 10th Figure 1). Average daily biomass from Churchill, MB in 2014 was 29.44 ± 27.16 mg/trap (range 0 -166.8 mg/trap). The daily average varied from a low of 16.27 ± 9.28 (July 22nd) to a high of 49.22 ± 37.26 mg/trap (July 16th; Figure 2). Spatial variation across sites in 2014 on a given day exhibited a coefficient of variation (CV = 0.75) of up to 75% on the most variable days (July 16th; Figure 2). Meanwhile at East Bay daily arthropod biomass averaged 157.82 ± 129.67 mg/trap (range 0 – 633 mg/trap), with the daily average ranging

from a low of 34.08 ± 43.32 mg/trap (July 15th) to a high of 239.03 ± 152.66 mg/trap (July 21st; Figure 3). Spatial variation across East Bay in 2018 on a given day had a coefficient of variation (CV = 0.64) up to 64% on the most variable day (July 21st; Figure 3).

I found temporal variation in microclimate but much less spatial variation than expected. The average temperature across stations in Churchill, MB in 2014 was 15.9 ± 3.28 °C for the brood rearing period. The daily average varied across the season, ranging from a low of 11.05 ± 1.21 °C (July 14th) to a high of 21.15 ± 2.08 °C (July 16th; Figure 4). Spatial variation in temperature for Churchill in 2014 on a given day exhibited a coefficient of variation (CV = 0.08) of 8.03% on the most variable day (July 8th; Figure 4). For East Bay in 2018 average temperature for the study period was 10.77 °C ± 3.27 °C, with daily average ranging from a low of 5.75 ± 0.43 °C (July 17th) to a high of 15.91 ± 1.05 °C (July 13th; Figure 5). Spatial variation in temperature for 2018 at East Bay on a given day exhibited a coefficient of variation (CV = 0.09) of 9.20% on the most variable day (July 23rd; Figure 5).

Please note that the remaining results below using chick data are based on data from Churchill 2011 data only due to low sample sizes (Table 1).

Movements and Home Range of Broods

The average distance per day between detections of known age broods was 272.64 m ± 233.92 m (range 27.75 to 1036.29 m). Variation in distance moved between detections was best described by a model including fixed effects of age with brood as a random effect (BIC = 512.30; Table 3). Distance moved increased with age, with broods moving an estimated ~ 22.79 m farther per day from their previous detection (Figure 6).

Mean home range size was 10.33 ± 10.88 hectares ($n = 6$) ranging 0.84 to 33.05 hectares over the brood rearing period (Table 7). Home range overlap averaged 57%, ranging from 16% to 99% overlap (Table 7, Figure 7).

Habitat use in relation to arthropod biomass

Variation in presence/absence of Dunlin broods was best described by a model including insect biomass as a fixed effect and brood as a random effect (BIC = 75.07; Table 4). Based on the logistic regression, the log of odds of Dunlin presence in an area decreased by 0.04 as insect biomass increased by 1 mg. The odds ratio of Dunlin present versus absence in an area of high insect biomass was lower by a factor of 0.96 which is equivalent to a 3.92% lower probability of being present in an area of high arthropod biomass. Therefore, I did not find higher rates of brood occupancy in foraging areas of higher arthropod biomass at fine spatial scales as predicted.

The average biomass at observed brood locations (51.71 ± 24.44 mg) was not significantly different than the average biomass at potential brood location sites (56.78 ± 24.44 mg; $t = -1.0271$, $df = 96$, $p = 0.3069$). Contrary to my prediction, broods did not actively select foraging areas of high arthropod biomass.

Chick Growth

Growth of known-age chicks was best modeled with a 4-parameter Log-logistic growth model. Variation in growth residuals was best described by the null model (BIC = 330.30; Table 8). Contrary to my prediction, broods foraging in areas of high arthropod biomass did not have higher growth residuals.

Chick Survival

Also contrary to my prediction, broods foraging in areas of high arthropod biomass did not have higher apparent survival rates. Variation in chick apparent survival rates were best described by constant survival across the study period, with the probability of detection varying between observation events (Table 6). Based on the top model, the estimated apparent survival rate across the 26-day observation period was 0.85 (CI 0.78, 0.91).

DISCUSSION

I examined how Dunlin broods responded to small spatial and temporal scale changes in arthropod biomass and how this affected growth and survival of chicks. I did not find evidence to support the original hypothesis that adult shorebirds respond to spatial and temporal microvariation in food resources in order to select the highest quality brood rearing areas to maximize chick growth and survival. Brood movements varied greatly; however, there was no clear positive impact of increased arthropod biomass on habitat selection, growth or survival of broods. I found no evidence of higher rates of brood occupancy in areas of higher arthropod biomass at relevant spatial scales and broods did not select areas of higher than average arthropod biomass. In terms of growth, chicks also did not have increased growth residuals or apparent survival in relation to increased arthropod biomass.

Movements and Home Range of Broods

For Dunlin broods in Churchill, MB older broods moved, on average, several hundred metres between detections. Broods movements increased with age, with 2-week-old broods moving up to 1km between detections that were 10-15 days apart. These movements are

comparable to other similarly sized shorebirds such as the Snowy Plover (*Charadrius nivosus*) and the Buff-breasted Sandpiper (*Tryngites subruficollis*). One day old Buff-breasted Sandpiper chicks were found to move 158 ± 78.5 m from their nest (Lanctot 1994) which is comparable to the estimated average distance of 195.8 m moved from the nest within two days in this study. Snowy Plover chicks moved an average of 518 ± 52 m in the first three days after hatch (Wilson & Colwell 2010), which is higher than the average 195.8 – 119.9 m moved by Dunlin within the first two to four days. Snowy Plover chicks decreased their movements as they got older perhaps because as temperate breeders there is more consistent temperature and food resources, therefore limiting their movements (Wilson & Colwell 2010).

Dunlin brood home ranges over the brood rearing period averaged approximately 10 hectares but varied greatly from less than one hectare to more than 30. However, the few studies completed on home ranges of shorebirds found relatively larger home ranges compared to Dunlin broods. European Golden Plover chicks (*Pluvialis apricaria*) exhibited average home ranges of 41 ha (range 18.3 – 86.2 ha, n=14 broods; Pearce-Higgins & Yalden 2004). In another species of temperate breeding shorebird, the Redshank (*Tringa tetanus*), chick home ranges averaged 0.56 ha (Jongbloed 2005). Redshank broods also overlapped an average of 5% as opposed to the 57% documented for Dunlin in my study. The high overlap found in my study may indicate that, in contrast to other shorebird species, Dunlin in Churchill, MB experience low intraspecific competition. Low intraspecific competition could imply an abundance of resources, or simply reduced territoriality during the brood rearing period. The high home range overlap could also be due to relatively low brood densities, since there were approximately ~11 broods per square kilometer. Nest densities for Arctic breeding shorebirds for instance, could be anywhere from 30-80 nests per square kilometer at some sites (Cotter & Andres 2000). It is important to note,

however that the overlap presented here does not necessarily show simultaneous detections and therefore may be overestimated.

Habitat use in relation to arthropod biomass

Contrary to my prediction, I did not find higher rates of brood occupancy in areas of higher arthropod biomass at relevant spatial scales. Though variation in presence/absence of broods was best described by arthropod biomass, the probability of brood presence was slightly higher (3.92%) in areas of lower arthropod biomass. Other studies have documented brood movements associated with shifts in habitat structure and food abundance. Kentish Plovers (*Charadrius alexandrinus*) for instance, led their broods away from salt marshes used for nesting towards lakeshores, which were more abundant in arthropod resources (Kosztolányi et al. 2007). In arctic-nesting shorebirds, habitat selection of broods generally varies by species; Western Sandpiper (*Calidris mauri*) and Rock Sandpiper (*Calidris ptilocnemis*) were found to select habitat based on proximity to tundra highlands (i.e. gravel ridges) during brood rearing (Johnson & McCaffrey 2004).

Patterns of larger scale habitat selection along with interspecific competition may mitigate the selection of preferred microhabitats. Whether breeding in the Arctic, where habitats are relatively homogeneous, or in temperate regions, shorebirds tend to nest in preferred habitat types to influence their nest success (Conway et al. 2005, Smith et al. 2007). Adult shorebirds also show habitat preference with species such as White-rumped Sandpiper (*Calidris fuscicollis*) and Red Phalarope (*Phalaropus fulicarius*) being detected in sites primarily composed of sedge meadows (Latour et al. 2005). However, it is unclear whether these habitats extend to the brood rearing period as well. Other habitat variables such as ground cover and predation risk were not measured in this study; however, based on their importance during the nesting season (Conway et al. 2005,

Latour et al. 2005, Smith et al. 2007), they may also be important factors in habitat selection during the brood rearing season.

Interspecific competition between shorebird species, especially in the relatively diverse shorebird community of Churchill, MB may have influenced habitat use. Habitat partitioning amongst shorebirds is well studied on the wintering grounds, where different species forage for prey using their unique body plans depending on tide and available habitat (Burger et al. 1977, Granadeiro et al. 2007). On the breeding grounds however, species forage freely on terrestrial sources, often in groups, with no apparent partitioning prior to egg laying (Baker & Miller Baker 1973). Dunlin are also one of the smaller species occurring in Churchill, MB with the next most abundant shorebird in our dataset, the Short-billed Dowitcher (*Limnodromus griseus*) being nearly double the size. These larger species require significantly more food resources to achieve optimal chick growth therefore, Dunlin may be excluded to intermediate areas of insect biomass with larger shorebird species selecting the areas of high insect biomass. Even between species, shorebirds with larger broods have been found to exclude broods with fewer chicks from areas of high food abundance (Lengyel 2007).

Chick Growth

Chicks did not grow faster when foraging in areas of higher arthropod biomass. These results differ from previous studies showing positive relationships between chick growth and arthropod resources. European Golden Plover chicks for example, had their highest growth rates in habitats rich in prey, both in abundance and quality (Pearce-Higgins & Yalden 2004, Machin et al. 2018). Similar results have also been reported for shorebirds in the *Calidris* genus. Growth in both Sanderling (*Calidris alba*) and Red Knot (*Calidris canutus*) have been both shown to be

positively correlated when food resources showed little variation across the breeding season or was high compared to previous seasons (Schekkerman et al. 2003, Reneerkens et al. 2016). However, in these studies arthropods were collected either at larger scales, with pitfalls sampled by habitat type across their study sites, or in the case of Schekkerman et al. (2003) using a small number of pitfalls in the area of highest brood densities to garner arthropod abundances; as opposed to this study which examined fine spatial scale of arthropod biomass within one general brood rearing habitat.

Additional abiotic factors such as wind can also negatively impact shorebird chick growth, especially in the first few days of hatch. Since chicks depend on adults in the first days after hatch for thermoregulation, exposure to elements can cause drops in body temperature as well as water loss, leading to low survival and reduced growth rates (Bakken et al. 2002). Weather conditions can make some areas inaccessible to chicks and reduce movements within a given year, especially when compounded with factors such as late snow melt and early emergence of insect prey. However, for Churchill MB there was no evidence the 2011 season had poor weather, resulting in adverse effects on growth or insect abundance (McKinnon et al. 2013, Corkery et al. 2019). Factors such as temperature and wind should be accounted for across seasons when studying growth of chicks.

Apparent Survival of chicks

Apparent survival (85%) was not higher for chicks foraging in areas of high arthropod biomass. Other studies found similar daily survival rates in both Arctic and temperate breeding shorebirds. However, it should be noted that in these studies shorebird chick survival increased as a factor of age and time. Some species such as Western Sandpipers and Snowy Plovers had overall

survival rates of 73% and 70% with chicks surviving to fledging respectively (Ruthrauff & McCaffrey 2005, Colwell et al. 2007). While these survival estimates are lower than the one reported here, the studies conducted by Ruthrauff & McCaffrey (2005) and Colwell et al. (2007) were completed over multiple seasons as opposed to the single season used in my analysis.

High energy requirements, especially for precocial chicks which forage for themselves and rely on their own thermoregulation, is critical in meeting developmental demands and overall survival (Schekkerman & Visser 2001, Ruthrauff & McCaffrey 2005, Krijgsveld et al. 2012). Previous studies found the most mortality occurred in the first few days of hatch when chicks were dependent on parents for thermoregulation and were fairly immobile (Krijgsveld et al. 2012). However, in years or at sites with high arthropod biomass and temperatures this early mortality may be avoided (McKinnon et al. 2012, Bolduc et al. 2013).

IMPLICATIONS FOR MONITORING AND RESEARCH

Given the challenges of studying shorebird chicks, especially in the Arctic, a standardized and comprehensive approach such as ours would be ideal for monitoring projects. Specifically, this is one of the few studies which has investigated how spatial and temporal changes in the food supply impacts chick growth and survival. However, future monitoring and research of shorebird chicks should take a more holistic approach when considering how habitat is used and how habitat use affects growth and survival. Future research should attempt to examine multiple shorebird species present in the area, in order to incorporate intraspecific and interspecific competition. Additionally, factors such as habitat type, predation risk and weather should be investigated in conjunction with food availability.

Though I did not find evidence to support my hypothesis regarding the importance of fine scale variation in arthropod biomass on habitat selection, this study is the first to provide apparent survival estimates for Dunlin chicks in the eastern Arctic, providing an important baseline for future research and monitoring. With as much as 80% of shorebird populations in North America in decline, and populations declining globally (Austin et al. 2000, Andres et al. 2012), and with shorebirds being excellent indicators of ecosystem health (Ogden et al. 2014a, Ogden et al. 2014b), there is an urgent need to increase our fundamental understanding of life history strategies, reproductive behaviour, and the variables that influence population dynamics in these species. Acquiring survival rates of chicks alone fills an important knowledge gap which will be useful for conservation strategies and population estimates. A comprehensive understanding of early life-history in Arctic-breeding shorebirds will be essential if efforts to stem population declines are to be successful.

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TABLES

Table 1. Number of Dunlin nests, broods, and resights/recaptures summarized by site, Churchill, MB or East Bay, NU, and by year.

Site	Year	Dunlin Nests	Dunlin Broods	Resights/Recaptures
Churchill	2011	35	20	53
	2014	24	6	14
East Bay	2018	3	0	0

Table 2. Summary of shorebirds which are regularly recorded to nest at both the Churchill, MB and East Bay Migratory Bird Sanctuary, NU sites.

Species	Scientific Names	East Bay Migratory Bird Sanctuary, Nu	Churchill, MB
American Golden Plover	<i>Pluvialis dominica</i>	X	X
Black-bellied Plover	<i>Pluvialis squatarola</i>	X	
Semipalmated Plover	<i>Charadrius semipalmatus</i>	X	
Dunlin	<i>Calidris alpina</i>	X	X
Least Sandpiper	<i>Calidris minutilla</i>		X
Stilt Sandpiper	<i>Calidris himantopus</i>		X
Short-billed Dowitcher	<i>Limnodromus scolopaceus</i>		X
Purple Sandpiper	<i>Calidris maritima</i>		X
White-rumped Sandpiper	<i>Calidris fuscicollis</i>	X	
Ruddy Turnstone	<i>Arenaria interpres</i>	X	
Red-necked Phalarope	<i>Phalaropus lobatus</i>		X
Red Phalarope	<i>Phalaropus fulicarius</i>	X	

Table 3. Linear regression models describing distance travelled by broods between detections compared using Bayesian Information Criterion (BIC scores). Models with $\Delta BIC < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC and difference between highest ranked model BIC value are included.

<i>Model</i>	<i>k</i>	<i>BIC</i>	<i>ΔBIC</i>
Distance varies with age and brood as random	3	512.30	0.00
Distance varies with brood as random	2	523.00	10.70
Distance varies with age and brood	3	548.84	36.54
Distance varies with brood	2	551.47	39.17

Table 4. Generalized Linear Models describing presence/absence of broods at a site compared using Bayesian Information Criterion (BIC). Models with $\Delta BIC < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC, difference between highest ranked model BIC value and loglikelihood are included.

<i>Model</i>	<i>k</i>	<i>BIC</i>	<i>ΔBIC</i>	<i>Loglikelihood</i>
Chick presence varies with insect biomass (site and brood as random)	4	75.1	0.00	-24.95
Chick presence varies with insect biomass (brood as random)	4	75.22	0.12	-25.03
Null model (brood as random)	2	79.48	4.38	--
Chick presence varies by day and insect biomass (site and brood as random)	5	81.35	6.25	-24.94
Chick presence varies with insect biomass (site, day, and brood as random)	5	81.37	6.27	-24.96
Null model	2	316.07	240.97	--
Chick presence varies with insect biomass (site as random)	3	323.3	248.2	-152.21
Chick presence varies with insect biomass	3	327.64	252.54	-154.38
Chick presence varies with insect biomass (site and day as random)	4	328.64	253.54	-151.73
Chick presence varies by day and insect biomass (site as random)	4	329.11	254.01	-151.97

Table 5. Linear regression models describing chick growth residuals compared using Bayesian Information Criterion (BIC). Models with $\Delta BIC < 2$ are considered competitive as the best fitting models. The model, number of parameters (k), BIC and difference between highest ranked model BIC value are included.

<i>Model</i>	<i>k</i>	<i>BIC</i>	<i>ΔBIC</i>
Null model (chick growth ~ brood)	2	330.30	0.00
Residual mass varies with insect biomass (site & brood as random)	4	341.08	10.78
Residual mass varies with insect biomass (site, Julian date, & brood as random)	5	345.20	14.9
Residual mass varies with insect biomass (Julian date & brood as random)	4	344.23	13.93
Residual mass varies with Julian date & insect biomass (site & brood as random)	5	349.33	19.03
Null model (chick growth ~ 1)	2	352.78	22.48
Residual mass varies with insect biomass (site as random)	3	358.38	28.08
Residual mass varies with insect biomass (site & Julian date as random)	4	360.46	30.16
Residual mass varies with Julian date & insect biomass (site as random)	4	365.75	35.45
Residual mass varies with insect biomass (Julian date as random)	3	367.28	36.98

Table 6. Survival models rate from best fitting to least with delta AIC, AIC weight, number of parameters, and deviance.

<i>Model</i>	ΔAIC	<i>AIC Weight</i>	<i>No. Par</i>	<i>Deviance</i>
Survival (constant) + Detection prob. (time)	0.00	0.68	8	282.31
Survival (time) + Insect Biomass	1.62	0.30	9	281.66
Survival (time) + Detection prob. (constant)	7.93	0.01	6	294.68
Survival (time) + Detection prob. (constant) + Insect Biomass	9.59	0.01	7	294.13
Survival (constant) + Detection prob. (constant)	47.74	0.00	2	343.00

Table 7. Home range reported in hectares calculated using minimum convex polygons on six Dunlin broods with five or more detections, sampled in Churchill, MB 2011.

<i>Brood ID</i>	<i>Area (Hectares)</i>
11DU07	10.32
11DU14	33.04
11DU24	13.14
11DU28	0.84
11DU30	8.46
11DU32	9.01

Table 8. Proportion of home range overlap for six Dunlin broods from Churchill, MB in 2011 using utilization distribution (UD) calculations.

	11DU07	11DU14	11DU24	11DU28	11DU30	11DU32
11DU07	1.0	0.50	0.73	0.65	0.99	0.98
11DU14	0.74	1.0	0.98	0.68	0.83	0.52
11DU24	0.62	0.57	1.0	0.65	0.73	0.47
11DU28	0.38	0.27	0.45	1.0	0.54	0.40
11DU30	0.60	0.35	0.52	0.57	1.00	0.71
11DU32	0.44	0.16	0.25	0.30	0.52	1.00

FIGURES

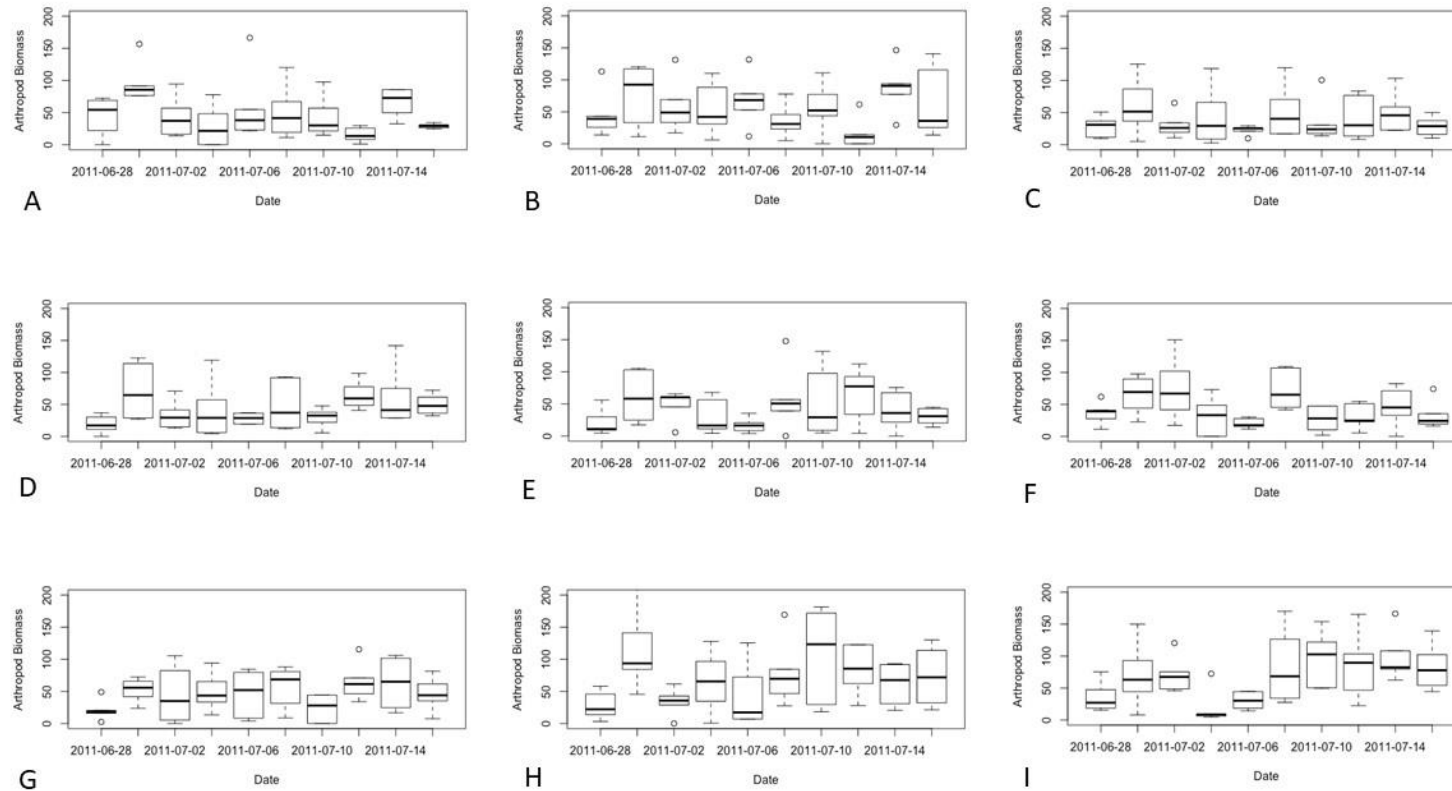


Figure 1. Variation in average arthropod biomass (mg/trap) at Churchill, MB from June 28, 2011 to July 16, 2011 across nine transects designated by letter.

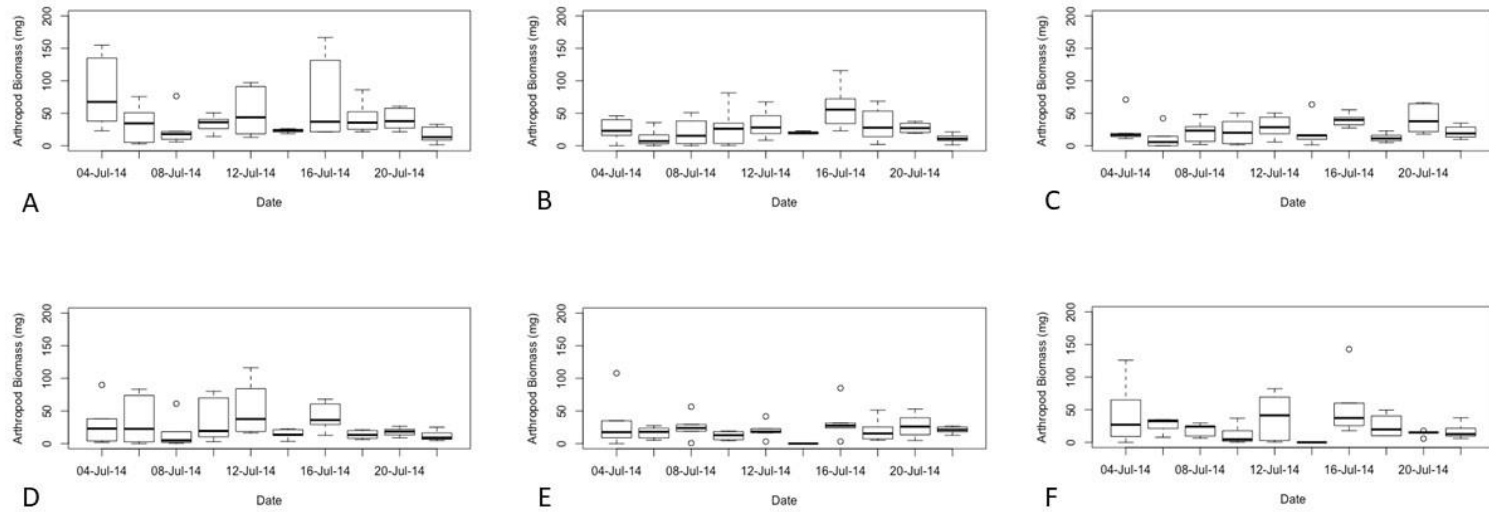


Figure 2. Variation in average arthropod biomass (mg/trap) at Churchill, MB from July 4, 2014 to July 16, 2014 across six transects designated by letter.

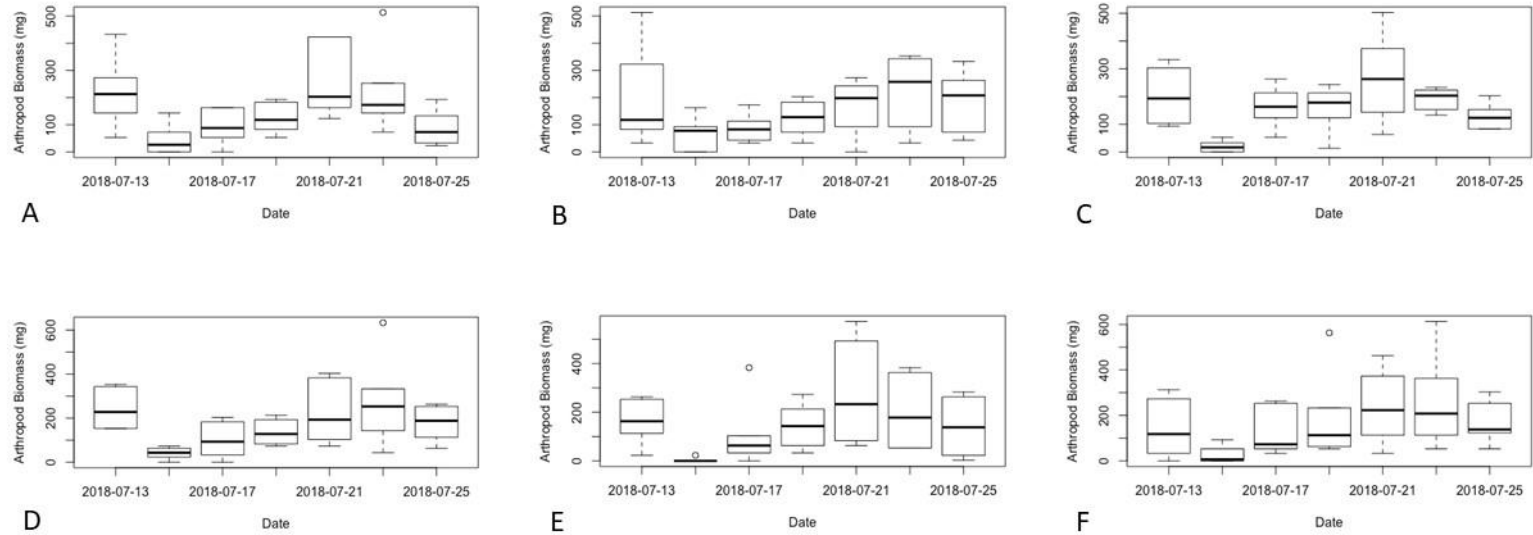


Figure 3. Variation in average arthropod biomass (mg/trap) at East Bay Migratory Bird Sanctuary, NU from July 13, 2018 to July 25, 2018 across six transects designated by letter.

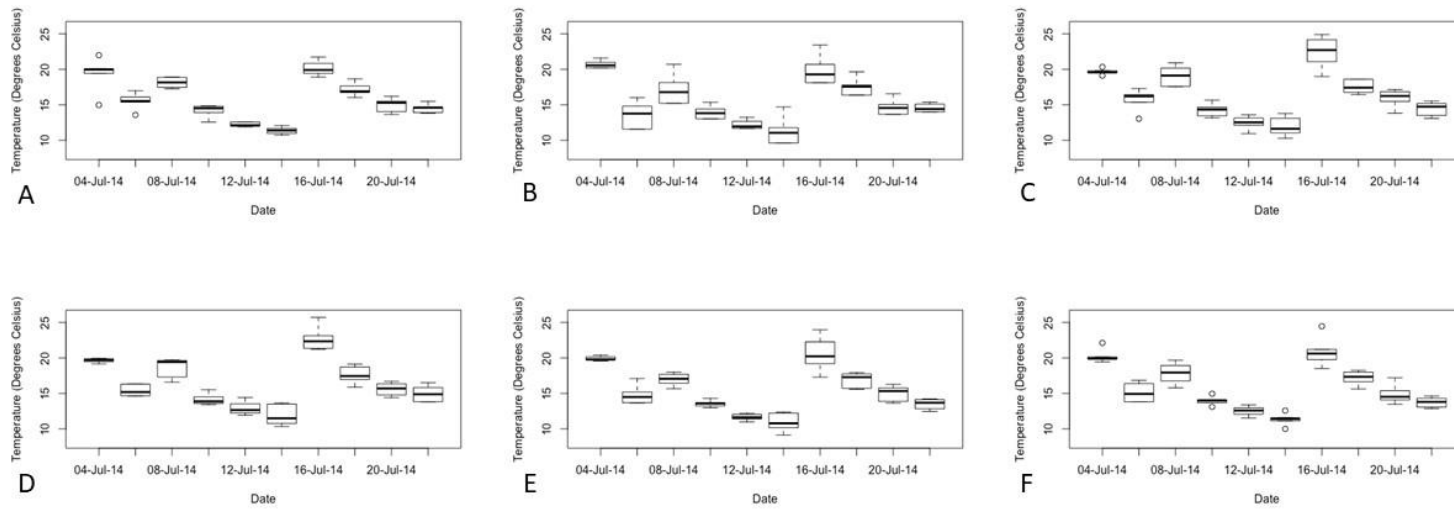


Figure 4. Variation in average temperature (degrees Celsius) at Churchill, MB from July 4, 2014 to July 16, 2014 across six transects designated by letter.

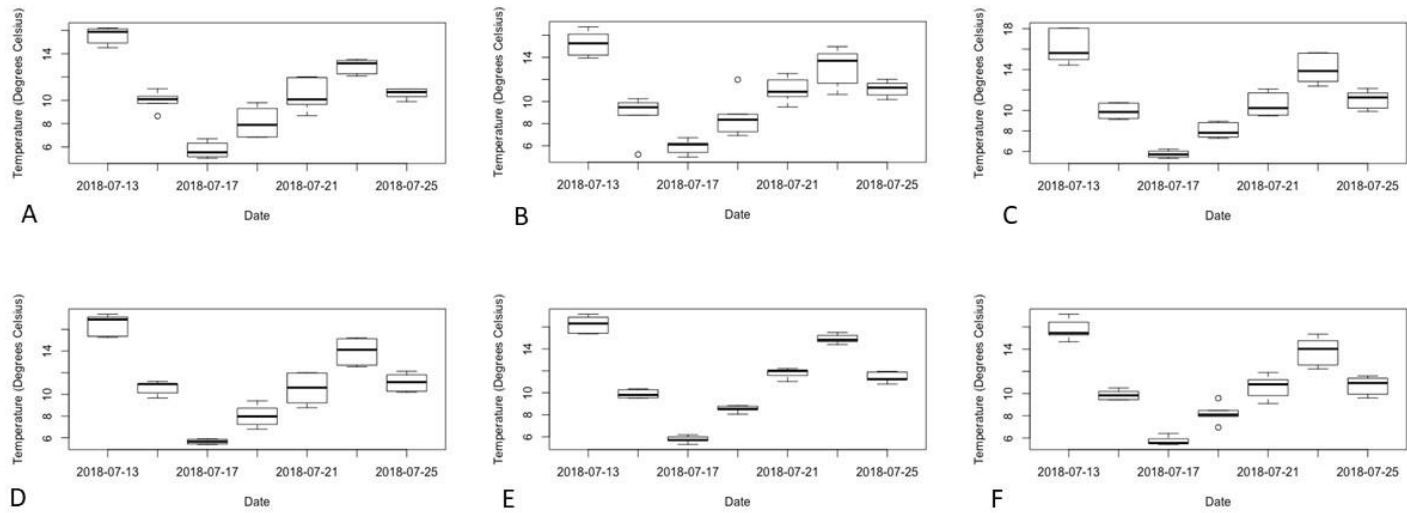


Figure 5. Variation in average temperature (degrees Celsius) at East Bay Migratory Bird Sanctuary, NU from July 13, 2018 to July 25, 2018 across six transects designated by letter.

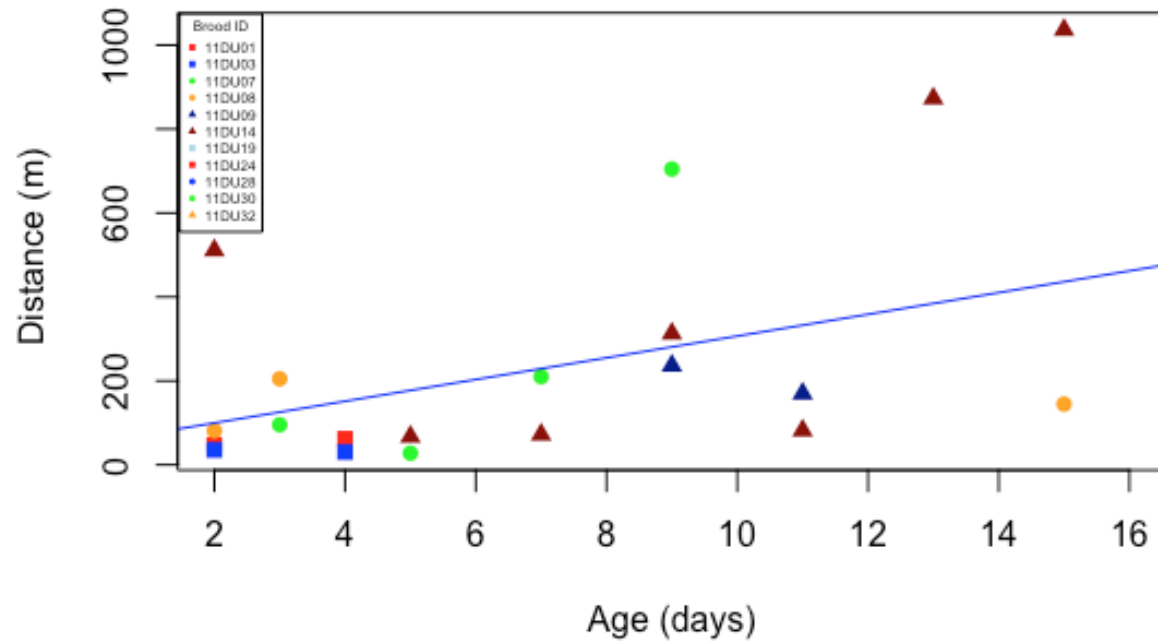


Figure 6. Scatter plot showing the relationship between age (days) of Dunlin chicks after hatching and distance travelled (m) by broods between subsequent detections. Brood identification is indicated by a unique colour and shape.

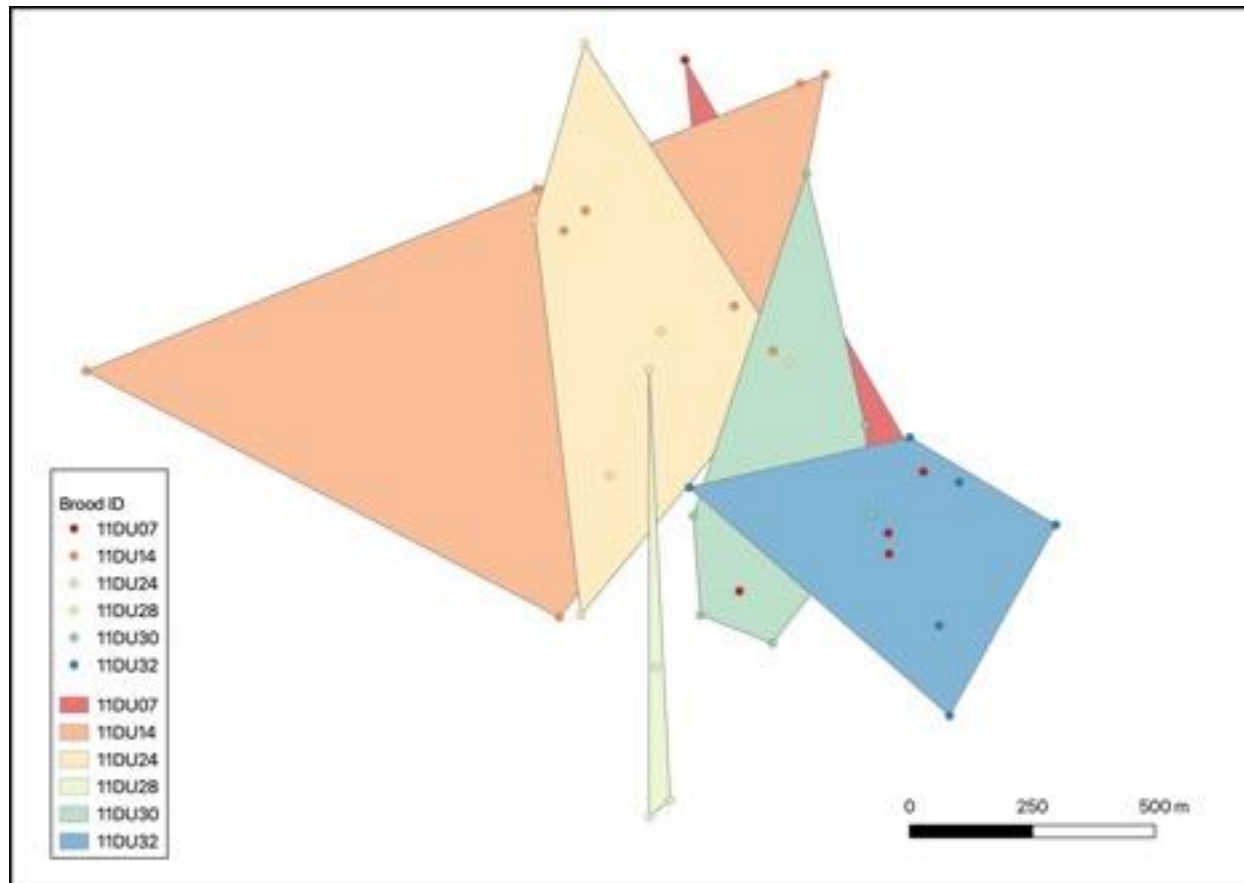


Figure 7. Home ranges and overlap of six Dunlin broods sampled in Churchill, MB in 2011 using Minimum Convex Polygons. Points indicate detections of broods identified by a unique colour with the corresponding polygons identifying home ranges.