Assessing the relationships between weather, food limitation and breeding ecology in an Arctic top predator.

by

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Abstract

A long term project being conducted on a population of Peregrine Falcons (*Falco peregrinus*) breeding near Rankin Inlet, Nunavut, Canada, has chronicled a steady decline in annual productivity over 30 years. By documenting the direct effects of summer rainfall on nestling mortality, a recent study on this population suggested that an increasing frequency of heavy rainfall may partially explain the observed declines. If the lower trophic communities that falcons rely on as prey are also affected by rainfall, reductions in food availability may be further limiting peregrine breeding success. The intent of this project was to determine if the Rankin Inlet population is generally food limited, and to determine if food limitation varied according to yearly precipitation. To answer these questions, I implemented a food supplementation experiment over three breeding seasons (2013 – 2015). After nestlings hatched each year, randomly selected broods periodically received an amount of commercially produced Common Quail (*Coturnix coturnix*) that correlated to 50% of the brood's age-specific energetic demand. The first two breeding seasons in which data were collected were uncharacteristically dry with total monthly rainfall amounts well below the 30 year average. The final season of data collection occurred in a summer with total monthly rainfall exceeding the 30 year average, and thus provided us with an opportunity to contrast food limitation across varying environmental conditions.

Over 3 years, I food supplemented a total of 93 individuals from 29 broods, and monitored 100 individuals from 32 broods that were not supplemented. Supplementation resulted in higher nestling survival, and more consistent growth between years. Based on these results, I suggest that the Rankin Inlet population is generally food limited during the breeding season.

Although I recorded an effect of rainfall on nestling growth, I failed to detect a relationship between nestling mortality and rainfall-induced food limitation. However, population-wide decreases in brood size during the wet year may have acted in a compensatory manner by reducing nestling energetic requirements. Overall, this project increases our understanding of how food availability relates to Peregrines breeding in the Arctic, and outlines important variables that influence productivity.

Preface

This thesis is an original work by Erik Hedlin. The study was conceived and designed by Erik Hedlin, Alastair Franke, and Lee Foote. Erik Hedlin and Vincent Lamarre collected the data, while Erik Hedlin both completed the analysis, and wrote the dissertation with edits from Alastair Franke and Lee Foote. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Multi-Scale Investigation of the Ecology of Raptors in Nunavut", AUP00000042, valid from May 1 2013 – May 12016.

Dedication

I dedicate this thesis dissertation to Sylvan Skarsgard. Although I spent much of my childhood, teen, and adult years with him, I remained completely oblivious to many of his incredible life achievements. This is a testimony to his modesty, and practiced abilities of steering conversations away from himself. Traits I respect in a man I deeply admired.

Acknowledgements

Between the adventures in Rankin Inlet and Edmonton, the solid friendships I formed over the past 2 years, and the development of my career ambitions, I'm indebted to my supervisors Dr.'s Alastair Franke and Lee Foote. I can't imagine I was the top candidate for this position, but I'm incredibly grateful they responded to my emails and eventually ended up saying: "what the hell, let's give this guy a shot". It's been a seriously enriching experience which will undoubtedly influence my future direction.

As I quickly found out, research in the North is *hard*; I couldn't have completed this work without the help and support of many technicians and fellow grad students. Special thanks go to Vincent Lamarre and Andy Aliyak. They tolerated my terrible attempts at speaking French and Inuktitut, my often chaotic methods of keeping track of keys, and most impressively my terrible jokes for 3 years. They not only tolerated my quirks, but somehow made the combination of stressful field work and a lack of sleep a *lot* of fun. Additional thanks in this regard go to Mathieu Tétreault, Barry Robinson, Philippe Galipeau, Pascal Pettigrew, Alexandre Paiement, and Kevin Hawkshaw.

I received a lot of feedback and guidance during the production of this dissertation, and a disproportionate amount of this help came from Helen Sofaer and Gabriel Oltean. Helen patiently walked me through some analytical methodology she developed despite there being no obvious reward, and Gabriel essentially put himself "on call" to answer any questions I had about coding, study design, or life in general. Their help not only enhanced my analysis, but enabled me to develop the necessary skills to address other obstacles in my project.

Lastly, none of this work would have occurred without financial aid and logistical support provided by Agnico Eagle Mining, Mitacs, Canadian Circumpolar Institute, and Environorth.

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"I strongly suspect that the deepest insight into a population comes from studying how survival and fecundity are influenced by the conditions in which the animals live. Such an approach cuts deeper into the problem of population ecology than do any of the others."

-Graeme Caughley (1980)

Introduction

Understanding factors that affect juvenile survival is imperative due to the strong relationship that exists between annual breeding productivity and population dynamics (Arcese et al. 1992, Johnson and Geupel 1996, Gaillard et al. 1998, Finkelstein et al. 2010, Saether et al. 2013, Fay et al. 2015). For birds however, survival rates in young are often low due to vulnerability from predation, anthropogenic disturbance, parasitism, sibling competition, habitat degradation, weather, and variability in food availability (Ricklefs 1969). Even if an individual survives beyond juvenile stages, evidence suggests that poor conditions during the growth and development periods can have lasting implications on fitness (Lindstrom 1999, Monaghan 2008, Cam and Aubry 2011).

In the context of rapidly changing climate and projected increases in frequency and intensity of extreme weather in North America (IPCC 2013), the effects of inclement weather, particularly rainfall, on breeding populations of birds has received a growing amount of attention (Both et al. 2006, Robinson et al. 2007, Oro et al. 2010, Anctil et al. 2013, Fisher et al. 2015, Laux et al. 2015). For example, heavy rainfall during the laying period has resulted in smaller egg sizes (Polak and Kasprzykowski 2013), and heavy rainfall during the incubation period has altered incubation behavior when coupled with variations in temperature (Coe et al. 2015). During the brood-rearing period, heavy rainfall has been linked to altered brooding behavior (Erikstad and Andersen 1983, Laux et al. 2015), decreased nestling growth rates (Erikstad and Andersen 1983), changes in host-parasite interactions (Manzoli et al. 2011, Soler et al. 2014), increased nestling mortality through direct exposure to rain or nest flooding (Sexson and Farley 2012, Anctil et al. 2013, Fisher et al. 2015), and overall decreases in reproductive success (Sexson and Farley 2012, Anctil et al. 2013, Fisher et al. 2015, Oberg et al. 2015). Furthermore, changes in prey species abundance and distribution resulting from variation in yearly precipitation has the potential to affect trophic interactions (Robinson et al. 2014), and thus for some species, food availability. For example, Vincenzi and Mangel (2013) demonstrated that a climate-induced increase in availability of foraging patches had strong implications for food availability, and therefore, on population dynamics of Kittiwake colonies on the Bering Sea. Using a food manipulation experiment, Fisher et al. (2015) established a link between weather and food availability by documenting the increased survival of food supplemented burrowing owls during bouts of heavy rainfall.

Food availability is considered to be the most prominent limiting factor during the brood rearing period among birds (Lack 1954, Martin 1987, 1995). Increases in frequency and intensity of inclement weather during this period could contribute to further increases in food limitation (Dawson and Bortolotti 2000). Therefore, examining the manner in which extreme weather and food abundance relates to breeding productivity is a vital component of understanding the way in which populations may respond to climate change.

Understanding the effects of climate change on wildlife is of particular concern in the Arctic. Globally, northern latitudes are expected to experience some of the greatest changes in climate, including increases in precipitation intensity and frequency (Serreze et al. 2000, Kusunoki et al. 2015). Moreover, birds breeding in the north may be more vulnerable to rapid climate change due to shorter breeding seasons relative to southern latitudes, and relatively simplistic food chains that are sensitive to alterations in trophic interactions (Ims and Fuglei 2005, Pearce-Higgins et al. 2005, Robinson et al. 2014).

Due to its unusually high density, a population of Peregrine Falcons (*Falco peregrinus*) breeding in Rankin Inlet, Nunavut, Canada, has been the focus of many research projects (Court et al. 1988, Court et al. 1989, Court et al. 1990, Bradley and Oliphant 1991, Johnstone et al. 1996, Bradley et al. 1997, Franke et al. 2010, Franke et al. 2011, Anctil and Franke 2013, Anctil et al. 2013, Franke et al. 2013, L'Herault et al. 2013). Among these, a breeding productivity comparison between the years 1982-1989 and 2002-2009 revealed that roughly half the number of young reached banding age (Franke et al. 2010). Although persistent organic pollutants have historically resulted in compromised reproductive success among peregrines, population-level pesticide loads during the study period had decreased below levels known to cause egg shell thinning and reproductive failure, indicating other causes for the observed declines (Franke et al. 2010). The authors used images captured by motion sensitive cameras to suggest that the direct effects of rainfall likely explained the long-term decline in reproductive success.

To investigate whether the direct effects of rainfall was associated with long-term changes in precipitation, Anctil et al. (2013) conducted a nest box experiment over three breeding seasons, and established that survival of nestlings raised in nest boxes was higher than those raised on natural ledges. The authors further demonstrated that ongoing changes to the precipitation regime over the course of population monitoring (1980-2010) was the most important factor explaining the reduction in reproductive success. Although Anctil et al. (2013)

identified the negative consequences of the direct effects of rainfall, the authors also indicated that a large proportion of nestlings died regardless of whether they were protected from the direct effects of rain. Using a combination of motion sensitive cameras and nest visits, the authors indicated that starvation was the main cause of mortality for nestlings that were spared from the direct effects of rainfall, and suggested that the indirect effect of rain (through reduced prey abundance) had also contributed to the long-term decline in reproductive success. Although supplemented with small mammals in years of high microtine abundance, Arctic breeding Peregrine falcons rely heavily on populations of shorebirds and passerines as prey (Court et al. 1988, Bradley and Oliphant 1991). Such populations are vulnerable to heavy rainfall through decreased arthropod activity and thus reduced food availability(Schekkerman et al. 2003, Seward et al. 2014), increases in juvenile mortality due to decreases in parental care (Oberg et al. 2015), and decreases in adult survival (McCleery et al. 1998). Such impacts on populations of shorebirds and passerines would make them less abundant across the landscape, and thus affect food availability for peregrines in the area.

The overarching goal of this project was to examine the relationship between precipitation and food limitation for Peregrine Falcons by conducting a food supplementation experiment. By manipulating the amount of food available to a population, food supplementation experiments have been widely implemented to examine the extent in which a population is food limited, and how such food limitation is manifested through ecological variables of interest (Boutin 1990). Because juvenile survival is tied to population dynamics and studies have indicated that the breeding productivity in the Rankin Inlet population of peregrines has declined, my project focused on the brood rearing period. Specifically my objectives were to 1) determine if the population was food limited during the brood rearing period, 2) to investigate how such food limitation may affect juvenile survival across breeding variables of known importance, and 3) examine the relationship between rainfall and food limitation.

Based on both observational evidence from Anctil et al. (2013) indicating the prevalence of starvation within this population, and the well documented effects of rainfall upon Peregrine prey species, I predicted that food supplementation would buffer nestlings against the direct and indirect effects of rainfall. Resulting from this buffer, I expected survival and growth in supplemented nestlings to be more consistent across years, while survival and growth in nestlings not being supplemented to fluctuate according to yearly precipitation.

Methods

Study Area

The study area was located on the western coast of Hudson Bay, and encompasses a 422 km^2 area that surrounds the community of Rankin Inlet, Nunavut, Canada (62°49'N, 92°05'W)(Figure 1). The terrestrial portion is characterized by rolling mesic tundra interspersed with numerous lakes and streams, and supports communities of passerines, shorebirds, ducks, geese, and small mammals. The marine portion is composed of numerous islands of varying size and also supports bird communities, in addition to small mammals. Rocky outcrops that form cliffs are common throughout both terrestrial and marine areas, and provide ideal nesting habitat for raptor species such as Rough Legged Hawks (*Buteo lagopus*), Peregrine Falcons (*Falco peregrinus*), Common Ravens (*Corvus corax*) occasionally Golden Eagles (*Aquila chrysaetos*), and Gyrfalcons (*Falco rusticolus*).

Peregrine Falcon Population Monitoring

Over three breeding seasons (May to August, 2013-2015), I monitored the study population using a combination of repeated nest site visits (to collect morphometric data) and motion sensitive cameras (RECONYX, Holmen Wisconsin, USA, models PC85 and PC800, 2013 n=11, 2014 n=22, 2015 n=22) to estimate lay date, hatch date, and causes of nestling mortality.

Camera Monitoring

RECONYX cameras were placed 60 to 200 cm from the nest bowl. For nest sites without cameras, hatch date was determined following Cade et al. (1996). Motion sensitive cameras were programmed to take one image followed by a quiet period of 2-5 seconds (the time period in which the camera did not respond to movement). Additionally, cameras were programmed to take a time lapse image every 15 minutes. All images were stored on 8 – 16 GB compact flash and SD memory cards, which were replaced during each nest visit. Nest visit were timed to occur approximately every 5 days.

Nest and Weather Monitoring

Beginning in mid-May as Peregrines arrived on territory, the study area was surveyed by helicopter, all-terrain-vehicle and snowmobile. Unoccupied sites were checked until occupancy by Peregrine Falcons was confirmed or the breeding season was sufficiently advanced to conclude the site was vacant. Rain gauges were installed adjacent to all occupied nest sites, and were checked and emptied if necessary during each site visit. In addition, weather data was recorded by the local Environment Canada weather station, and by two portable weather stations (Rainwise PortLog, Trenton Maine, USA) placed within the study area (Figure 1).

Site visits were scheduled approximately every 5 days until nestlings were 30 days of age to collect nestling mass data using an electronic scale accurate to ±1 gram, maintain cameras (replace batteries and memory cards), and record mortality. Nestlings were uniquely marked using Approved Product certified non-toxic ink (The Art & Creative Materials Institute, Inc., Hingham, Massachesetts, USA).

Supplementation Experiment

Each year, twenty occupied sites that held young were randomly allocated to one of two treatments; food supplemented (*n* = 10) and control (not supplemented, *n* = 10). Supplemented broods received commercially produced grown Common Quail (*Coturnix coturnix*) that corresponded to 50% of the brood's age specific energetic demand. Such demand was derived at the individual level from the observed amount of food necessary to suppress begging among captive bred falcon nestlings (Lynn Oliphant, personal communication, May 14, 2013). To avoid disturbance immediately after hatch, supplementation was started once nestlings were 5 days of age, and was stopped prior to 30 days of age to avoid pre-mature fledging. Broods that failed before reaching 5 days of age, or for reasons unrelated to food limitation (e.g., predation), were excluded from analysis.

In an effort to reduce disturbance, I only food supplemented broods during the scheduled nest visits which occurred approximately every 5 days. An amount of supplemental quail was left at each visit to account for the energetic demands of each nestling until the following scheduled nest visit. This resulted in the deposits of large amounts of food, however I expected that females would exhibit normal caching behaviour (Booms and Fuller 2003), and that supplemented quail would therefore be rationed over the following days.

Data Analysis

Survival

To estimate the probability of nestling survival between treatment groups, and across years in which different amounts of precipitation were recorded, I modeled the probability of nestling survival (1=lived, 0=died) using the glmer function in the lme4 package in R (Bates et al. 2015, R Development Core Team 2015) to generate generalized linear mixed effects models. For model selection, I used an information-theoretic approach based on second order Akaike's information criterion (AICc) for corrected for small sample size, and multi-model inference (model averaging) to estimate parameters from the best models (Burnham and Anderson 2002). I compared the modeled survival probabilities between treated and control nestlings to determine the extent of food limitation within the population, and then examined whether this effect varied across yearly climate conditions by adding an interaction between the treatment variable, and a variable denoting yearly weather (0 = dry, 1=wet). Other variables included in the models were hatch date (standardized against the median for each breeding season), within brood hatch order (1st hatch to 4th hatch), and asynchrony (the number of days that had passed since the oldest sibling hatched). An important assumption of generalized linear models is that the response of unit i, is independent given covariate x_i. Because treatment was allocated at the brood level and my sample unit was the individual, my data violated this assumption. To account for this lack of independence, random intercepts for the year, and nest site in which individuals were raised were included in every model. I used averaged survival probability in the grouping variables (nest and year) across hatch order, and relative hatch date to visualize how survival probabilities changed accordingly throughout the range of those two variables.

Growth

Growth analysis employed the methodology outlined by Sofaer et al. (2013) to examine differences in growth curves between years of varying weather conditions. Because peregrines exhibit distinct reverse sexual size dimorphism (males =607 g ± 42.42, females = 920 ± 55.28)(Court et al. 1988), and sex could not be confidently assigned until nestlings reached ~25 days of age, growth analysis incorporated only the individuals that survived to this age. I modeled growth separately for each sex by generating 3 parameter mixed effects logistic models using the nlme package in R (Pinheiro et al. 2015, R Development Core Team 2015) where w_t = mass at time t (g), A = asymptotic mass (g), K = growth rate constant, I = inflection point of the growth curve (days), and t = nestling age (days). Two levels of random effects – nest and nestling – were included in the models to account of for 1) shared genetic backgrounds and common levels of parental care, and 2) repeated measurements on individuals. These random effects were applied to one or more of the three parameters in the models for both sexes, and the models were then ranked based on AICc scores to determine the best random effect structure to describe each sex (Sofaer et al. 2013). The mass for the *k*th measurement on the *j*th nestling in the *ith* nest was therefore:

$$w_{ijk} = \frac{A + A_i + A_{ij}}{1 + e^{((K+K_i+K_{ij})(I+I_i+I_{ij}+t_{ijk}))}} + \varepsilon_{ijk}$$

In all models, both levels of random effects and the random errors were assumed to be normally distributed with a mean of zero. I followed Sofaer et al. (2013) and discarded over-parameterized models that were signified by a) a failure to converge, b) a random effect standard deviation equal to zero, or c) an absolute value of the correlation between two random effects that was >0.9.

To determine whether treatment groups differed in growth among wet years, and dry years (2015 vs. 2013 and 2014 respectively), growth curves were fitted to each treatment group within each sex separately, and a fixed "condition" (i.e.,. X_{con}) effect that reported differences between wet and dry years was added to each of the three parameters.

$$w_{ijk} = \frac{A + A_i + A_{ij} + A_{con}}{1 + e^{((K+K_i+K_{ij}+K_{con})(I+I_i+I_{ij}+ I_{con}-t))}} + \varepsilon_{ijk}$$

Any differences in the fixed condition effect between treatment groups in the three parameters (A_{con}, k_{con},I_{con}) were assumed to be related to amount of food since the only difference between groups was whether they were being food supplemented or not.

I also wanted to determine whether supplementation in wet years had a greater effect on growth than food supplementation in dry years. To do so, I employed the above methodology, but replaced the fixed condition effect with an interaction between treatment and yearly condition to denote differences in all three parameters.

$$w_{ijk} = \frac{A + A_i + A_{ij} + A_{t*w}}{1 + e^{((K+K_i+K_{ij}+K_{t*w})(I+I_i+I_{ij}+ I_{t*w}-t))}} + \varepsilon_{ijk}$$

Results

Nestling Monitoring

A total of 193 nestlings from 61 broods were monitored (2013, *n* = 63, 2014, *n* = 68, 2015, *n* = 62), with a total of 133 (70 %) that survived the brood rearing period (2013: *n*=47, 2014: *n*=44, 2015: *n*=42). Of the 60 individuals that died, 40% (24/60) succumbed to starvation, 18% (11/60) from the direct effects of rainfall (in some instances starvation was exacerbated by rainfall), 7% by predation (4/60), 2% (1/60) by siblicide, and 33% (20/60) of the mortalities could not be classified.

I food supplemented a total of 93 individuals from 29 broods, and monitored 100 individuals from 32 broods that were not supplemented.

Rainfall

The summers of 2013 and 2014 were dry, compared to the summer of 2015. Total monthly rainfall for June, July, and August was 7.8mm, 24mm, and 3.6mm respectively in 2013, 16mm, 16mm, and 40.6mm in 2014, and 33.2mm, 61.6mm, and 55.2mm in 2015 (Figure 2). Only the total rainfall for June and July of 2015 exceeded the 30 year mean (1981-2012, Figure 2). Average daily rainfall was also higher in all three months of 2015 (Figure 2). Because of the distinct differences in total precipitation between 2013, 2014, and 2015, yearly weather was categorized as dry (2013 and 2014) or wet (2015).

Survival

Out of 14 candidates, the two most parsimonious models to explain nestling survival included the variables treatment, relative hatch date, asynchrony, weather, and an interaction between treatment and weather (Table 1). The interaction between treatment and weather variable was used to test the hypothesis that the effect of supplementation was different in dry vs. wet years, however this variable was not included in the top model and there was substantial variation surrounding the estimate (estimate: 1.30, SE: ±1.41). Treatment was positively associated with survival, while relative hatch date, asynchrony, and weather were negatively associated to survival (Table 2). Given the set of candidate models, the probability that the top model best explains survival is high (AICc weight = 0.74, Table 1), and importance should therefore be placed on the variables used within that model (treatment, relative hatch date, and asynchrony).

The effect of treatment, hatch date and asynchrony on survival

To characterize the manner in which survival varied with treatment, hatch date and asynchrony, I averaged survival among years, and broods (random effects), and let the averaged survival probabilities vary across relative hatch dates while holding treatment and hatch order constant (Figure 3). Due to the high level of correlation between hatch order and asynchrony (r = 0.71), I used hatch order to categorize asynchrony for the purpose of visualization. I assumed trends associated with hatch order reflected asynchrony. Relative to first hatch nestlings, asynchrony for second, third and fourth hatched nestlings was 0.64 ± 0.73, 1.67 ± 1.14, and 2.8±1.70 days respectively.

Generally, survival was highest when an individual was supplemented, hatched first within their brood, and hatched early in the season, and lowest when individuals were not supplemented, hatched last within broods, and hatched late in the season.

Although supplementation increased survival overall, the negative trend between survival, hatch date, and hatch order was apparent in both experimental groups. The probability of survival for supplemented individuals that hatched first within their brood ranged from 0.99 when hatched early in the season (relative hatch date: -5), to 0.68 when hatched late (relative hatch date = 10). The positive effects of supplementation, along with the negative effects of hatch date and hatch order are also evident in the model estimates averaged across the top two models (Table 2).

The additive effect of supplementation given hatch order and relative hatch date.

To estimate the effect of supplementation with variation in relative hatch date and hatch order, I calculated the marginal difference in survival between supplemented and control groups (Figure 4). For each hatch order, the effect of supplementation was parabolic, initially resulting in increased survival with relatively later hatch date (i.e., peak supplementation effect), followed by decreased survival indicting that the negative effect of relative hatch date on survival was greater than the effect of supplementation (Figure 5). Increases in hatch order resulted in in two general trends: 1) the peak supplementation effect increased in magnitude, and 2) the peak supplementation effect occurred at earlier hatch dates. For example, supplementation resulted in a maximum increase in survival probability of 0.34 at relative hatch date = 7 for first hatch individuals, and a maximum increase in survival probability of 0.48 at relative hatch date = -2 for fourth hatch individuals.

Growth

Because I included only those nestlings that survived to banding age (~25 days), and because I modeled growth for each sex separately, my sample size for growth analysis was a subset of nestlings included in the survival analysis (females: *n* = 51, males: *n* = 76). Overall, I averaged a total of 6.0 ± 0.9 measurements on each individual starting at 5 days of age, and ending at 30 days. Overall, food supplementation decreased the amount of variation in growth between wet and dry years for both sexes. The variation I observed in the control group however was limited to inflection points and growth rate constants. Asymptotes did not significantly differ between wet and dry years in any experimental group.

I found evidence for the inclusion of random effects in my growth models for both sexes (Table 3 and Table 4

Table 4). The most parsimonious model for females included a nestling level random effect on asymptote and inflection (Table 4

Table 4), while the most parsimonious model for males included a nest level random effect on asymptote, inflection, and the growth rate constant (Table 3). I then used the top models for both sexes to estimate the effect of treatment on growth among wet and dry years (Table 5 and Figure 7). The only significant difference in parameters when wet years were compared to dry for supplemented males was an earlier inflection (I_{wet}= -0.9 days at p=0.0064), while control males showed a significant decrease in the growth constant (k_{wet} = -0.05 at p=0.0088) and a delayed inflection (I_{wet} = 3.00 at p=0.0001). No significant differences were exhibited by supplemented females in wet years, while control females showed a delayed inflection of 2 days (I_{wet}= 2.09 at p=0.015).

Next, I replaced the fixed “condition” effect with an interaction between weather and treatment to determine how the magnitude of the effect of supplementation changed between wet and dry years. Despite a different fixed effect in the models, the most parsimonious random effect structures were similar to those which incorporated a condition effect on all parameters. Using these models, I could not detect any difference between wet and dry years in regards to the effect of supplementation upon growth (Table 6 Three parameter estimates for growth models, and how each estimate changes given an interaction between food supplementation and greater summer precipitation. Both random and fixed effect structures of male and female growth models were the same as in table 5. I found no significant differences in the magnitude of the effect of supplementation in wet years.

Discussion

The intent of this project was to determine if food limitation during the brood rearing period was exacerbated by the indirect effects of rainfall. Among prey species on which peregrines rely, prolonged and heavy rainfall has been shown to decrease adult and juvenile survival, as well as reduce parental foraging capabilities (McCleery et al. 1998, Schekkerman et al. 2003, Seward et al. 2014, Oberg et al. 2015). This introduces the potential for an indirect effect of rainfall on peregrine falcon breeding that should result in altered nestling growth, and increased mortalities related to food limitation.

Survival

In light of increased probability of survival from food supplementation, I suggest that peregrine falcon nestlings are generally food limited in the Rankin Inlet population. A supplementation effect release from this limitation was evident in all years and therefore all weather conditions, and across all variables used to model survival.

Consistent with Anctil et al. (2013), I found a strong negative relationship between hatch date and nestling survival. Decreased reproductive output with later hatch dates is evident in most birds, and is often represented by smaller clutch sizes, lowered nestling survival, and lowered post-fledging survival (Klomp 1970, Perrins 1970, Daan et al. 1988, Rohwer 1992). Although it is most commonly believed that declining reproductive output with later hatch dates is best explained by seasonal trends in food availability (Daan et al. 1988, Brinkhof and Cave 1997), some have suggested other pressures such as seasonal trends in weather conditions (Bengtson 1972, Erikstad and Andersen 1983), predation rate (Eldridge and Krapu 1988), or parasite loads (Moller 1994). In my study population, supplementation resulted in overall increases in survival, and the pattern in which it increased survival suggests increasing food limitation with later hatch dates (Figure 4 and Figure 6).

Due to logistical constraints, I could not conduct prey population surveys during the experiment, and therefore I cannot explore the mechanisms driving seasonal patterns in food limitation. For example, it is possible that more pronounced food limitation among later hatch birds is not entirely caused by seasonal decreases in prey abundance/availability, but also by variation in parental quality. Individuals who are able to initiate breeding at advanced dates may be older with more breeding experience, and of generally higher phenotypic quality (Perdeck and Cave 1992, Moreno 1998). These traits would likely result in better parental care and provisioning rates, which would lead to decreased food limitation among early hatch nestlings.

Although model averaged estimates for rainfall and the interaction between rain and supplementation suggests a negative, food-related effect of rain, these variables were not present in the most parsimonious model. Additionally, these estimates were surrounded by substantial variation, indicating noise in the response. Rainfall may not have had the expected effect on food related mortality due to population-wide decreases in clutch size during the wet year. During the dry years, an average of 47% of the breeding pairs attempted to raise broods of four (2013 = 10/19, 2014=9/22), while this number was 25% in the wet year (2015=5/20). Reductions in brood size, even by one nestling, would reduce the total amount of energy parents need to invest throughout the brood rearing periodand likely reduce weather related food limitation, and weaken the signal obtained from mortalities.

Growth

Mortality is the most extreme manner in which an individual can respond to an environmental pressure. Because individuals can survive the brood rearing period but still be affected by food limitation, it is expected that more subtle responses to food limitation would appear through the analysis of growth. However, my growth analysis relied on the confident identification of sex, and therefore only included the individuals that survived to banding age. Because this resulted in the inclusion of only the most competitive individuals within their broods (i.e., those who outcompeted siblings for food), it is assumed that the growth measurements used in my analysis represented the best possible growth given the yearly conditions. I therefore expected to see less pronounced differences between experimental groups.

Despite my predictions, supplementation significantly affected growth. Growth curves of supplemented nestlings varied little between dry and wet years, and I interpret this to indicate a buffering effect of food supplementation. Comparatively, growth curves for both control males and females varied substantially between wet and dry years (Figure 7). Because the only difference between experimental groups was food supplementation, I conclude that the increased variation observed among control individuals was caused by variation in food availability between wet and dry years.

It is important to note that changes in food availability across dry and wet years does not necessarily imply changes in food abundance. Although variation in nestling growth across wet and dry years among the control group was likely caused by variation in food availability (indicated by the lack of variation in the supplementation group), I cannot conclude that such a result originated from weather induced decreases among prey species. It is well established that rainfall negatively affects several aspects of passerine and shorebird ecology (McCleery et al. 1998, Schekkerman et al. 2003, Seward et al. 2014, Oberg et al. 2015), but rainfall may also affect peregrine hunting efficiency. Prey species may become less active and thus less conspicuous during bouts of rainfall which may decrease encounter rates for hunting peregrines. Although it is likely that increased rainfall affects prey abundance, a lack of data from prey populations in the wet years restricts my conclusions about the mechanisms that cause reduced prey availability.

Despite the reduced growth rate constants in control males, and delayed inflections in control groups for both sexes, asymptote values did not significantly differ. These findings indicate that despite the slower growth caused by rainfall in 2015, individuals that survived the brood rearing period reached asymptote masses comparable to those obtained in dry years. Although I can only infer this much, such a conclusion may be underestimating the effects of rain on food availability. Due to increased bottlenecks in parental food provisioning, larger brood size reduces nestling growth (Dijkstra et al. 1990, Sicurella et al. 2015). Again, the signal of rain-induced changes to growth may have been substantially weakened by the fact that peregrines were generally raising larger broods in the dry years.

Suggested areas of improvement

More data - weather, and hatching asynchrony

Not surprisingly, the best way to improve this study is by collecting more data. By extending this experiment and collecting more data in wet years, one could decrease the confounding effect of smaller brood sizes in 2015, and create more robust models to better isolate the effect of weather on peregrine food limitation. By using the methodology presented here, one can obtain empirical values related to food limitation for each hatch order (i.e.,. the hatch date when food limitation overwhelms supplementation), and with more data one could therefore determine how food limitation changes from dry to wet conditions across the range of hatch positions. This is important, because nestlings may experience weather induced food limitation differently according to the sequence in which they hatched.

Although there are many theories as to why hatching asynchrony occurs in birds, the most widely known and debated is the brood reduction hypothesis posited by (Lack (1947)). The brood reduction hypothesis states that when breeding adults cannot predict how abundant food will be when nestlings hatch, it is advantageous to create a feeding hierarchy within the brood. Therefore if the laid clutch turns out to be too large for the available food, the nestlings hatching late (i.e.,. the runts) will succumb to starvation and effectively reduce the clutch to a manageable size. This means that in years of lower food availability, food limitation affects nestlings according to their hatch position, and the effects of weather would therefore be more accurately described within the levels of this variable.

Isolating the indirect effects of rainfall

Although logistically difficult to implement, this study could have benefitted from nest boxes. It is possible that the delayed growth I observed in wet years resulted from the fact that nestlings were persistently wet and experienced increased energetic costs related to compromised thermoregulation. Supplemented individuals may not have exhibited delayed growth because they could match the increased energetic costs with the extra food they were receiving. By placing all individuals in both experimental groups in nest boxes, one could eliminate the direct effects of rainfall from the experiment and thus make more confident conclusions about the indirect effects of rainfall.

Prey surveys

Because this project attempts to link weather with peregrine breeding success through its impact on prey communities, information on annual variation in prey abundance would complement the supplementation experiment. The methodology the supplementation experiment was designed to observe the results of rainfall on food limitation; not to conclude about the mechanisms driving food limitation. By including information on annual variation in prey abundance, this project would gain an explanatory component, and better describe the ways in which increased rainfall affects breeding success through food availability.

Conclusion

This project is the first to study in-depth how breeding productivity in the Rankin Inlet population is affected by food. Through this supplementation experiment, I have been able to determine that a substantial portion of the variation in survival across hatch order and hatch date is related to food availability. Furthermore, by determining at which hatch dates food limitation begins to overwhelm supplementation, I can now more precisely predict the survival of individuals based on these two important variables. The extension of this experiment in to the future would likely yield results in additional wet years, and decrease the confounding effect of smaller brood sizes in 2015. When combined with simultaneous surveys on prey populations, such additional data would greatly extend the knowledge I now have on food limitation and nestling survival.

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Figures and Tables

Table 1

Table 1 Generalized linear mixed candidate models in descending order from most to least parsimonious. Columns indicate the variables included in each model, the number of parameters (K), corrected AIC scores (AICc), change in AICc (ΔAICc), AIC weight (AICcWt), and the log-likelihood.

Variables	K	AICc	ΔAICc	AICcWt	LL
Relative Hatch, Asynchrony, Treatment	6	196.86	0.00	0.74	-92.20
Relative Hatch, Asynchrony, Treatment:Weather, Treatment, Weather	8	200.24	3.38	0.14	-91.73
Asynchrony, Treatment, Weather	6	202.40	5.54	0.05	-94.98
Treatment:Asynchrony, Treatment, Asynchrony	6	202.50	5.64	0.04	-95.02
Treatment:Relative Hatch, Treatment, Relative Hatch	6	204.31	7.45	0.02	-95.93
Relative Hatch, Treatment, Weather	6	204.48	7.62	0.02	-96.01
Hatch order, Relative Hatch	7	209.36	12.50	0.00	-97.38
Relative Hatch, Asynchrony, Weather	6	214.28	17.42	0.00	-100.91
Hatch Order	6	217.51	20.65	0.00	-102.53
Treatment	4	218.26	21.40	0.00	-105.03
Asynchrony	4	218.53	21.67	0.00	-105.16
Treatment:Weather, Treatment, Weather	6	219.66	22.80	0.00	-103.60
Weather	4	237.86	41.00	0.00	-114.82

Table 2

Table 2 Model averaged parameter estimates from the two most parsimonious models. *Treatment*: 1 = supplemented, 0 = control. *Hatch Date*: hatch date relative to the yearly median (0 = median). *Asynchrony*: number of days since oldest sibling hatched. *Weather:* yearly precipitation (1=wet, 0 = dry). *Supplementation x weather*: interaction between food supplementation and weather

Parameters	Treatment	Hatch Date	Asynchrony	Weather	Treatment x Weather	Intercept
B	2.13	-0.24	-0.53	-0.68	1.30	1.15
SE	0.63	0.12	0.20	0.98	1.41	0.60
Lower CI	0.90	-0.48	-0.92	-2.60	-1.46	-0.03
Upper CI	3.36	-0.0048	-0.14	1.24	4.06	2.33

Table 3

Table 3 Fourteen models were used to select the most parsimonious random effect structure for male growth. Model parameters include *a:* asymptote, *i:* inflection, *k*: growth rate constant. The fixed effect structure of all models was a three parameter logistic model.

Random Effect Structure					
Nest Level	**Nestling Level**	**Total # of *k***	**Delta AICc**	**AIC**	**LL**
aik	-	10	0	4772	-2370
-	ai	7	5.397	4778	-2376
i	i	6	11.406	4784	-2376
ai	ai	10	11.406	4784	-2376
a	a	6	45.322	4818	-2397
-	a	5	45.914	4818	-2401
a	-	5	149.767	4922	-2453
ai	-	7	129.369	4902	-2438
-	i	5	159.074	4931	-2455
i	-	5	187.3	4960	-2469
k	-	5	205.057	4977	-2480
k	k	6	205.533	4978	-2477
-	k	5	207.767	4980	-2479
-	-	4	209.674	4982	-2481

Table 4

Table 4 Twelve models were used to select the most parsimonious random effect structure for female growth. *a:* asymptote, *i:* inflection, *k*: growth rate constant. The fixed effect structure for all models was a three parameter logistic model.

Random Effect Structure					
Nest Level	**Nestling Level**	**Total # of *k***	**Delta AICc**	**AIC**	**LL**
-	ai	7	0	3219	-1600
a	a	6	35.424	3255	-1618
-	a	5	35.984	3255	-1620
aik	-	10	58.807	3278	-1625
a	-	5	64.606	3284	-1634
-	i	5	104.108	3323	-1654
i	i	6	106.108	3325	-1654
i	-	5	128.076	3347	-1666
k	-	5	134.664	3354	-1669
k	k	6	136.668	3356	-1669
-	k	5	139.396	3358	-1671
-	-	4	141.289	3360	-1672

Table 5

Table 5 Three parameter estimates for growth models, and how each estimate changes for both sexes and both experimental groups across wet and dry years. Estimates are presented with standard deviations, along with notation that denotes the level of significance. The random effect structure for males included a nest level random effect on asymptote, inflection, and the growth rate constant, while the random effect structure for females included a nestling level effect on the asymptote and inflection. The fixed effect structure was a three parameter logistic model.

Sex	Treatment	K	K_{wet}	A	A_{wet}	I	I_{wet}
Male	Supplemented	0.2±0.009*	-0.006±0.01	608.8±8.0*	-12.9±10.7	13.6237±0.2*	-0.9±0.3*
Male	Control	0.3±0.01*	-0.05±0.02*	558.9±23.89*	73.6±40.0***	12.3±0.4*	3.0±0.7*
Female	Supplemented	0.2±0.008*	0.02±0.02	840.5±19.0*	22.1±33.6	14.5±0.2*	0.6±0.4
Female	Control	0.2±0.01*	-0.04±0.03	780.4±24.4*	82.02±63.5	13.9±0.2**	2.1±0.8**

*P<0.001, **P<0.05, ***0.05<P<0.10

Table 6

Table 6 Three parameter estimates for growth models, and how each estimate changes given an interaction between food supplementation and greater summer precipitation. Both random and fixed effect structures of male and female growth models were the same as in table 5. I found no significant differences in the magnitude of the effect of supplementation in wet years.

Sex	**K**	**K_{t*w}**	**A**	**A_{t*w}**	**I**	**I_{t*w}**
Male	0.24±0.00584*	-0.006±0.01	608.8±8.0*	-23.7±18.5	13.0±0.2*	-0.6±0.4
Female	0.2±0.009*	0.02±0.02	813.6±11.5*	35.6±27.8	14.2±0.2*	0.5±0.1

*P<0.001, **P<0.05, ***0.05<P<0.10

Figure 1

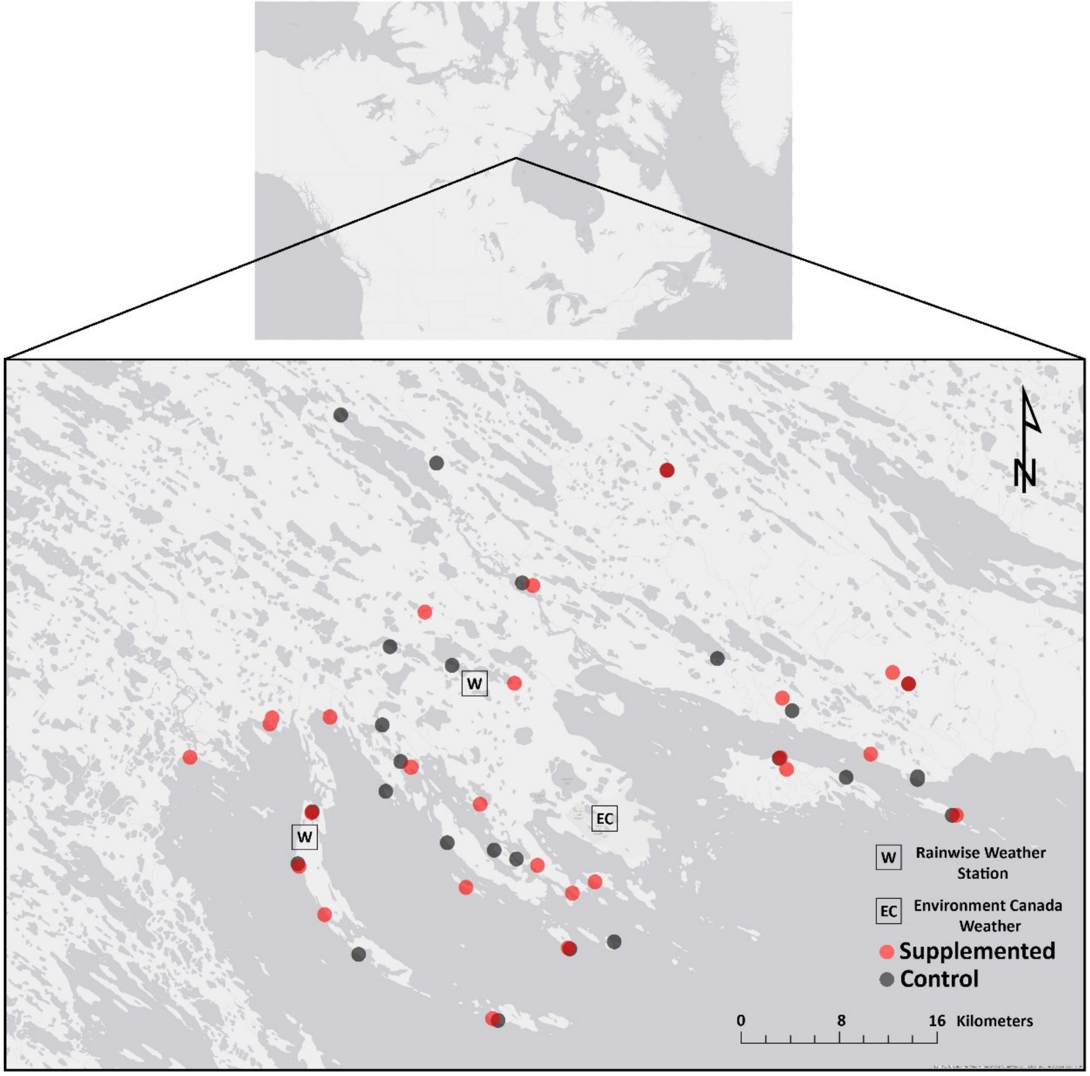

Figure 1 The distribution of supplemented and control broods of Peregrine Falcons over three years (2013-2015). This map also shows the placement of weather stations within the study area.

Figure 2

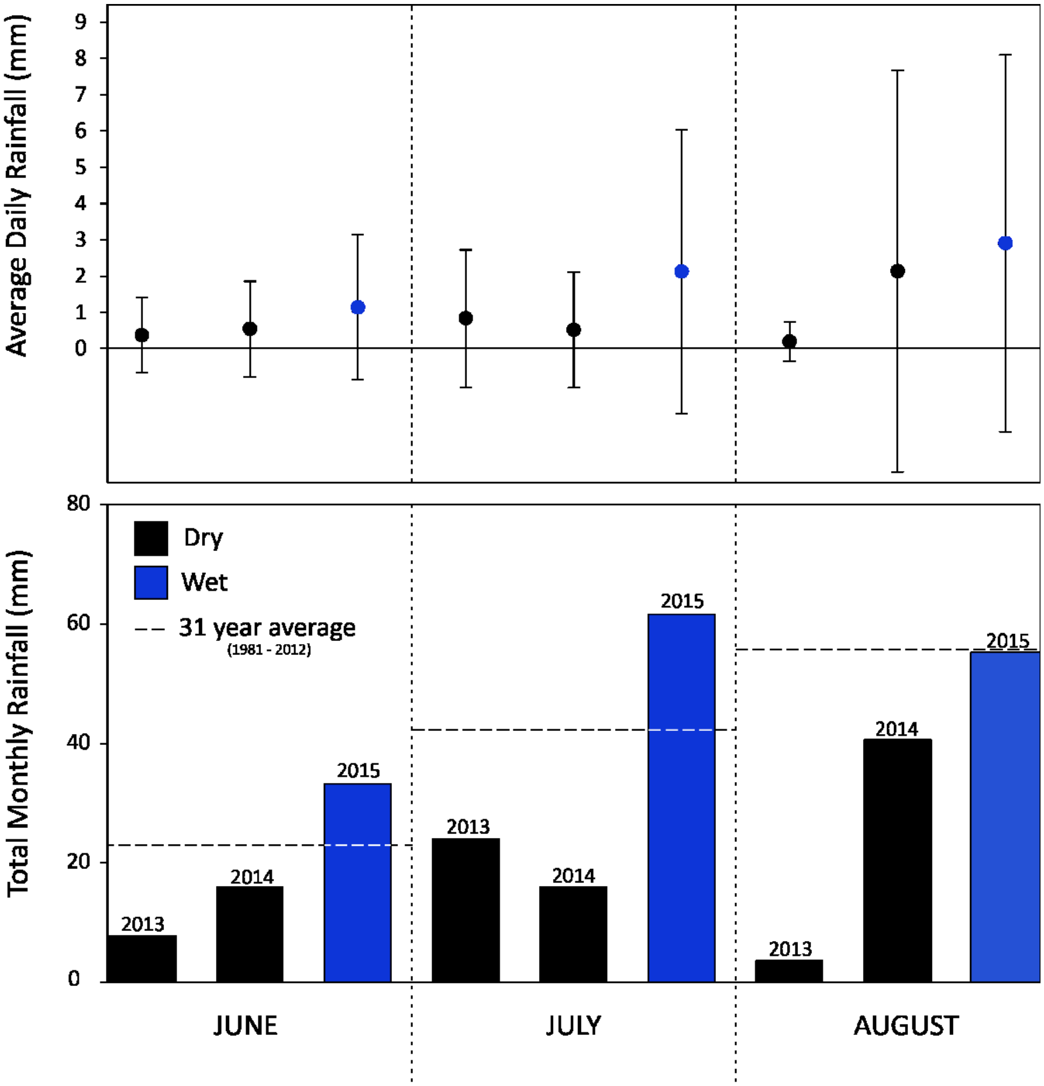

Figure 2 Displays the total monthly rainfall, and the average daily rainfall (per month, ± 1 standard deviation) in the three years this study took place (2013 – 2015). Rainfall data was obtained from the Environment Canada weather station located at the Rankin Inlet Airport.

Figure 3

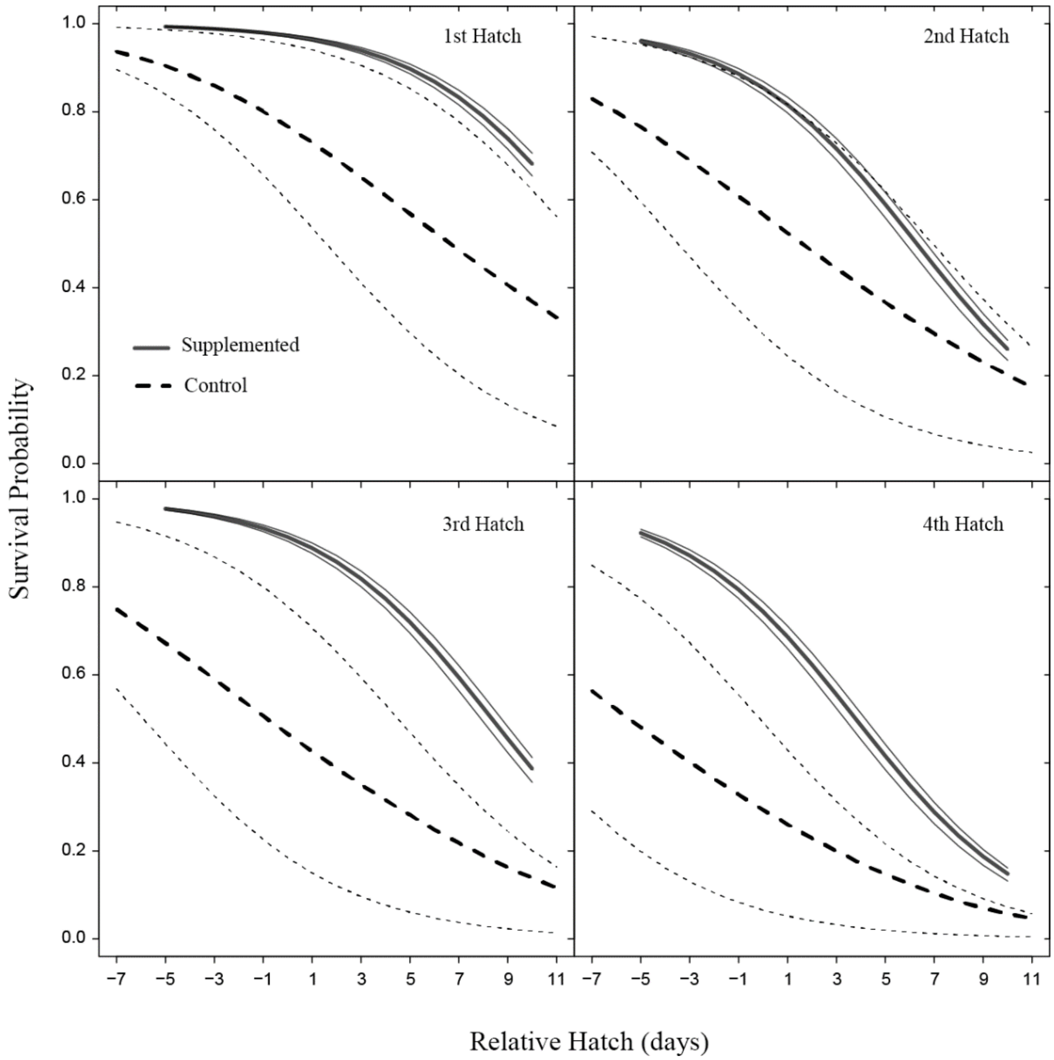

Figure 3 Survival probabilities for supplemented and control individuals monitored from 2013-2015 as a function of hatch order, and relative hatch date (where negative hatch dates indicate hatching prior to the yearly median). Survival probabilities were obtained by averaging the fitted probabilities for each individual across the grouping variables year, and nest used in a mixed effects logit model (survival = Relative hatch date + hatch order + treatment). Theseprobabilities were then plotted across relative hatch date, while holding hatch order and treatment constant. Error lines depict the upper and lower quartiles (upper = 75%, and lower = 25%). Mean asynchrony for hatch 1: 0±0, hatch 2: 0.64±0.73, hatch 3: 1.67±1.14, hatch 4: 2.8±1.70.

Figure 4

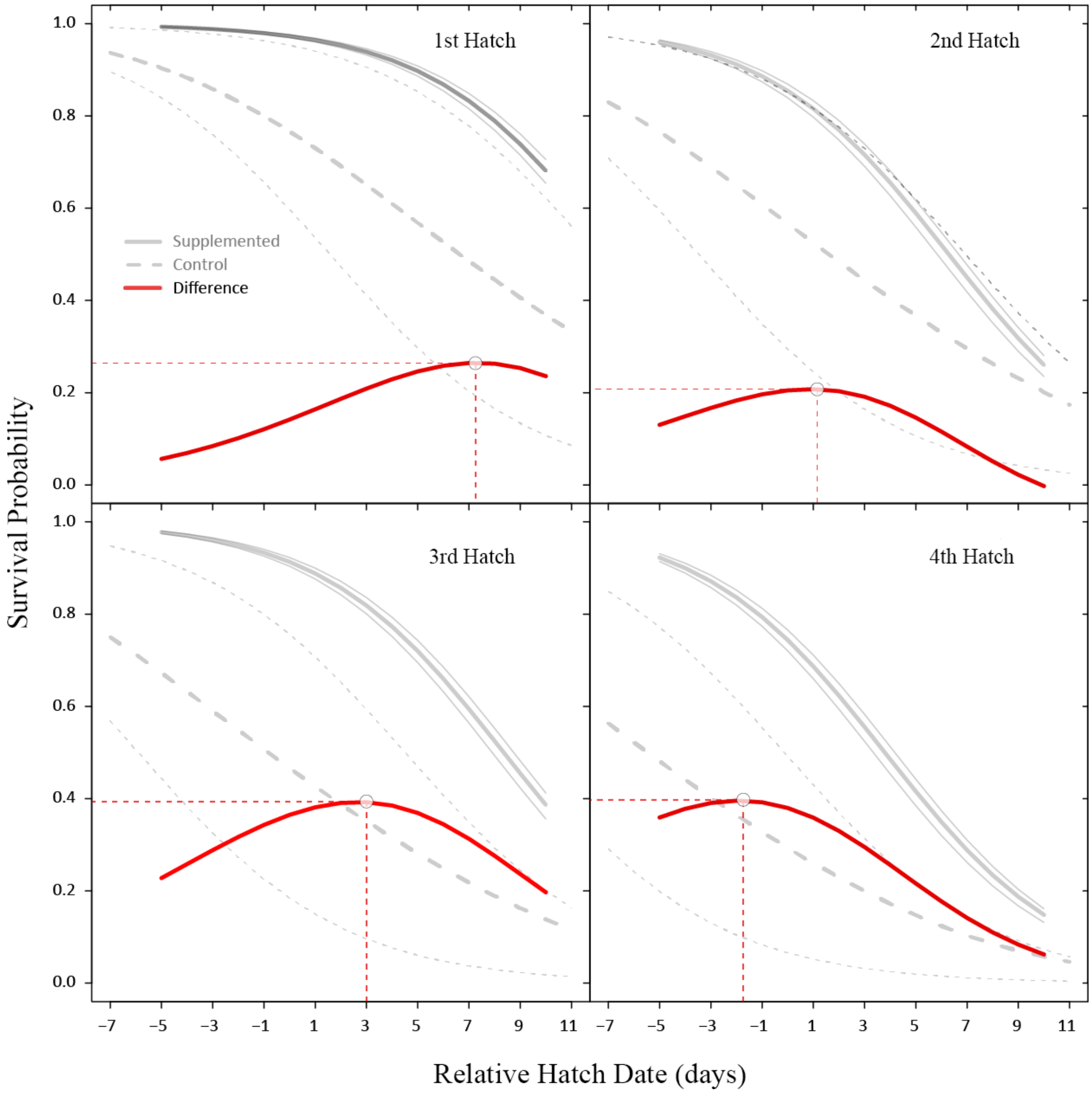

Figure 4 This figure expands on figure 3, and highlights the difference in survival probabilities between supplemented and control nestlings. The red line can be interpreted as the effect of supplementation across relative hatch date, and for each hatch position.

Figure 5

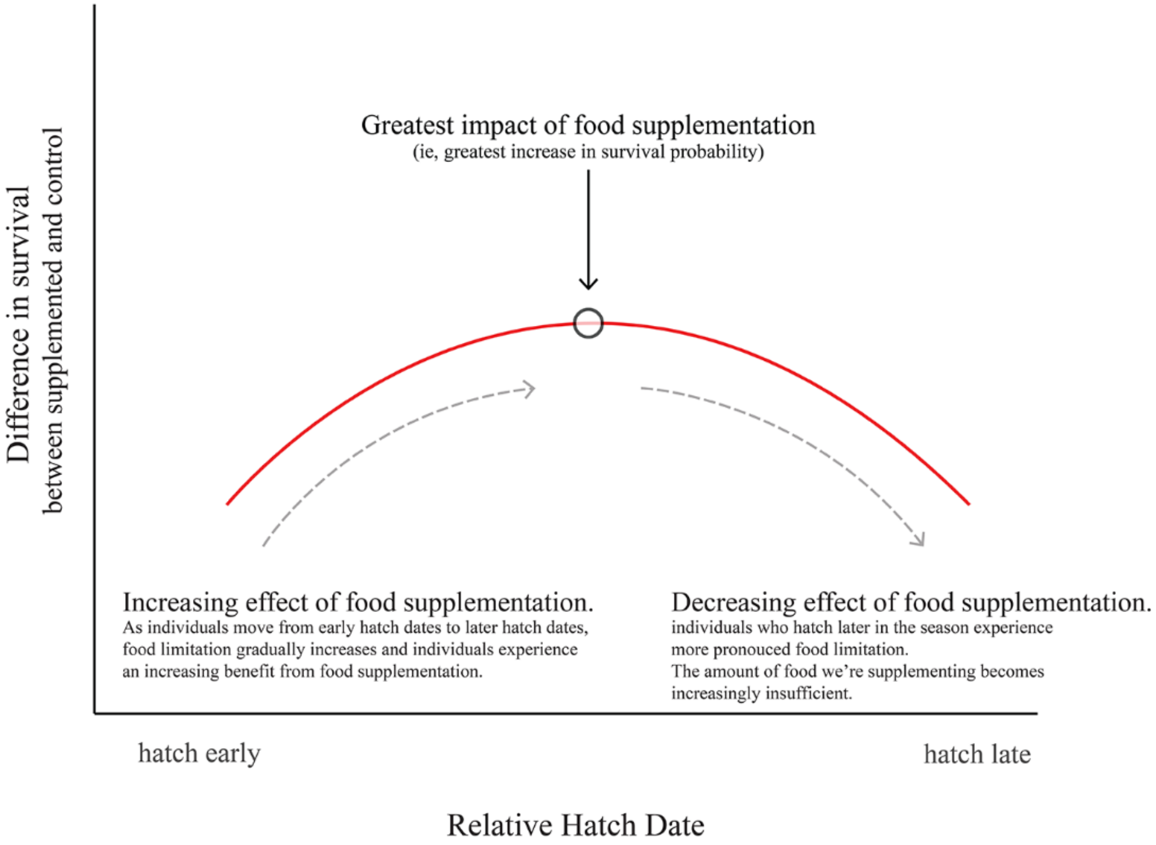

Figure 5 An illustration that explains my interpretation of how the effects of supplementation vary according to relative hatch date.

Figure 6

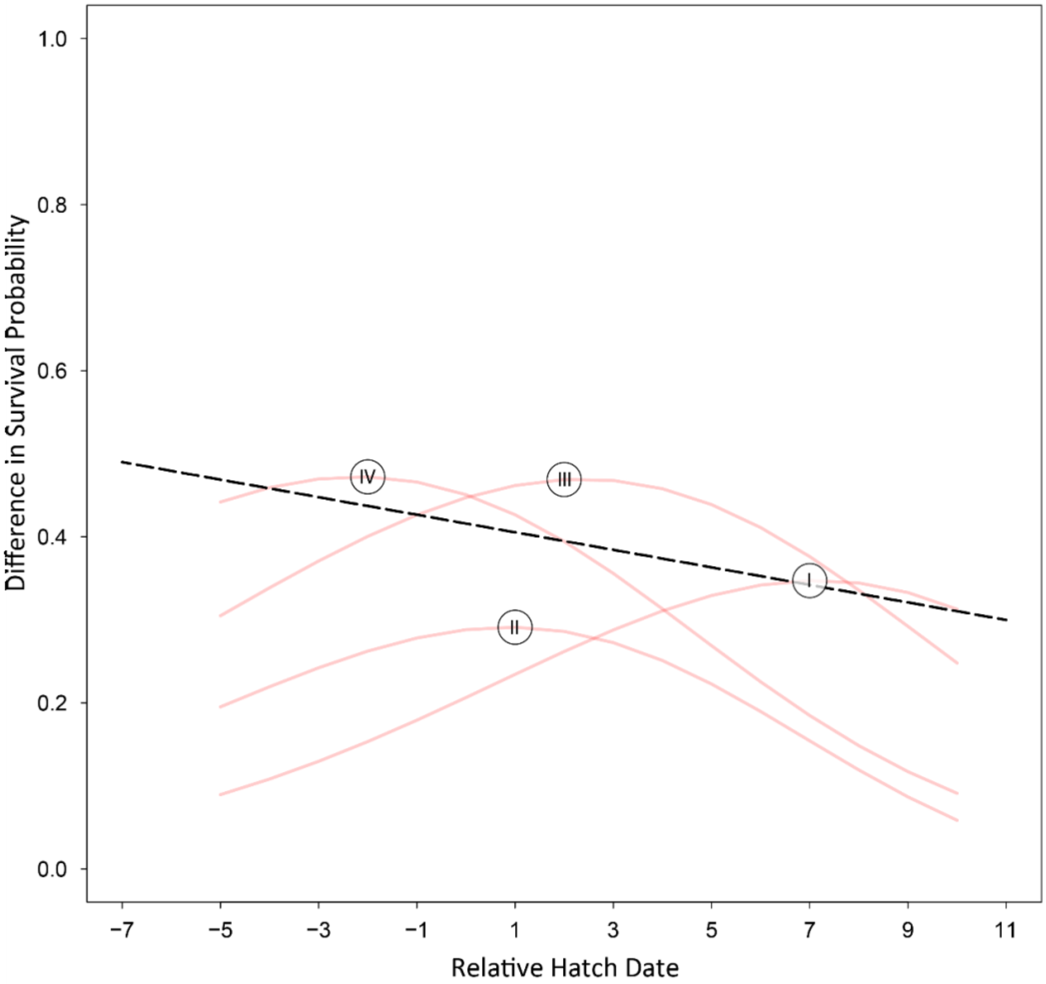

Figure 6 Difference in survival probabilities between experimental groups (supplemented - control) to illustrate how the effect of supplementation increases with hatch order (I = 1st hatch through to IV = 4th hatch), and how the maximum difference in survival probability caused by supplementation occurs at earlier hatch dates for each hatch order.

Figure 7

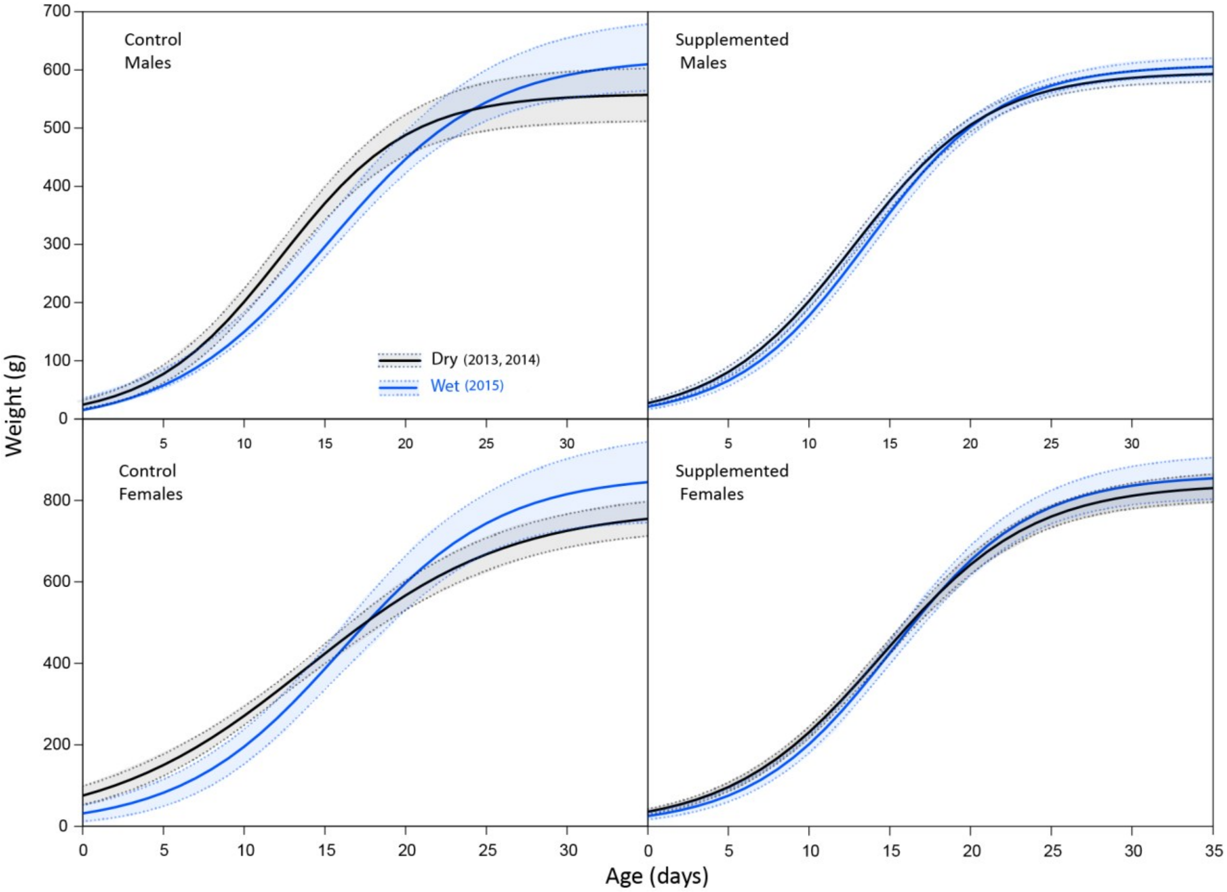

Figure 7 The growth curves for both sexes in both experimental groups, and between wet and dry years. Male growth was modeled with a brood level random effect on the asymptote, inflection, and growth rate constant, while female growth was modeled using a nestling level random effect on asymptote and inflection.