

# THE ARCTIC RAPTORS PROJECT: 2013 REPORT TO GOVERNMENT OF NUNAVUT

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## BACKGROUND

The Rankin Inlet Peregrine Falcon study population was discovered in the late 1970s, but its size and density was not appreciated until intensive surveys were conducted in 1980-81. Critical nesting habitat and an abundance of marine and terrestrial prey make the area ideal for Peregrine Falcons and other nesting predatory birds. The 455 km<sup>2</sup> study area surrounds the hamlet of Rankin Inlet (15 km radius) and contains the highest density of Peregrines in the Arctic and the second highest density ever recorded for the species (1 pair/17 km<sup>2</sup>). Though at a relatively southern latitude (62°N 92°W), environmental conditions are as, or more, severe than any encountered in the range of the species. Hudson Bay accounts for 44% of the study area and it remains frozen well after egg-laying has commenced. In the spring, cliffs are often snow-covered which may temporarily restrict the location that Peregrine Falcons choose to nest. However, ease of access makes the area ideal for studying the ecology of these birds. The entire area is accessible by snowmobile, ATV, and boat, allowing a systematic search of the thirty-six (36) known sites (four with alternates) for banded and unbanded adult birds. Climbing into nest-sites for collecting productivity data and banding of young poses few problems.

A variety of research partners and the Government of Nunavut have been involved in the project since 1981. Up to 1996, graduate students from the Universities of Alberta and Saskatchewan conducted and managed the project and the government provided field equipment and logistical support. Research projects included detailed studies of life history, pesticide contamination, diet, and a series of investigations based on individually identified (banded) birds. These studies, and on-going monitoring by the government, have produced one of the longest continuous data sets on reproductive success and contaminant burdens for nesting Peregrine Falcons

anywhere in the world. These data allow for an assessment of trends in pesticide residues from peregrines and their primary prey species over three decades. These data, combined with detailed information on Peregrine Falcon reproductive performance, have been referenced numerous times in

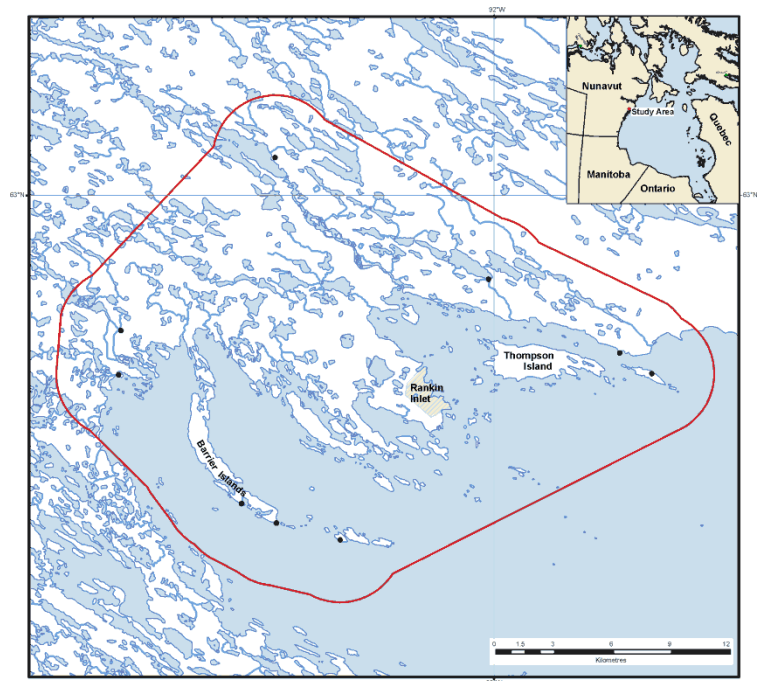


Figure 1 Rankin Inlet Study area.

research journals and status reports that provide management actions for falcons throughout North America. Additionally, data collected at Rankin Inlet has allowed immediate assessment of factors that may impact falcon populations throughout Nunavut. As such, the falcon population at Rankin Inlet is widely recognized as one of the best "indicator" populations of Peregrine Falcons in North America.

The unique, detailed, long-term data set includes demographic attributes such as the annual number of occupied territories, the number of pairs to produce young, and the total number of young fledged. Both the University of Alberta and the University of Saskatchewan were involved closely with graduate students until 1996. No monitoring was conducted in 2001. However, with funding from the Government of Nunavut (GN DoE), Department of Environment, monitoring of the population resumed in earnest in 2002 and 2003. The GN DoE contributes approximately \$20 000.00 per year to the project (or approximately 10% of the overall annual budget required to fund the project)

### Surveys for Occupancy and Reproductive Success

The Rankin Inlet study has provided unparalleled monitoring of occupancy and reproductive success on Arctic-nesting peregrine falcons in Canada (Figure 2). These measures are integral to computer population models that are used by wildlife managers to assess the viability of other falcon populations throughout the world, and have been of considerable value to wildlife managers seeking to predict the recovery of the peregrine falcon in southern Canada.

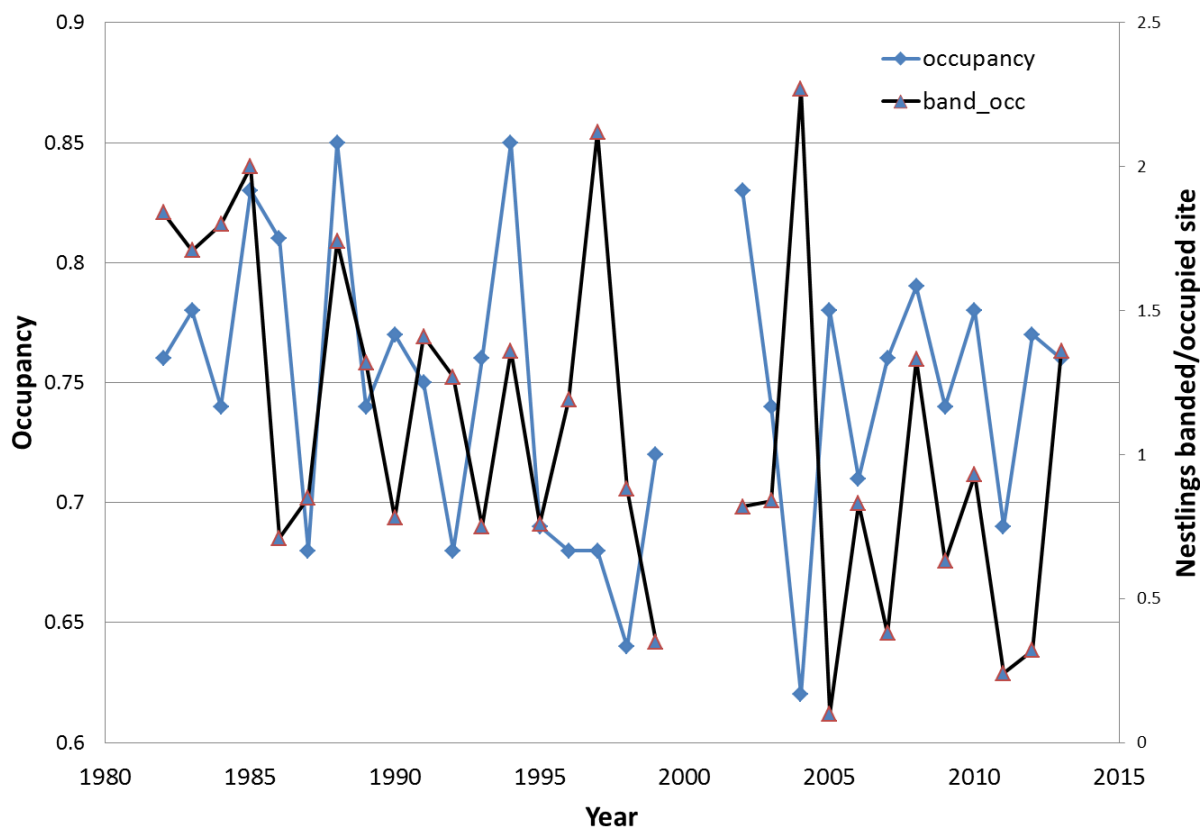


Figure 2. Occupancy and reproductive success of peregrine falcons nesting near Rankin Inlet, Nunavut from 1982 - 2013

On-going declines in productivity have been documented in Peregrine Falcons breeding near Rankin Inlet despite decreased organochlorine contamination to below levels known to cause reproductive failure (Franke et al. 2010). Using a nest box experiment Ancil et al. (2013) demonstrated that the nestlings raised in nest boxes survived the negative effects of exposure to rainfall better than those raised on natural ledges (Figure 1). More importantly, the authors found that the increase in the frequency of heavy rain over the last three decades is likely an important factor explaining the recent decline in falcon nestling survival rates, and hence the decrease in annual breeding productivity of the population. Our study is among the first experimental demonstrations of the direct link between rainfall and survival in wild birds, and clearly indicates that top arctic predators can be significantly impacted by changes in precipitation regime.

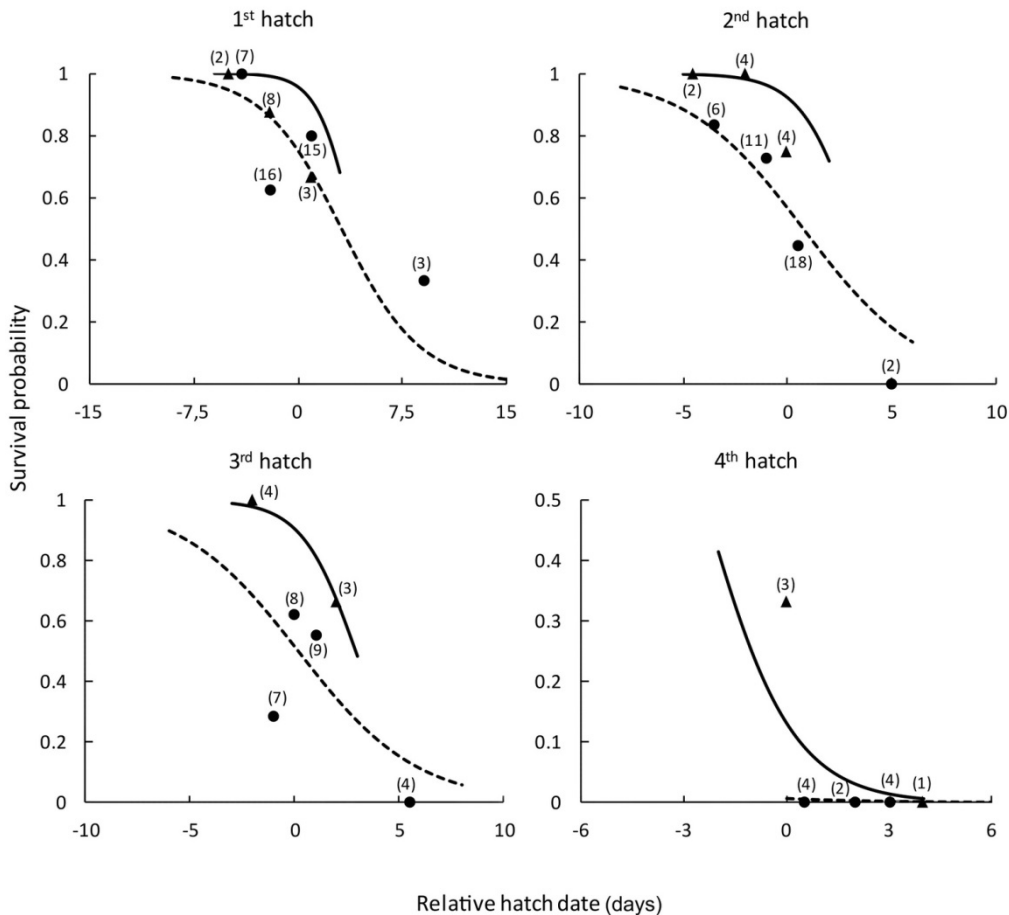


Figure 3 Survival probability of Arctic-nesting peregrine falcon nestlings up to 25 days old in relation to their relative hatch date (values standardized relative to yearly median) and within brood hatch sequence (a–d). Lines represent values of the fitted logistic regression model [nestlings sheltered in a nest box (solid line), unsheltered nestlings (dashed line)].

## Camera monitoring

We use cameras to estimate several reproductive parameters and causes of mortality. We observed a unique case of infanticide and cannibalism in Peregrine Falcons in 2011, and published a note on this in 2013. A marked adult female and unmarked adult male produced and hatched two eggs at a known and regularly monitored nest site. Motion sensitive camera images indicated that two nestlings were

attended to by the adults and were fed in a manner that resulted in growth and development typical for the nestlings produced in the study population. During a period of intense rainfall both nestlings were left unattended for several hours; both nestlings were clearly distressed and one was close to death. When the visibly wet marked adult female returned to the nest ledge, she killed and partially consumed the smaller and weaker of the two nestlings. The female flew from the nest ledge without feeding the remaining nestling and returned shortly afterward to kill and partially consume the second nestling.



### [Banding Effort](#)

A total of 93 raptors were banded in 2013; of these, 67 were peregrines (58 nestlings and nine adults), and 26 were rough-legged hawk nestlings. In addition 15 adult peregrines previously marked in the study area were recaptured, and one foreign recapture was encountered; and adult female banded in Texas in 2010.

### [New and ongoing projects](#)

Erik Hedlin, a graduate student registered at the University of Alberta conducted the first year of data collection. The overarching goal of this project is to examine the relationship between precipitation and food limitation in peregrine falcons by implementing a food supplementation experiment. Specifically we will investigate the effects of food on nestling growth and survival among years of varying precipitation, and across ecological variables such as hatch asynchrony, hatch order, and hatch date.



Vincent Lamarre completed his second field season collecting data to examine the effect of body condition on laying date. There were no issues associated with conducting field work in 2013, and no fuel was cached.

### **Peer reviewed journal articles published in 2013**

Anctil A., Franke, A., and Bêty, J. 2013. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons. *Oecologia*. DOI 10.1007/s00442-013-2800-y

L'Hérault, V., Franke, A., Lecomte, N., Alogut, A. and Bêty, J. 2013. Landscape heterogeneity drives intra-population niche variation and reproduction in an arctic top predator. *Ecology and Evolution*. doi:10.1002/ece3.675

Anctil, A. and Franke, A. 2013. Intraspecific Adoption and Double Nest Switching in Peregrine Falcons (*Falco peregrinus*). *ARCTIC*. Vol. 66 (2): 222-225

Franke, A., Galipeau, P., Nikolaiczuk. 2013. Brood Reduction by Infanticide in Peregrine Falcons. *ARCTIC*. Vol. 66 (2) : 226-229.

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Anctil, A., Franke, A. and Bety, J. 2013. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in Peregrine Falcons. -*Oecologia*.

Franke, A., Settingington, M., Court, G. and Birkholz, D. 2010. Long-term trends of persistent organochlorine pollutants, occupancy and reproductive success in Peregrine Falcons (*Falco peregrinus tundrius*) breeding near Rankin Inlet, Nunavut, Canada. -*Arctic*, 63: 442-450.

# Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons

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**Abstract** Although animal population dynamics have often been correlated with fluctuations in precipitation, causal relationships have rarely been demonstrated in wild birds. We combined nest observations with a field experiment to investigate the direct effect of rainfall on survival of peregrine falcon (*Falco peregrinus*) nestlings in the Canadian Arctic. We then used historical data to evaluate if recent changes in the precipitation regime could explain the long-term decline of falcon annual productivity. Rainfall directly caused more than one-third of the recorded nestling mortalities. Juveniles were especially affected by heavy rainstorms ( $\geq 8$  mm/day). Nestlings sheltered from rainfall by a nest box had significantly higher survival rates. We found that the increase in the frequency of heavy rain over the last three decades is likely an important factor explaining the recent decline in falcon nestling survival rates, and hence the decrease in annual breeding productivity of the population. Our study is among the first experimental demonstrations of the direct link between rainfall and survival in wild birds, and clearly indicates that top arctic predators can be significantly impacted by changes in precipitation regime.

**Keywords** Climate change · Precipitation · Breeding success · Avian predator · Survival

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## Introduction

Variation in annual breeding productivity has been shown to have considerable repercussions on animal population dynamics (Johnson and Geupel 1996; Gaillard et al. 1998). Understanding the mechanisms that influence annual reproductive success is challenging because numerous factors can interact. Trophic interactions (e.g., predation, cannibalism, competition and food availability) and anthropogenic activities (e.g., disturbance and contaminants) have been identified as potential causes of variation in breeding success in various species (Potapov 1997; Ims and Fuglei 2005; Morrissette et al. 2010). The effect of weather is also regarded as one of the key factors influencing breeding output (Steenhof et al. 1997; Moss et al. 2001), and climatic oscillations have often been correlated with population dynamics of both consumers and prey (Grindal et al. 1992; Forchhammer et al. 1998). Weather can affect individuals, and hence populations, directly (e.g., increasing thermoregulation and movement costs; Machmer and Ydenberg 1990) or indirectly through interactions with biotic and abiotic components of the ecosystem (Grant et al. 2000).

In the context of rapid climate change, weather patterns are predicted to be strongly modified (IPCC 2007). In order to assess the vulnerability of animal populations to such changes, an understanding of the nature of the mechanisms linking weather and individual breeding success is crucial. However, our knowledge of the main climatic factors affecting populations remains limited because the exact causes by which weather affects individuals have been mostly inferred rather than experimentally tested (Redpath et al. 2002; Molnár et al. 2010).

The Arctic will experience, during all four seasons, some of the most severe effects of climate change on the planet (Screen and Simmonds 2010), which will undoubtedly

affect animals inhabiting this area (Hunter et al. 2010; Ims et al. 2011). However, our knowledge of the consequences of climate change on arctic wildlife is relatively poor (Post et al. 2009) although some progress has been made in a few well-studied species [e.g., geese (Dickey et al. 2008); seabirds (Gaston et al. 2005); polar bears, *Ursus maritimus* (Stirling and Derocher 2012); lemmings (Kausrud et al. 2008)]. Moreover, some bird groups, such as raptorial species, have received much less attention than others (Møller et al. 2010).

Rain is an important component of weather that is often related to breeding success of avian species (Kostrzewa and Kostrzewa 1990; Skinner et al. 1998). Rainfall at different time periods has been associated with either increases or reductions in nest success rates (Olsen and Olsen 1989; Rodriguez and Bustamante 2003), and also with timing of breeding and duration of the breeding season (Carrillo and Gonzalez-Davila 2010). In addition, negative correlations between rainfall and nestling survival (Potapov 1997; Jovani and Tella 2004; Bionda and Brambilla 2012) have been reported. However, previous studies on this topic were correlative and, to our knowledge, experimental manipulations to clearly test for the direct effect of rainfall on nestling have not been conducted.

The main goal of this study was to investigate the direct effect of rain on nestling survival of a top avian predator of the arctic tundra, the peregrine falcon (*Falco peregrinus tundrius*), nesting in the Rankin Inlet area of the Canadian Arctic. In this population, no temporal trend in apparent survival of adults was observed over the last three decades (Franke et al. 2011), but a long-term decrease in annual productivity, despite concomitant declines in persistent organochlorine residues, has been reported [reduction of 0.65 young per territorial pair between 1982 and 1989 and 2002–2009 (Franke et al. 2010)]. Mortality of nestlings in this population is known to vary with the annual amount of rain recorded during rainstorms (Bradley et al. 1997), and a change in precipitation regime was thought to be the most likely mechanism explaining the recent decline in Arctic-nesting falcon productivity (Franke et al. 2010).

To investigate the mechanisms linking rain and falcon productivity, we used direct observations (i.e., camera monitoring) to determine the main causes of nestling mortality and we experimentally manipulated nest site (using artificial shelters) to test for the direct effects of rain on survival of nestlings. We hypothesized that nestlings that received improved shelter from rain would experience higher survival rates than those that remained unprotected. Finally, we examined historical weather data for evidence of changes in precipitation regime that could explain the observed long-term decline in annual productivity of the breeding population. This study uniquely combined direct

near real-time observations, field experimentation, long-term population monitoring data and historical weather data to better understand the vulnerability of an arctic top predator to the effects of ongoing climate change.

## Materials and methods

### Study area

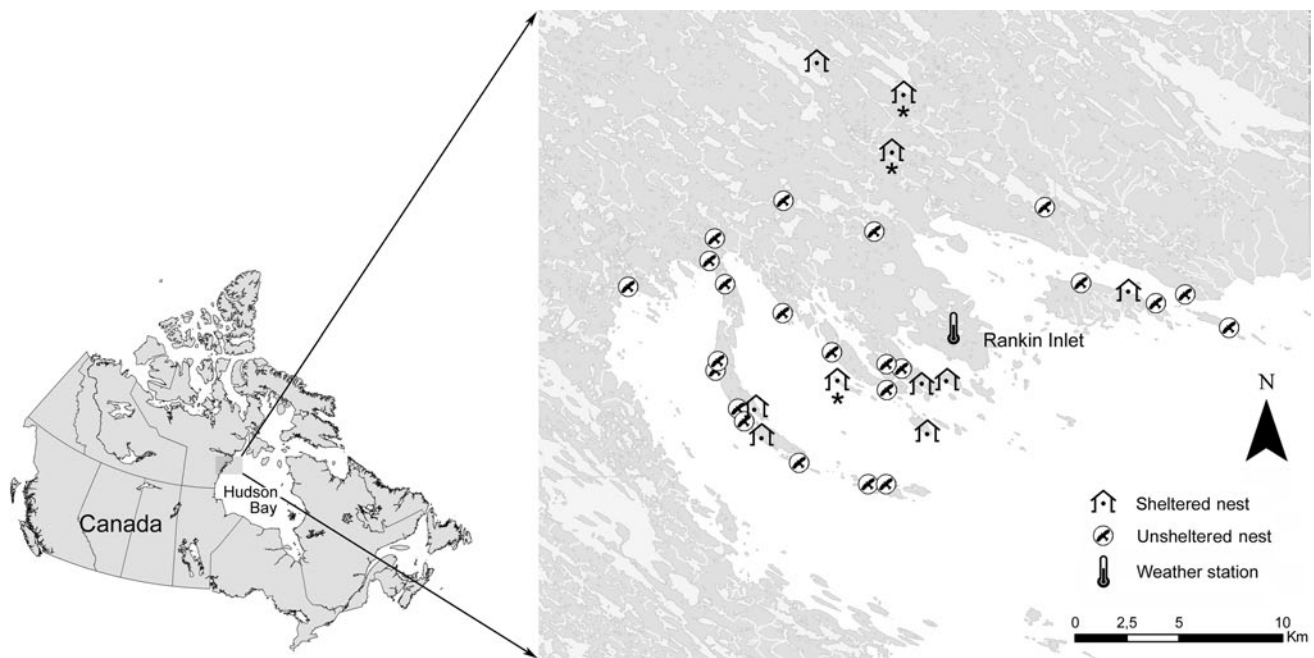
The study area is located on the west shore of Hudson Bay, near the community of Rankin Inlet (62°49'N, 92°05'W), Nunavut, Canada. Geographically, the region is typified by rolling uplands and lowlands with frequent outcrops of exposed bedrock and eskers. Freshwater lakes, ponds, and wetlands are numerous. The Hudson Bay comprises about half of the study area, and encompasses a barrier island system extending from the mainland as well as several isolated islands (Fig. 1). The peregrine falcon is a cliff-nesting species and suitable nesting sites are found through the study area on islands, along the coast and on the mainland. For more details on vegetation and geology, see Court et al. (1989).

### Study species

The peregrine falcon is a long-lived raptor with world-wide distribution (White et al. 2008). The subspecies *F. peregrinus tundrius* breeding in the Rankin Inlet area is a long-distance migrant and a generalist top predator (White et al. 2008). At peak density, the population reached 29 territorial pairs (one pair per 12 km<sup>2</sup>), making it one of the densest breeding populations recorded for the species worldwide (Franke et al. 2010). Egg laying takes place from early to late June, incubation lasts 33.5 days on average (Burnham 1983) and nestlings hatch asynchronously in July [mean hatch date typically occurs in the second week of July (Court et al. 1988)]. Nestlings are able to thermoregulate independently at approximately 21 days of age (Hovis et al. 1985) and are therefore more vulnerable to cold and wet weather in the first 3 weeks after hatching.

### Data collection

Beginning in May, as falcons arrived from their wintering grounds, territories were surveyed by snowmobile to determine the presence or absence of territorial, breeding-aged adults. All known sites (i.e., cliff or rock outcrop used by a single pair of peregrines including known alternate nest sites within a breeding territory) were checked until occupied or until the breeding season was sufficiently advanced to conclude that the site was vacant (Franke et al. 2010).



**Fig. 1** Location of the study site in the Rankin Inlet area, Nunavut, Canada. Detailed study area is shown on the *right panel*, including freshwater bodies (*light gray*), continent (*dark gray*), Hudson Bay (*white*), location of the weather station and positions of sheltered

and unsheltered nests of peregrine falcon followed during the nesting rearing period between 2008 and 2010. All sheltered nests were tracked in only 1 year except for three cases (marked with an *asterisk*) that were monitored for 2 years

### Camera monitoring

Motion sensitive cameras (RECONYX models PM35T25, PC85 and PC800 Hyperfire; 2009,  $n = 15$ ; 2010,  $n = 17$ ) were installed at a distance of 1–4 m from the nests to determine hatch date and hatch sequence of the nestlings (i.e., hatching order among siblings) during the 2009 and 2010 summers. The nestling's development stage recorded during the early brood rearing period was used to determine hatch date and hatch sequence in 2008 and for nests with no camera in 2009 and 2010 (see Cade et al. 1996). When triggered, cameras were programmed to immediately capture from one to three photographs followed by a quiet period of 5–15 s (the time period after a trigger during which the camera did not respond to motion events). In addition, cameras were programmed to collect a single time-lapse image every 15 min. Each year cameras were immediately removed from failed nests and transferred to an active nest to ensure that we monitored as many broods as possible. Over both years, nestlings  $\leq 25$  days old were monitored with cameras at 23 different nest sites (2009,  $n = 14$ ; 2010,  $n = 15$ ) for a combined total of 588 days (average = 22, minimum = 2, maximum = 28). We analyzed images from the cameras to examine feeding rate of juveniles, exposure to rainfall or other external events, to determine the causes of nestling mortality.

Based on recorded observations, we summarized the causes of mortality into one of four categories; exposure to rain, starvation, other, and unknown. Using the photographs, we analyzed daily feeding events for every nestling 0–25 days of age. We determined that healthy nestlings of <25 days old were typically fed at least three times per day. Therefore, those that were routinely fed on three or more occasions per day, but were exposed to rain (i.e., visibly wet in camera images) and died during the rainstorm were assumed to have died as a result of direct exposure to rain. Conversely, nestlings that were fed fewer than three times per day for 3 or more consecutive days and that did not die during or soon after a rainstorm were assumed to have died from starvation. Nestlings that died of known causes that were not related to rain or starvation were classified as “other” (see “Results”), while nestlings that died for reasons that remained unclear were classified as “unknown.”

### Experimental nest box manipulation

We deployed 13 (2008,  $n = 2$ ; 2009,  $n = 5$ ; 2010,  $n = 6$ ) wooden nest boxes at nest sites soon after nestlings hatched in order to shelter them from the combined effects of rain and wind during heavy rainfall events. Nest boxes of  $56 \times 56 \times 81$  cm with an opening of  $38 \times 76$  cm (see Fig. 2) were painted to resemble the nesting cliffs. Typical nesting substrate consisting of a mix of sand and gravel





**Fig. 2** Wooden nest box (56 × 56 × 81 cm) with an opening of 38 × 76 cm used to shelter peregrine falcon nestlings and test for the direct effect of rain on early survival

was added to each nest box to ensure good drainage and to provide sufficient weight to prevent shifting. Sites that received a nest box were selected randomly from those available each year. However, not all occupied nest sites were suitable for a nest box as some ledges were too small for them (2008,  $n = 4$ ; 2009,  $n = 4$ ; 2010,  $n = 3$ ). We nonetheless included these control sites in our analyses because their exclusion generated similar results.

Nest box deployment was attempted only on days when the weather conditions were mild. A shallow depression mimicking the natural scrape that is usually built and maintained by adult falcons was excavated in the substrate and the nestlings were placed into it. A small prey item was placed conspicuously at the entrance of the nest box to encourage adult falcons to return quickly to nestlings and engage in normal feeding behavior. A site that received a nest box was monitored continuously until at least one of the adults had accepted it (i.e., feeding or brooding behavior was observed). Adults usually adopted a nest box very quickly (usually in less than 10 min). However, when pairs (three of 16) failed to return to normal brooding behavior within 1.5 h, the nest box was removed. A prey item was left on the natural nest ledge when deployment of a nest box was abandoned, and the site was monitored to ensure that adults resumed normal nestling rearing behavior. No nests were abandoned following the disturbance. In August 2010, ambient temperature was recorded every 30 min inside and outside six nest boxes using temperature data loggers (Thermochron; accuracy  $\pm 1$  °C) to verify that sheltered nestlings would be exposed to similar thermal environments as unsheltered ones. Five nest boxes had a positive but weak effect on ambient temperature while one had a weak negative effect (mean difference inside vs. outside nest boxes was 0.3 °C;  $t$ -value = 15.3,  $p < 0.01$ , 95 % confidence interval = 0.27–0.35 °C).

### *Nest and weather monitoring*

We typically visited nest sites every 5–7 days, on days when weather conditions were mild. Each nestling was color marked using non-toxic, permanent markers to identify individuals. At approximately 25 days, nestlings were marked permanently using unique alphanumeric color-coded and US Fish and Wildlife Service federal bands.

Breeding productivity was calculated as the number of surviving nestlings per territorial pair. A nestling that lived 25 days was considered to have survived. We selected 25 days of age rather than fledging (average 35–40 days) because after 25 days nestlings often move several meters from the nest ledge restricting our ability to document mortality events and causes. The sex of nestlings that died at an early stage was not determined and therefore the potential effect of sex on survival was not taken into account (see “Discussion”).

Weather data recorded at the Rankin Inlet airport were downloaded from the Environment Canada (2011) website. Daily rainfall was retrieved from this meteorological station, which is situated approximately in the middle of the study area (Fig. 1).

### Data analysis

#### *Nest box experiment*

We modeled the probability of nestling survival using a generalized linear mixed effects model [logit link function in the package lme4 version 0.999375-39 (Bates et al. 2011)] in R Statistical Environment version 2.13.0 (R Development Core Team 2010). We compared survival of nestlings at sites with nest boxes to those on naturally exposed ledges (control nests with no nest box) by modeling the probability of nestling survival (binomial response, lived = 1, died = 0). Models included the variable Nest Box (1 = yes, 0 = no) as well as the covariates Hatch Date (hatch dates transformed as deviation from the median hatch date in each breeding season) and within-brood Hatch Sequence (1st hatch to 4th hatch). To account for variation in survival over time and space, Year and Site were modeled as random effects. In addition, we tested for interactions between Nest Box and Hatch Date, and between Nest Box and within-brood Hatch Sequence. Nine different combinations of these variables were tested and models were ranked based on second-order Akaike’s information criterion (AICc) to control for small sample size. Models with  $\Delta AICc < 2$  were selected (Burnham and Anderson 2001). We used model averaging to estimate parameters from the selected models to reduce bias and increase precision (Burnham and Anderson 2002).

## Precipitation

In the same study area, Bradley et al. (1997) reported that mean falcon nestling mortality was correlated with annual precipitation recorded during storms (defined as  $\geq 3$  days of consecutive rain). However, our camera data indicated that weather-related mortalities occurred during very short periods ( $< 24$  h, but sometimes within as little as 2 h when not brooded) of intense rainfall. These observations allowed us to identify days during which some nestlings died because of direct effects of rainfall. Local weather data recorded on those days indicated that 8 mm was the daily minimum amount of rain that caused mortality. We thus used this value as the “precipitation threshold” (daily minimum amount of rain) that was known to be associated with nestling mortality during our study period (hereafter referred to as “heavy rain”). As lower amounts of rain could possibly cause nestling mortality, we performed sensitivity analyses using lower threshold values to evaluate the strength of our conclusions. We calculated the number of days of heavy rain in July and August for all years of the study (i.e., 1981–2010). We used July and August because this period encompasses the 25-day time frame when nestlings are considered to be most vulnerable to weather (Hovis et al. 1985). We used linear regression to examine temporal trend in the annual number of days with heavy rain from 1981 to 2010.

We examined the relationship between the number of days with heavy rain and nestling survival using a generalized linear model. Actual number of surviving nestlings was used as the dependent variable while the total number of nestlings at hatch was used as an offset. We limited our analysis to 17 years (1982–1995 and 2008–2010) as the number of nestlings at hatch was not recorded in other years. We used a similar model to test for a temporal trend in nestling survival before and after controlling statistically for the effect of heavy rain. We also used a generalized linear model to test for temporal trends in the number of eggs laid with territorial pair as an offset, the number of nestlings at hatch with the number of eggs laid as an offset and annual breeding productivity (number of young produced) with territorial pair as an offset. Finally, we also tested for a temporal trend in annual breeding productivity after controlling statistically for the effect of heavy rain. For all analyses, data were log transformed to achieve normality (Kolmogorov–Smirnov, all  $p \geq 0.2$ ) and graphical inspection of the residuals revealed no trend.

For all analyses testing for temporal trends, we computed the Durbin–Watson statistic to test for autocorrelation problems, which could bias the parameter estimates of the regression (Box et al. 1994). However, no autocorrelation was detected for any of the tests. All analyses were done in the R Statistical Environment.

## Results

### Causes of mortality

Motion-sensitive cameras captured the death of 26 nestlings ( $< 25$  days old; 2009,  $n = 11$ ; 2010,  $n = 15$ ) from 14 broods (2009,  $n = 5$ ; 2010,  $n = 9$ ). In 2009, the resident female of a nest site vanished well into the nestling rearing period, which is a highly unusual event in our study population. Her three nestlings died a few days later after not being taken care of. The female was likely killed and although we included her nestlings’ deaths in the mortality summary, we decided to exclude this nest from all other analyses.

Overall, 38 % (10/26) of deaths were caused by the direct effect of rainfall. These mortalities occurred in 16 % of the nests (5/31) and affected one to four nestlings per nest. This includes a nestling that was knocked off of the cliff by the resident female as she flew from the nest ledge while brooding three large nestlings during a heavy rainstorm. Four nestlings (15 %) died as a result of starvation and four other (15 %) from events not related to either rain or starvation. These included the three nestlings of the female that was likely killed (see above) as well as a nestling that died shortly after being bitten and grabbed aggressively by the resident female. Finally, eight deaths (31 %) occurred due to reasons that could not be confirmed (though a combination of rainfall and starvation were suspected in four cases). Four deaths were recorded for nestlings raised in a nest box, but none were attributed to rainfall. Of these, one was killed by the female and three died of an unknown cause clearly not related to the direct effect of rain. Moreover, there were no nestling deaths attributed to predation in either sheltered or unsheltered nests.

### Nest box experiment

Over 3 years (2008–2010), we followed 34 nestlings from 13 broods raised in nest boxes and 117 nestlings from 41 broods raised on natural ledges. We found strong evidence for an effect of hatch date on nestling survival (Table 1; Fig. 3). Nestlings that hatched later in the season had much lower survival than those that hatched earlier. For example, the survival probability of the first-hatched nestlings not raised in a nest box was on average 97 % lower in late-hatched chicks relative to those hatched 24 days earlier (Fig. 3). Within a given brood, nestlings that hatched first, second or third had similar survival probability. However, young that hatched fourth experienced lower survival than first-hatched nestlings (Table 1; Fig. 3).

After controlling for the effect of hatch date and within-brood hatch sequence, nest boxes had a positive influence on survival (Table 1; Fig. 3). We also found some evidence

**Table 1** Variables, number of parameters (*k*), second-order Akaike's information criterion (*AICc*),  $\Delta AICc$ , *AICc* weight (*AICcWt*) and log-likelihood (*LL*) of the candidate models explaining peregrine fal-

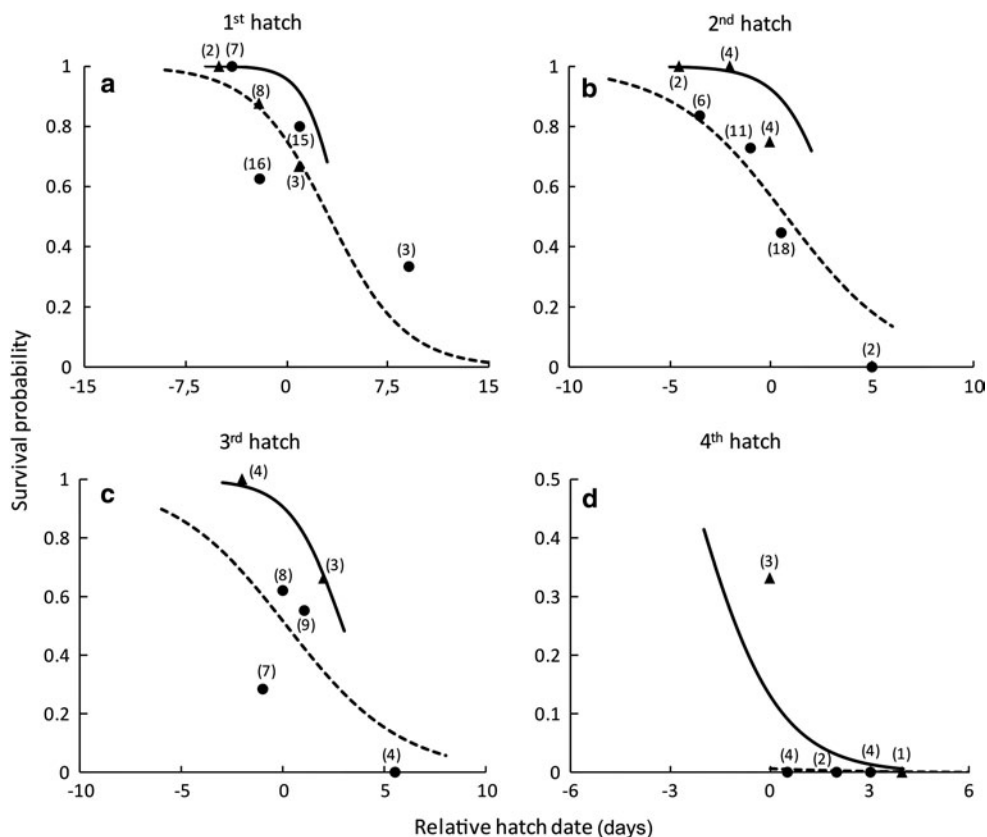
con nestling survival, and model-averaged parameter estimates from the two most parsimonious models, unconditional SE and 95 % confidence intervals (*CI*; lower CI and upper CI)

Selected models							
Variables	<i>k</i>	<i>AICc</i>	$\Delta AICc$	<i>AICcWt</i>			<i>LL</i>
Nest box, Hatch date, Hatch sequence	8	160.93	0.00	0.51			-71.96
Nest box, Hatch date, Hatch sequence, Hatch date $\times$ Nest box	9	161.97	1.04	0.30			-71.35
Nest box, Hatch date, Hatch sequence, Hatch date $\times$ Nest box, Hatch sequence $\times$ Nest box	12	164.28	3.35	0.10			-69.01
Nest box, Hatch date, Hatch sequence, Hatch sequence $\times$ Nest box	11	165.68	4.75	0.05			-70.89
Nest box, Hatch sequence	7	166.51	5.58	0.03			-75.86
Hatch date, Hatch sequence	7	169.27	8.34	0.01			-77.24
Hatch sequence	6	176.16	15.23	0.00			-81.79
Hatch date, Nest box	5	176.81	15.88	0.00			-83.20
Hatch date	4	178.85	17.82	0.00			-85.24
Parameters	Nest box	Hatch date	Second hatch	Third hatch	Fourth hatch	Hatch date $\times$ Nest box	Intercept
B	2.45	-0.35	-0.84	-1.08	-5.77	-0.42	0.96
SE	0.98	0.13	0.56	0.63	1.73	0.42	0.54
Lower CI	0.54	-0.61	-1.94	-2.31	-9.15	-1.25	-0.10
Upper CI	4.36	-0.10	0.26	0.14	-2.38	0.41	2.02

A random effect of Year and Site is included in all models

*Nest box* presence or absence of a nest box, *Hatch date* value relative to the annual mean hatch date, *Hatch sequence* within-brood hatch order (1st, 2nd, 3rd and 4th; 1st hatch is included in the intercept), *Hatch date*  $\times$  *Nest box* interaction between the hatch date and the presence of a nest box

**Fig. 3** Survival probability of Arctic-nesting peregrine falcon nestlings up to 25 days old in relation to their relative hatch date (values are standardized relative to the yearly median) and within-brood hatch sequence (a-d). Lines represent values of the fitted logistic regression model [nestlings sheltered in a nest box (solid line), unsheltered nestlings (dashed line)]. Values were obtained using the average random effect calculated for each hatching position, with or without shelter, separately. To illustrate the adequacy of the model, each point represents the proportion of surviving nestlings grouped by similar hatch date [sample size is shown near each point; sheltered nestlings (triangles), unsheltered nestlings (circles)]



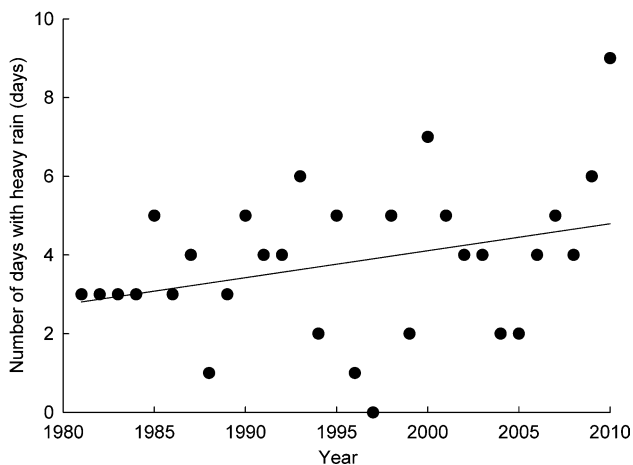
(second-best model) that the positive effect of a nest box was reduced in nestlings that hatched relatively late in the breeding season (Table 1).

### Precipitation

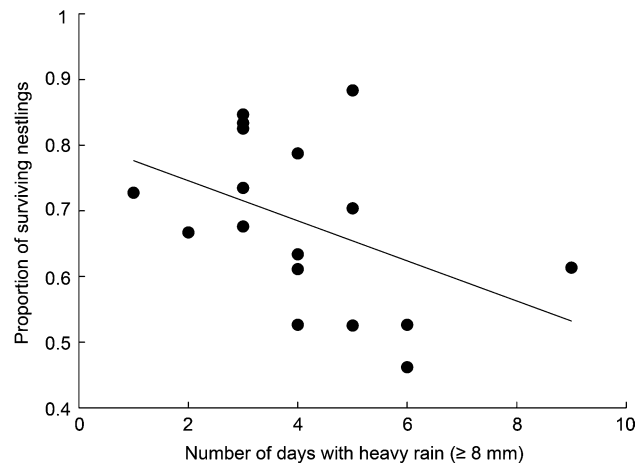
Using scouting cameras, we detected mortality as a result of the direct effects of rain (see above) on four distinct rain events (2009,  $n = 2$ ; 2010,  $n = 2$ ). The frequency of heavy rain events has shown an increasing trend from 1981 to 2010 ( $\beta = 0.07$ ; similar trends were found with thresholds of 5–7 mm of rain,  $\beta = 0.08$ – $0.12$ ). Overall, about 2 additional days of heavy rain were recorded in recent years compared to the early 1980s (Fig. 4). For the period 1981–2010, the annual rainfall recorded for July and August showed an increasing trend of about 3.1 mm per decade. The mean daily temperature recorded in July and August was 10.1 °C and also showed an increasing trend ( $\beta = 0.055$  °C/year).

Nestling survival during the study period tended to be lower in years with more days with heavy rain ( $\beta = -0.03$ , SE = 0.02,  $p = 0.08$ ,  $R^2 = 0.19$ ,  $n = 17$ ; Fig. 5; similar trends and slightly better fit were found with critical daily thresholds of 5–7 mm of rain,  $\beta = -0.02$  to  $-0.03$ , SE = 0.01,  $p = 0.02$ – $0.05$ ,  $R^2 = 0.23$ – $0.32$ ). No significant relationship was found when we used the total annual amount of precipitation recorded during the nestling rearing period ( $\beta = -0.001$ , SE = 0.0008,  $p = 0.19$ ,  $R^2 = 0.11$ ).

We found a long-term temporal decrease in nestling survival ( $\beta = -0.013$ , SE = 0.005,  $p = 0.01$ ,  $n = 17$  years). However, this trend was no longer statistically significant ( $\beta = -0.011$ , SE = 0.006,  $p = 0.10$ ) after controlling for the effect of frequency of heavy rain (i.e., by using the variable year and number of days with heavy rain in the same



**Fig. 4** Number of days with heavy rain ( $\geq 8$  mm/day) recorded by the Rankin Inlet airport weather station in July and August between 1981 and 2010



**Fig. 5** Relationship between the number of days with heavy rain ( $\geq 8$  mm/day) recorded in July and August, and the proportion of peregrine falcon nestlings surviving up to 25 days old in the Rankin Inlet area (1982–1995 and 2008–2010). To illustrate the adequacy of the regression model (line), we show the annual proportion of surviving nestlings (points). The annual number of nestlings at hatch varied from 26 to 77 (mean 44)

model). This suggests that the temporal decline in nestling survival partly resulted from the increase in the frequency of heavy rain in recent years. Using the same 17 years of data, we found no temporal trend in the number of eggs laid per territorial pair ( $\beta = -0.004$ , SE = 0.004,  $p = 0.34$ ) or in the number of nestling at hatch per egg laid ( $\beta = -0.01$ , SE = 0.007,  $p = 0.12$ ), but a temporal decrease in annual breeding productivity was found ( $\beta = -0.03$ , SE = 0.01,  $p = 0.01$ ). However, this negative trend was no longer significant ( $\beta = -0.02$ , SE = 0.01,  $p = 0.19$ ) after controlling statistically for the effect of heavy rain.

### Discussion

Although the greatest impacts of climate change are expected to occur in the Arctic (Screen and Simmonds 2010), little is known about the mechanisms linking weather to reproduction and survival of most Arctic-breeding species (but see Dickey et al. 2008; Kausrud et al. 2008; Stien et al. 2012; Stirling and Derocher 2012). This is especially true for arctic predators, which are seldom studied. The direct effects of weather have long been suspected to influence early survival in northern wildlife (e.g., Stirling and Smith 2004; Mallory et al. 2009). In peregrine falcons, rainfall has previously been identified as a potential driver of nestling mortality (Ratcliffe 1984; Mearns and Newton 1988; Olsen and Olsen 1989). Using a short-term experiment combined with camera-recorded observations and a long-term database, we found that the direct effect of rain accounted for a high proportion of falcon nestling



mortalities in an Arctic-breeding population. Despite a relatively small sample size, our field experiment showed that protecting nestlings from direct exposure to rainfall significantly increased their survival. In addition, we found strong evidence for the link between the increase in the frequency of heavy rain and the long-term decline in annual reproductive success of the study falcon population. In this regard, our detailed study provides crucial information in the assessment of the vulnerability of a top arctic predator to climate change.

The lower survival rate of nestlings exposed to heavy rain compared to those that were sheltered is, to our knowledge, the first experimental demonstration of the causal mechanism linking precipitation and nestling survival. Although nest boxes likely sheltered nestlings from a combined effect of rain and wind, no deaths were attributed to wind alone, while some deaths attributed to rain occurred on days with relatively slow wind speed. This suggests that, although wind likely increases the effect of rain, protection from rainfall is the main reason explaining increased survival in sheltered nestlings. During heavy rain events, cameras recorded unsheltered nestlings often getting wet unless very well protected by the parent. Indeed, parents can brood their young for several hours, but camera data showed that even short absences can lead to nestling mortality. Wet downy feathers lose their insulation properties and therefore heat loss increases rapidly (Nye 1964). On the other hand, sheltered nestlings remained dry most of the time even in the absence of an adult. In such cases, siblings would huddle together to conserve heat.

Although the sex of an individual can influence survival in dimorphic species (Roskaft and Slagsvold 1985), we did not include this variable in our analyses as individuals that died at an early age could not be sexed using external cues. However, we are confident that it did not generate a bias in our study as we deployed the nest boxes randomly (and hence the sex ratio after hatch was likely similar between treatments). Moreover, sex-biased mortality is often due to a difference in food requirement (Roskaft and Slagsvold 1985) and our study was limited to the first 25 days after hatch, a period during which males and females have similar feeding rates (Boulet et al. 2001).

The effect of hatch date on nestling survival was much stronger than that reported in most bird studies (e.g., Dawson and Clark 1996; Riley et al. 1998), but was similar to that for some other Arctic-breeding species experiencing sharp seasonal changes in environmental conditions (Lindholm et al. 1994). In birds breeding in northern environments, hatching synchrony is important due to a seasonal peak in food abundance (Visser et al. 1998; McKinnon et al. 2012). A decline in food supply throughout the season has been shown to be one of the main factors reducing growth and survival in late-hatched nestlings in other

species (Daan et al. 1988; Brinkhof and Cavé 1997). Although this remains untested, we suggest that a seasonal decline in prey availability and vulnerability is likely the main factor explaining decreased survival of late-hatched falcon nestlings. Assuming adults initiate a clutch as soon as possible in the spring to avoid the cost of a delay (Rowe et al. 1994), they may face important trade-offs when selecting nest sites. Indeed, sites that offer the best sheltering capacity (e.g., caves and recesses) are present in the study area, but often remain packed with snow and are unavailable in early spring (A. Franke, personal observations). Falcons may then prefer to select sites well exposed to solar radiation and hence available in early spring, leaving nestlings more vulnerable to direct effect of rainfall during the brood-rearing period. This pattern is not unique to the study population and was observed in areas characterized by lower nest densities (A. Ancil and A. Franke, unpublished data), indicating that intra-specific competition is likely not the driving force explaining the use of unsheltered sites by most breeding birds.

Our results strongly suggest that the frequency of heavy rain has a much greater impact on nestling survival than the total amount of precipitation recorded during the rearing period. The latter parameter is, however, typically used in most ecological studies (e.g., Bradley et al. 1997; Lehikoinen et al. 2009). In our study system, direct observations showed that fatalities can occur in less than 2 h of heavy rain. The long-term precipitation data for our study site are consistent with the increase in extreme precipitation events noted in climate studies (e.g., Stone et al. 2000; Groisman et al. 2005) and it is predicted that the frequency of rainstorm events will continue to increase at a rapid pace, especially in the Arctic (Min et al. 2011). The negative effect of rainstorms on annual breeding productivity of Arctic-nesting falcons is therefore predicted to increase. However, a periodic boom in productivity due to a low frequency of heavy rain in a given year could allow population maintenance of a long-lived species like the peregrine falcon. Furthermore, although the direct effects of heavy rain explained an important proportion of the annual variation in nestling survival at our study site, other environmental factors, such as food availability (Potapov 1997; González et al. 2006), could strongly affect breeding success. Heavy rain could also interact with other factors and indirectly drive breeding productivity. Overall, the consequences of environmental change on population dynamics remain unknown and merit further study. Moreover, in order to better assess the impact of these changes at the regional and global scale, it would be important to understand the spatial variability in the vulnerability of falcons by conducting studies at other locations across their distribution range.

Birds and mammals have evolved powerful mechanisms to maintain their body temperature to avoid mortality (Hillenius

and Ruben 2004). Hence, indirect effects of weather (i.e., through the food chain) are likely to play a larger role on their population dynamics than direct effects of weather (Berteaux and Stenseth 2006). However, young of many species are unable to maintain their body temperature (Evans 1984; MacArthur and Humphries 1999). Some species (e.g., cavity nesters, denning species and species that build elaborate nest structures) guard against inclement weather during their early stages of life and therefore might be expected to experience mainly the indirect effects of poor weather. Conversely, the young of other species that rely solely on parental brooding and chick huddling to maintain body temperature (Kirkley and Gessaman 1990), such as peregrine falcons, are much more likely to experience the direct effects of weather, especially during the critical period following birth. Variability in juvenile survival of long-lived vertebrates can play an important role in population dynamics (Gaillard et al. 1998). Hence, in species like the peregrine falcon, where rainfall can directly affect nestling survival, rapid changes in the precipitation regime could increase the vulnerability of the population. However, because long-lived species have delayed sexual maturity, the effects of climate change via reduced recruitment, if any, are unlikely to be noticed immediately due to a time-lag delay (Thompson and Ollason 2001).

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## Landscape heterogeneity drives intra-population niche variation and reproduction in an arctic top predator

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### Keywords

Arctic top predator, central place forager, intra-population niche variation, landscape heterogeneity, peregrine falcon, reproductive success.

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### Abstract

While intra-population variability in resource use is ubiquitous, little is known of how this measure of niche diversity varies in space and its role in population dynamics. Here we examined how heterogeneous breeding environments can structure intra-population niche variation in both resource use and reproductive output. We investigated intra-population niche variation in the Arctic tundra ecosystem, studying peregrine falcon (*Falco peregrinus tundrius*, White) breeding within a terrestrial-marine gradient near Rankin Inlet, Nunavut, Canada. Using stable isotope analysis, we found that intra-population niches varied at the individual level; we examined within-nest and among-nest variation, though only the latter varied along the terrestrial-marine gradient (i.e., increased among-nest variability among birds nesting within the marine environment, indicating higher degree of specialization). Terrestrial prey species (small herbivores and insectivores) were consumed by virtually all falcons. Falcons nesting within the marine environment made use of marine prey (sea birds), but depended heavily on terrestrial prey (up to 90% of the diet). Using 28-years of peregrine falcon nesting data, we found a positive relationship between the proportion of terrestrial habitat surrounding nest sites and annual nestling production, but no relationship with the likelihood of successfully rearing at least one nestling reaching 25 days old. Annually, successful inland breeders raised 0.47 more young on average compared to offshore breeders, which yields potential fitness consequences for this long-living species. The analyses of niche and reproductive success suggest a potential breeding cost for accessing distant terrestrial prey, perhaps due to additional traveling costs, for those individuals with marine nest site locations. Our study indicates how landscape heterogeneity can generate proximate (niche variation) and ultimate (reproduction) consequences on a population of generalist predator. We also show that within-individual and among-individual variation are not mutually exclusive, but can simultaneously arise and structure intra-population niche variation.

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## Introduction

Intra-population variability in resource use is ubiquitous and several empirical studies identified among-individual niche variation as a main driver (reviewed in Bolnick et al. 2003). A recent study further showed that decoupled variation in population and individual niches could also arise via increased within-individual variation under conditions of ecological release from competition (Bolnick et al. 2010). Prior studies have highlighted the tendency for top predators to exhibit niche variation, and also their sensitivity to variation in prey abundance (Urton and Hobson 2005; Matich et al. 2011; Dalerum et al. 2012). To help cope with uncertainty, predator species commonly use a cocktail of resources coming from various ecosystems, a factor contributing to niche expansion (Ben-David et al. 1998; Rose and Polis 1998; Restani et al. 2000; Tarroux et al. 2012). Along with this resource subsidization, several factors (biological, ecological or environmental) can interact to shape niche variation (Bolnick et al. 2003; Svanback and Bolnick 2007; Tinker et al. 2008). For example, Darimont et al. (2009) demonstrated that grey wolves (*Canis lupus* Linnaeus) inhabiting different landscapes in a large-scale coastal gradient had increased their niche width through both a surge in consumption of marine-based subsidies and release from inter-specific competition.

Beyond niche variation and its causal mechanisms, few studies have addressed the links between individual niche variation and demographic processes such as reproductive performance (but see Annett and Pierotti 1999; Golet et al. 2000; Votier et al. 2004). Recent work of Giroux et al. (2012) provided evidence that differences in resource abundance within a heterogeneous landscape can influence both resource use and reproduction probability in a generalist predator, the arctic fox (*Vulpes lagopus* Linnaeus). Their study pointed out the importance of fine scale investigation using both spatial and behavioural perspectives to understand consumers' variation in trophic niche and reproductive output (Giroux et al. 2012).

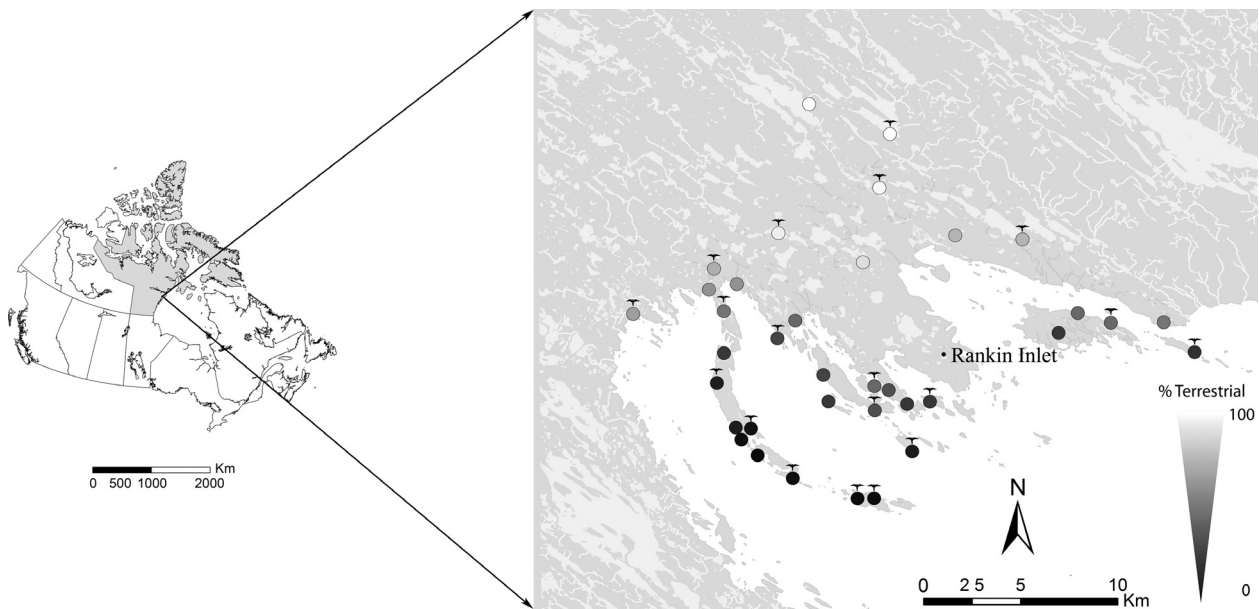
On the northwestern end of Hudson Bay near the community of Rankin Inlet (Nunavut, Canada) an extensive monitoring program of a top predator, the peregrine falcon *Falco peregrinus tundrius* White, has been ongoing since 1982 (Court et al. 1988; Franke et al. 2011) (Fig. 1). Initially launched to study contamination levels of dichloro-diphenyl-trichloroethane (DTT) after the peregrine falcon was listed as a threatened species under the Canadian *Species at Risk Act* (Cooper and Beauchesne 2007), this program provides long-term monitoring of breeding success and short-term sampling of resource use, an avian parallel to what was done on arctic foxes by Giroux et al. (2012). The multi-species diet of the arctic-breeding pere-



**Figure 1.** Male peregrine falcon (*Falco peregrinus tundrius*) standing next to his nest on the mainland at the beginning of the nestling rearing period (July) in summer 2008 near Rankin Inlet, Nunavut, Canada.

grine falcon (Cade 1960; Hunter et al. 1988; Rosenfield et al. 1995) makes it an ideal study species for examining niche variation. Compared with their southern counterparts which rely on a bird prey base (Ratcliffe 1980; White et al. 2008), peregrine falcons nesting in the Arctic are regularly observed using mammalian prey species (lemmings -*Lemmus trimucronatus* and *Dicrostonyx groenlandicus* Traill- and ground squirrel *Spermophilus paryii* Richardson) and this behaviour may bear consequences on demographic processes (e.g., lemmings spp.; Court et al. 1988; Bradley and Oliphant 1991 in the Canadian Arctic, Lecomte, A. Sokolov and V. Sokolov, pers. comm., in the Russian Arctic).

Our study was conducted at the junction of the tundra and marine ecosystems, with a mosaic of mixed terrestrial and marine habitat. During the breeding season, the peregrine falcon population is distributed along an environmental gradient (<20 linear kilometers), which provides a unique opportunity to gain insight into how ecological patterns (i.e., intra-population niche variation and reproduction) change relative to environmental factors (Keddy 1991). The landscape heterogeneity generated among-individual variation in the type of the habitat available around nest sites, which varied from terrestrially dominated rock outcrops, to cliffs on small islands surrounded by sea (Figs. 1, 2). Because peregrine falcons stay near their nest and behave as central place foragers (Orians and Pearson 1979), foraging costs for breeding adults may be proportional to the distance between breeding and foraging sites. As a consequence, resource use and reproductive success in peregrine falcons could vary according to the type of habitat (i.e., terrestrial *versus* marine) locally available around nest sites (hereafter; heterogeneity of the breeding environment), if individuals experience different foraging costs along the environmental gradient.



**Figure 2.** Location of the peregrine falcon study area near Rankin Inlet, Nunavut, Canada. The enlargement shows the study area with the mainland (shaded gray) and marine (blank) habitats. Circles represent breeding sites ( $n = 36$ ; 1982–1999, 2002–2010) and bird symbols above circles highlight falcon breeding sites ( $n = 19$ ) that were successful in raising offspring up to 25 days old in 2008. The intensity of gray shading within circles is proportional to the amount of terrestrial habitat within the falcon's pseudo home range (PHR), from black (0%) to white (100%; see Materials and Methods for details).

The main objectives of our study were to determine the influences of the heterogeneity of the breeding environment (1) on intra-population niche variation (i.e., within-individual variation and among-individual niche variation) and (2) on individual resource use and annual reproductive success of a generalist predator. We predicted that the use of terrestrial prey would be the greatest by peregrine falcons nesting within or near to the mainland habitat and would decrease with increasing distance between nest sites and the mainland. We also predicted that the annual reproductive success of peregrine falcons would be inversely proportional to the availability of terrestrial habitat within their nest neighbourhood. We examined our predictions using stable isotope sampling (Layman et al. 2012) and long-term monitoring of breeding performance.

## Materials and Methods

### Study area

Our work was conducted near the community of Rankin Inlet, on the western coast of Hudson Bay, Nunavut, Canada ( $62^{\circ}49'N$ ,  $92^{\circ}05'W$ ; Fig. 2). Our study area encompassed  $349 \text{ km}^2$ , shared between the terrestrial tundra (mainland) and marine ecosystems. The inland tundra is composed of low rolling hills with mesic tundra

interspersed with wetlands, while the marine ecosystem includes numerous inner and outer islands covered by mesic tundra (Fig. 2). Rocky outcrops and cliffs are prominent features and attract breeding raptors. Outcrops large enough for falcon nests occur up to 9 km inland and on islands up to 4 km from the coastline. Average peregrine falcon nest site density in the study area is one nest per  $8.73 \text{ km}^2$  (A. Franke, M. Bradley, G. S. Court, C. Hotson, N. Lecomte and M. Settingington, unpubl. data). The terrestrial fauna found in the study area is typical of the low arctic tundra (Callaghan et al. 2004); see Appendix 1.

### Study design: quantifying the heterogeneity of the breeding environment

To assess whether the heterogeneity of the breeding environment influenced the diet of nestling falcons and adult reproductive success for nestling rearing falcons (mid July to late August), we first calculated a pseudo home range for each pair of breeding falcon by buffering each nest with a 5 km radius circle (Hunter et al. 1988; Byholm et al. 2007). Five kilometers was selected because it is within the typical range of foraging distance for breeding peregrine falcon observed in other studies (A. Franke, M. Prostor, V. L'Hérault and J. Bety, unpubl. data). Secondly, we characterized these pseudo home ranges by cal-

culating the proportion of terrestrial (mainland plus islands) to marine (sea water) habitat present within the 5 km buffer using ArcGIS 9.2 software (ESRI, Redlands, CA). We then used the pseudo home range of the nests distributed along the terrestrial-marine continuum and isotopic ratios of nestlings to assess relationships between habitat, diet heterogeneity and the production of young, as a measure of adult reproductive success.

### Peregrine falcon monitoring and prey sampling

During the breeding seasons from 1982 to 2010 (except 2000 and 2001; no data available), we monitored peregrine falcon nests across the study area and recorded the number of young produced. During the 28 years of monitoring, all active falcon nests within the study area were visited at least once to count and band nestlings when they were approximately 25 days old, prior to their fledging age (~35–40 days old; Ratcliffe 1980). We classified a nest as successful if at least one nestling reached 25 days old (banding age). Additionally between 1982 to 1995, and 2008 to 2010, we systematically recorded breeding activities from laying to fledging; this provided a more detailed description of breeding parameters including clutch size and number of young hatched.

During the summer of 2008, we monitored nestling diet at all active nests, starting 14 days after hatch date (mid-July) until nest departure around mid August (Appendix 3). To capture diet variation over the course of this nestling period we used stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of blood plasma to track nutrients consumed and assimilated over a very fine temporal window (weekly) (Hobson and Clark 1993) (Appendix 3). We collected blood samples (1 mL) from the ulnar vein every 5–12 days ( $7.7 \pm 1.6$  standard deviation [SD] days) from 50 nestlings at 20 nests ( $1.8 \pm 1.3$  SD nestlings per breeding nest). We obtained an average of  $2.5 \pm 0.7$  SD (range 1–3) blood measurements per nestling throughout the nestling period. Blood samples were sealed, stored in heparin in the field and centrifuged within 8 h of collection to separate plasma from red blood cells. All samples were stored frozen until further analysis (see below).

During the falcon nestling period, we opportunistically collected 86 specimens from 13 prey species in the study area (Appendix 2). The selection of prey items was based on previous years' observations made during the nestling period via analyses of prey remains (Court *et al.* 1988) and from information collected by scouting cameras placed at nests ( $n = 5$  evenly distributed within the environmental gradient; unpubl. data). Muscle samples were extracted from prey items and stored in 70% ethanol prior to analyses (Ehrich *et al.* 2010).

### Stable isotope analyses

To reconstruct the diet of the peregrine falcon nestlings, we first measured the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of nestlings' plasma and prey muscle samples. After initial preparation including lipid extraction of prey samples (see details in Appendix 4), we determined isotope signatures using a continuous flow Finnigan Mat Delta Plus isotope ratio mass spectrometer at Stable Isotopes in Nature Laboratory (SINLAB), University of New Brunswick, Canada. Stable isotope ratios are expressed as parts per thousand (‰) deviations from standards, namely Pee Dee Belemnite for C and atmospheric air for N (Appendix 4).

### Data analyses

All analyses were run using packages written for the R 2.12 software (R Development Core Team 2012).

### Intra-population niche variation

To investigate whether the heterogeneity of the breeding environment influenced within-individual and among-individual niche variation in falcons, we correlated the proportion of terrestrial habitat within the falcon's pseudo home range with two metrics, (1) the "mean within-nest distance" and (2) the "mean among-nest distance" calculated from the relative positioning of nestlings in the  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plot (Appendix 5) (Layman *et al.* 2007; Turner *et al.* 2010). We measured niche variation at the scale of the nest. This is a proxy of individual niche variation because the siblings from a single nest are all fed by the same individuals (parents) (Ratcliffe 1980).

We refer to the "niche" and "ecological specialization" concepts following the framework developed by Poisot *et al.* (2011). Individuals with higher degree of specialization are those for which the niche is substantially narrower than the population niche (Bolnick *et al.* 2003). The mean within-nest distance is positively correlated to individual generalization (greater within-nest distance reflects a larger individual niche width) and mean among-nest distance is positively correlated to individual specialization (greater among-nest distance reflects individual spread apart within the population niche). Because the metrics were calculated from data collected during the rearing season using short-term diet trackers, they represent niche variation for this particular time frame (from mid-July to mid-August).

We calculated the two metrics by first computing the centroid of each nest (a point representing the average position of siblings in the isotopic space) and then calculating the Euclidean distance between this nest centroid and the relative position of each sibling (mean



within-nest distance) or the relative position of the other nest centroids (mean among-nest distance; see Appendix 5 for an example) (Layman *et al.* 2007). In order to track the differences in among-nest variation along the environmental gradient (terrestrial to marine), we measured the Euclidean distances between a nest and the five nests with the closest values for the variable “proportion of terrestrial habitat within the falcon pseudo home range” (habitat neighbours). Calculating the mean distance among five neighbouring nests, rather than more or less, balanced both a minimal level of replication and discrimination of the among-nest variation along the environmental gradient. For instance, the mean distance calculated out of 4, or six neighbours, would lead to either insufficient replication or low discrimination; see Appendix 6 for a sensibility analysis using linear regression models.

## Diet

We used Stable Isotope Analysis in R (SIAR; Parnell *et al.* 2010) to reconstruct the diet of peregrine falcon nestlings. Our aim was to investigate the relative importance of terrestrial versus marine prey source for peregrine falcon nestlings across the terrestrial/marine continuum. Isotopic signatures of peregrine falcon nestlings sampled in 2008 were then modeled with respect to the nest they belonged to ( $n = 19$ ) so that the reconstructed diet could be compared according to the variable “proportion of terrestrial habitat within falcon’s pseudo home range.” Because we worked with a large number of potential sources (13 prey species, Appendix 2) and only two isotopic tracers, we used a multivariate analysis of variance (MANOVA) (tested for the two assumptions of normality of the distribution and homogeneity of the variance) to determine whether isotopic ratios of different prey sources were sufficiently clustered to be pooled together (Phillips and Koch 2002). We then pooled prey species to three distinct types: terrestrial herbivores (three species), terrestrial insectivores (seven species) and marine birds (three species) (MANOVA, Wilks’ Lambda:  $F_{2,83} = 149.9$ ,  $P < 0.001$ ,  $n = 86$ ; Appendix 2). We corrected isotopic ratios of peregrine falcon nestlings for isotopic discrimination (i.e., difference between the isotope signatures of the diet and the tissue of the consumers) using estimates developed for whole blood of adult falcons fed a simple diet composed of quail ( $\delta^{13}\text{C} = 0.2 \pm 0.01$  SD,  $\delta^{15}\text{N} = 3.3 \pm 0.4$  SD; Hobson and Clark 1992). Although discrimination factors may vary between plasma and blood cells, and between young and adult (Lecomte *et al.* 2011), using an average for the whole blood is a conservative approach. We also take into account the concentration dependence of C and N in tissues. We ran SIAR

using the following parameters: iterations = 1,00,000, burnin = 100,000, thinby = 10, and flat priors (Parnell *et al.* 2010).

## Reproductive success

To investigate whether the heterogeneity of the breeding environment influenced reproductive success in the population, we compared the number of young per nest at the time of nestling banding (~25 days old) over the 28 years of monitoring (1982–1999, 2002–2010) to two fixed predictors: the proportion of terrestrial habitat within falcon’s pseudo home range and the year. We integrated the nest site identity (nest site use varied over the duration of study) as a random variable in the linear mixed-effect models. The number of nestlings to reach banding age was the most consistently recorded variable across all years of the study. We lack details on nestling mortality therefore, only successful pairs (i.e., those pairs that raised at least one young to 25 days old and were detected during yearly nest visits) were included when modeling reproductive success. Additionally, we were able to model nest success (no young vs. 1 or more young produced) for 17 years (1982–1995; 2008–2010). We used a binomial distribution within a linear mixed-effect model to address the contribution of the proportion of terrestrial habitat within falcon’s pseudo home range (fixed), year (fixed), and nest identity (random) to variation in nest success. To ensure that the effect of the heterogeneity of the breeding environment was not related to phenomena occurring outside of the nestling period, clutch size together with the number of young hatched were also used as response variables in linear mixed-effect models. For all linear models used in our study, we verified the assumption of linearity and homoscedasticity.

## Results

### Heterogeneity of the breeding environment

The proportion of terrestrial habitat within a falcon’s pseudo home range was highly variable (5–100%) and averaged  $45 \pm 29\%$  SD ( $n = 36$  nests, Fig. 2). This variability was similar within the subset of nests sampled in 2008 for our isotope analysis ( $45 \pm 38\%$  SD,  $n = 19$  nests, Fig. 2). This suggests that the nest site distribution in 2008 was comparable that of the 36 nest sites monitored over 28 years (Fig. 2).

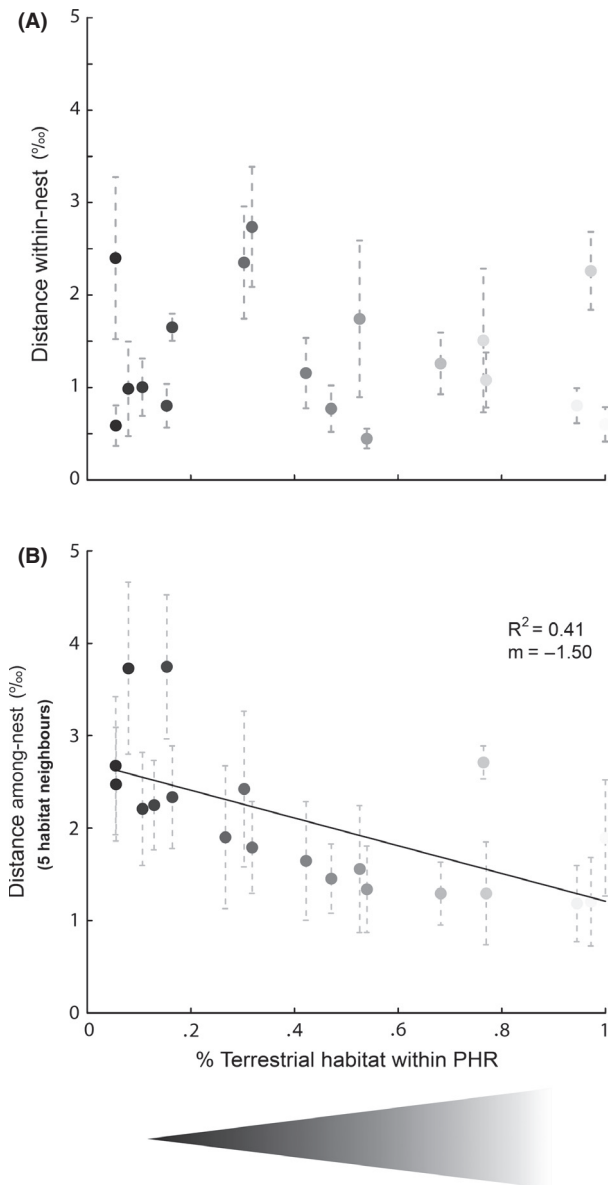
### Intra-population niche variation

At the population level, the value of the mean isotopic within-nest distances was  $1.3 \pm 0.5\%$  SD (ranging from

$0.4 \pm 0.2\text{‰}$  SD to  $2.7 \pm 1.3\text{‰}$  SD). A quarter of the nests (five nests) showed relatively high and variable values for their mean within-nest distance metric, whereas the majority of the nests showed lower and consistent values (Fig. 4A). Mean within-nest distance variation was independent of the proportion of terrestrial habitat within falcon's pseudo home range (linear regression model;  $m = -0.23 \pm 0.52$  standard error [SE],  $n = 17$ , Fig. 3A). Although possible diet generalists may exist in the population (increased within-nest variability), the majority of individuals were likely using a limited set of prey mixture over the rearing season. The mean isotopic among-nest distances (to five habitat neighbours) were higher (ranging from  $1.3 \pm 0.4\text{‰}$  SD to  $3.7 \pm 1.0\text{‰}$  SD) than the mean within-nest distances ( $1.3 \pm 0.5\text{‰}$  SD). In addition, the variation in mean isotopic among-nest distances was negatively related to the proportion of terrestrial habitat within the falcon's pseudo home range (linear regression model;  $m = -1.50 \pm 0.42$  SE,  $n = 19$ , Fig. 3B). This suggests individual's diet specialization (increased among-nest variability) was a driving mechanism structuring niche variation within the marine-dominated environment.

## Diet

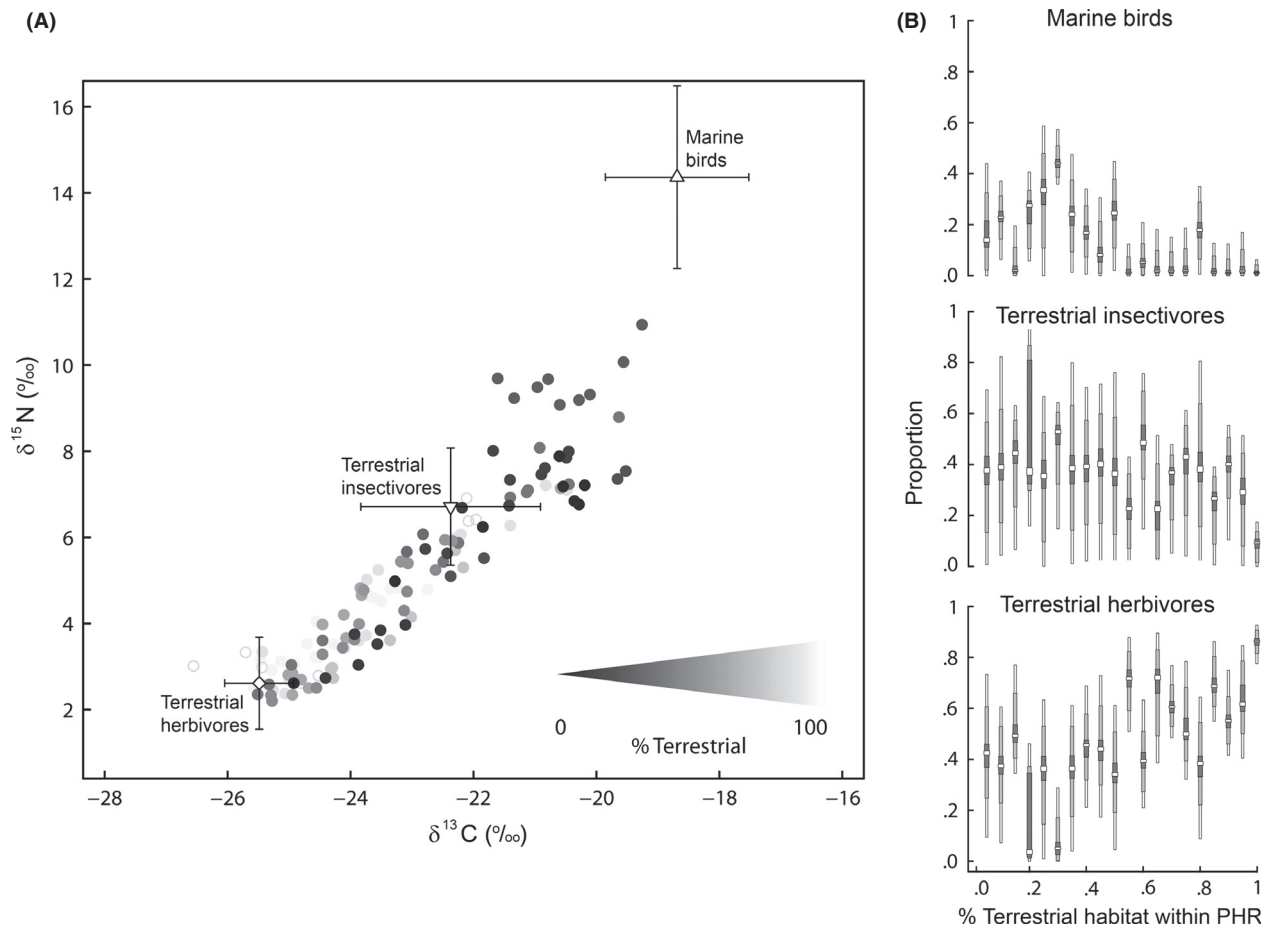
We recorded a steep increase in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios from terrestrial prey species compared to marine prey species (ranging  $-26.0$  to  $-17.4$  in  $\delta^{13}\text{C}$  and  $1.4$ – $16.7$  in  $\delta^{15}\text{N}$ : Appendix 2 and Fig. 4A). We found a large variation in stable isotope ratios of falcon nestlings raised along the terrestrial-marine continuum (ranging  $-26.6$  to  $-19.3$  in  $\delta^{13}\text{C}$  and  $2.2$ – $10.9$  in  $\delta^{15}\text{N}$ : Fig. 4A). **The contribution of terrestrial herbivores prey source in peregrine falcon nestlings diet notably increased with increased proportion of terrestrial habitat within falcon's pseudo home range, ranging from a CI 95% equalled to [0%, 30%] in an offshore nest site to a CI 95% [78%, 95%] in a mainland nest site (Fig. 4B).** However, the contribution of marine birds prey source in peregrine falcon nestlings diet notably decreased with increased proportion of terrestrial habitat within falcon's pseudo home range, ranging from a CI 95% equalled to [36%, 57%] in an offshore nest site to a CI 95% [0%, 9%] in a mainland nest site (Fig. 4B). Finally, the contribution of terrestrial insectivores prey source in peregrine falcon nestlings diet also varied among nest sites but to a lesser extent than for marine and terrestrial prey, ranging from a CI 95% equalled to [15%, 95%] in an offshore nest site to a CI 95% [0%, 18%] in a mainland site (Fig. 4B). The overall pattern indicates a predominance of terrestrial prey source regardless of nest positions within the terrestrial/marine landscape.



**Figure 3.** Mean within-nest distance (A) and mean among-nest distance (to five habitat neighbours) (B) relative to the proportion of terrestrial habitat within the pseudo home range (PHR) for peregrine falcon nestlings sampled up to three times during nestling period 2008 near Rankin Inlet, Nunavut, Canada. Circles illustrate the mean nest distances and bars represent standard deviation. The intensity of gray shading within circles is proportional to the amount of terrestrial habitat within the falcon's pseudo home range, from all black (0%) to all white (100%).

## Reproductive success

During the 28 years of monitoring,  $11.9 \pm 4.5$  SD peregrine falcon nests had at least one 25 day-old young (range: 1–20 nests/year;  $n = 36$  nest sites). The population averaged  $28.7 \pm 14.2$  SD young annually (range:



**Figure 4.** Influence of the proportion of terrestrial habitat within the falcon's pseudo home range (PHR) on (A) the isotopic signature of peregrine falcon nestlings and (B) the relative contribution of their potential prey species to their diet for summer 2008 near Rankin Inlet, Nunavut, Canada. Left panel (A): circles represent young falcons sampled up to three times during the nestling period, and arrows represent their potential prey species gathered in three clusters (mean  $\pm$  standard deviation). The intensity of gray shading within each circle is proportional to the amount of terrestrial habitat within the falcon's pseudo home range, from all black (0%) to all white (100%). Data are corrected for isotopic discrimination for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Right panel (B): Stable Isotope Analysis in R (SIAR) output distributions of the relative contribution of marine birds, terrestrial insectivores and terrestrial herbivores in the reconstructed diet of peregrine falcon nestlings. Boxplot showed the 5, 25, 75 and 95 credible intervals (white marks, dark grey, light grey and white boxes, respectively) of the SIAR posterior probability distributions.

3–61), with an average of  $2.4 \pm 0.4$  SD young produced per successful nest (range: 1–4).

The number of young produced per successful nest was positively related to the proportion of terrestrial habitat within the falcon's pseudo home range (number of young produced increased by 0.47 from a marine-dominated pseudo home range to a terrestrial-dominated one [ $m = 0.47 \pm 0.17$  SE,  $n = 36$ ]), and decreased over time (number of young produced decreased by 0.14 per 10 years [ $m = -0.014 \pm 0.006$  SE,  $n = 28$ ]) (Table 1A and Fig. 5). In contrast, peregrine falcon nest success (no young vs. 1 or more young produced) was not related to the proportion of terrestrial habitat within the pseudo home range ( $m = 0.17 \pm 0.52$  SE,  $n = 36$ ), (Table 1B). Similarly, clutch size ( $m = 0.04 \pm 0.16$  SE,  $n = 36$ ) and

number of eggs hatched ( $m = 0.25 \pm 0.33$  SE,  $n = 36$ ) were not related to the proportion of terrestrial habitat within falcon's pseudo home range, (Table 1A). This suggests that the effect of the heterogeneity of the breeding environment on the number of young produced was associated with events occurring during the nestling period.

## Discussion

It has been known that landscape heterogeneity can influence ecological processes such as intra-population niche variation, (e.g., Darimont et al. 2009), but little is known about the underlying mechanisms, and their demographic consequences on populations. By combining analyses of an individual's isotope niche with long-term monitoring

**Table 1.** Summary of the linear mixed-effect models accounting for the effect of the proportion of terrestrial habitat within the peregrine falcon's pseudo home range (PHR) and year (Year) on the number of young produced (1982–1999 and 2002–2010) and on the nest success, number of young hatched and clutch size (1982–1995 and 2008–2010). Reported within the linear mixed-effect model are (A) a continuous distribution and (B) a binomial distribution. Models accounted for the effect of *nest identity* as a random variable but not presented here.

Response	Predictor	<i>b</i>	Standard error	df	<i>t</i>	<i>P</i>
(A)						
Young produced	PHR	0.47	0.17	34	2.69	0.01**
	Year	−0.014	0.006	283	2.37	0.02*
Young hatch	PHR	0.25	0.33	34	0.75	0.46 ns
	Year	0.011	0.009	290	1.22	0.22 ns
Clutch size	PHR	0.04	0.16	34	0.31	0.76 ns
	Year	0.007	0.005	290	1.53	0.13 ns
(B)						
Nest success	PHR	0.17	0.52	34	0.32	0.75 ns
	Year	−0.027	0.015	330	1.80	0.072 ns

Data collected near Rankin Inlet, Nunavut, Canada.

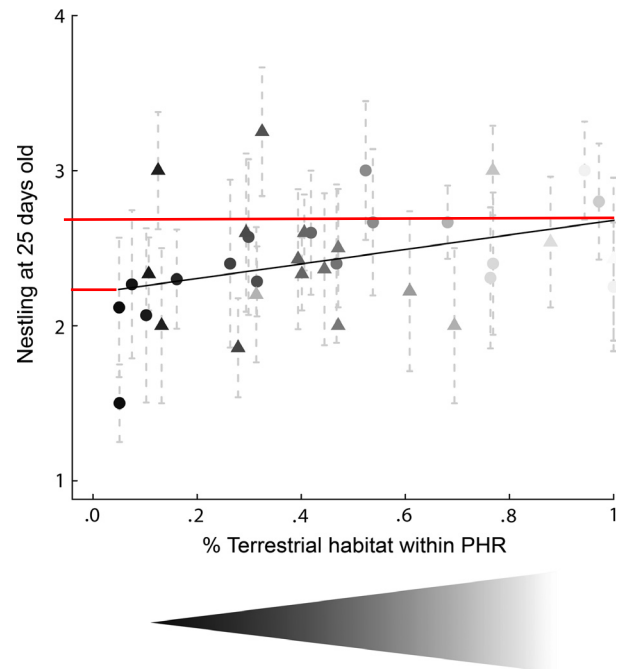
\*\* , \* , and ns represent  $P < 0.01$ ,  $P < 0.05$ , and  $P > 0.05$  (non-significant), respectively.

of reproduction, our study shows how landscape heterogeneity (terrestrial/marine gradient) can influence a generalist predator population: the proportion of terrestrial prey source within a peregrine falcon nestling diet and the brood size decrease with increasing nest site distance to the mainland. Breeding within the mainland habitat potentially yields a fitness advantage with this long-living species.

Here we present robust results from (1) the monitoring and sampling of all hatchlings in active nests for isotopes during 2008, and (2) the integration of all nests present during 28 years of population monitoring (nest detection probability was high due to high nest site fidelity; Franke et al., unpubl. data). Moreover, the distribution of nest sites in 2008 across the habitat gradient was representative of the distribution of all used nest sites ( $n = 36$ ; Fig. 2) recorded during the 28 years and allows for extrapolation of the niche/landscape relationship for a multi-year perspective (Figs. 2, 5). However, our understanding of the effect of landscape heterogeneity on resource use could be furthered by calculating the proportion of terrestrial habitat within actual foraging area in place of our pseudo home range.

### Landscape heterogeneity effects on intra-population niche variation

Bolnick et al. (2003) have demonstrated that many apparent generalist species can be in fact composed of a range



**Figure 5.** Influence of the proportion of terrestrial habitat within the falcon's pseudo home range (PHR) on the mean number of fledglings produced near Rankin Inlet, Nunavut, Canada (1982–1999, 2002–2010). Dots represent the average number of nestlings produced per nest ( $n = 36$ ) and arrows show standard error. The line indicates fitted values for illustrative purposes only. Triangles highlight the distribution of the nests sampled in 2008 for stable isotope work. The intensity of gray levels are proportional to amount of terrestrial habitat within the falcon's pseudo home range, from all black (0%) to all white (100%).

of ecologically variable individual specialists. Our results from isotope analyses indicated that niche variation within the peregrine falcon population arose from individuals with variable degree of generalization (high intra-nest variation) and specialization (high among-nest variation) in their prey use. **These findings show that (1) peregrine falcons, considered as generalist predators, can actually exhibit a higher-than-anticipated degree of dietary specialization during the breeding season and (2) individual specialization and generalization are not mutually exclusive phenomena but can simultaneously arise and structure intra-population niche variation (see also Tinker et al. 2008).** Interestingly, we found a higher degree of specialization with individuals nesting offshore than with those individuals nesting in terrestrial-dominated habitats, which is in contrast to conclusions drawn in recent studies dealing with similar ecological circumstances (i.e., generalist predator inhabiting a heterogeneous landscape). Darimont et al. (2009) reported that a coastal grey wolf population showed the most specialized individuals (sub-population with the largest trophic

niche) under conditions of increased species richness with resource input from the sea (spawning salmon), and Giroux *et al.* (2012) showed that arctic foxes breeding in the vicinity of a goose colony had increased niche breadth compared to more distant breeders. In our study, peregrine falcons nesting near the mainland (along the coast) had the widest diversity of prey resources in their nesting environment with access to both terrestrial and marine resources, but these individuals did not exhibit the widest niche; in fact, they extensively used terrestrial prey. We address this result with two possible, though not mutually exclusive, explanations.

First, we hypothesize that the peregrine falcon is limited in its ability to use marine resources, which would explain its minimal use by individuals nesting on or near the mainland (with low individual specialization). Under this scenario, the characteristics of marine birds (e.g., capable of diving under water to escape predation) do not complement the predator's traits (e.g., lack of hovering behaviour over the surface of the water, shorter wings, small size, and shorter claws than subspecies specializing on marine birds; Nelson 1990) to allow for a match that yield energetic benefits for the predator (Sih and Christensen 2001; Bolnick *et al.* 2003; Tinker *et al.* 2008). The availability of marine prey relative to terrestrial resources may be an important factor influencing profitability (prey use) and needs to be quantified by further studies since no quantitative data are currently available for our study area.

Second, we hypothesize that the abundance of terrestrial resources during 2008 within our study area was high enough to provide food for nesting peregrine falcons on or near the mainland, explaining the low use of marine resources (with low individual specialization and constant isotopic niche). The extensive use of herbivore prey items (rodents) by peregrine falcon nestlings (as shown by isotope modeling), along with measurements (lemming trapping) and observations (high breeding density [25 breeding pairs with the study area] and breeding success of a lemming specialist, the rough-legged hawk, *Buteo lagopus*) during summer 2008, support the hypothesis that lemmings were overabundant in 2008 and, consequently, that the consumption of marine resources may be a minimal estimate for this population over the long term. Other studies have demonstrated that inter-annual variation in preferred resources can modulate the relative contribution of marine resources in the diet of generalist consumers (e.g., Roth 2002). Quantifying the multi-annual variation in lemming abundance, as well as other terrestrial prey species, is necessary to further support our hypothesis and to understand its temporal extent. This could be done by quantifying the contribution of lemming versus marine resources to peregrine falcon diet

across different phases of the lemming cycle (peaks and crashes in particular). Despite the low contribution of marine resources to the overall falcon diet, our results show a significant use of marine resources by offshore nesting peregrine falcons. We address these results in the light of the optimal foraging theory that predicts the use of alternate prey (here marine resources) by a consumer to be quite low unless the availability of preferred prey (here terrestrial resources) is decreased (Schoener 1971; Sih and Christensen 2001).

### Landscape heterogeneity effects on reproductive performance

Although our results do not identify the mechanism underlying the decrease in the annual number of young produced by offshore nesting peregrine falcons, analyses of niche and reproductive success suggest a potential breeding cost for accessing distant terrestrial prey. The central place foraging theory (CPFT; an extension of optimal foraging theory; Orians and Pearson 1979) provides some support to this possible explanation. Our studied system fulfils the central premise of the CPFT, as peregrine falcons are bound to a fixed central place (their nest) during the nestling period. Suitable nest sites are available asymmetrically within the study area (most nest sites are available within the marine end of the gradient), yet the apparent preference of peregrine falcons for terrestrial prey (Fig. 4) results in many individuals being unable to choose a central place close to their preferred food distribution (Orians and Pearson 1979). Hence, CPFT expects that peregrine falcons nesting in the most distant location (offshore) relative to foraging areas (mainland) will experience higher traveling costs; this could in turn impact their reproductive output (Orians and Pearson 1979). Interestingly, CPFT also predicts that the most distant nesting peregrine falcons relative to their terrestrial resource would be more likely to integrate locally available resources (i.e., marine resources) to cope with the increased foraging cost, as observed in our study (Fig. 4B). Our results follow such pattern by using the angle of the niche theory to understand resource heterogeneity. This merges both niche theory and CPFT into a single framework.

Along with CPFT, recent empirical studies (Hakkarainen *et al.* 2003; Lambrechts *et al.* 2004; Byholm *et al.* 2007; Doligez *et al.* 2008; Golawski and Meissner 2008) have drawn parallels between habitat quality (resource availability), food delivery rates (energy intake for nestlings) and reproductive performance. For example, Byholm and Kekkonen (2008) experimentally demonstrated that small-scale variation in habitat quality, along with food availability, could influence demographic patterns in "habitat-sensitive" avian top



predator (goshawk *Accipiter gentilis* Linnaeus). Assuming increased traveling costs for peregrine falcons breeding offshore (as suggested by our results), how this could result in a decreased food provisioning would require the quantification of the delivery rates at nests and the correlation of these with the proportion of terrestrial habitat within the peregrine falcons' home range.

Since our study was not experimental, we cannot exclude the possibility that the observed relationship between reproductive response (and resource use) and landscape heterogeneity may be linked to other mechanisms. First, individual quality has been shown to influence reproductive performance (Carrete *et al.* 2006); in our study area individual quality could be confounded with landscape heterogeneity influences, as peregrine follow a despotic distribution where high quality individuals often monopolize high quality habitat (Sergio *et al.* 2009). However, as we detected no relationship between the proportion of terrestrial habitat within falcons' pseudo home range and clutch size (a proxy of individual quality; Sydeman *et al.* 1991), we argue that variation in individual quality could not solely explain the observed tendency linking landscape heterogeneity, trophic niche, and reproduction. Second, previous studies conducted in the same study area have documented the influence of weather as a major determinant of peregrine falcon nestling survival and reproductive success (Bradley *et al.* 1997; Añtil 2012). To assess whether weather could create variance in the nestling survival across the landscape gradient, we would need to measure nest sites exposure and weather events at the nest site scale.

### Generalist predators and tundra functioning

When compared to the large contribution of marine energy to the diet (Tarroux *et al.* 2012) and reproductive success (Roth 2003) of another top arctic predator, the arctic fox, marine inputs for peregrine falcons was only minimal, at least for summer 2008. This highlights the various consequences of marine resources input on generalist predators with contrasting life cycle characteristics. Nevertheless, the contribution of marine resources in the peregrine falcons' diet was significant for individuals with direct access to this resource and remote access to terrestrial resources, boosting breeding output. Assessing the role of marine prey on peregrine falcons' reproduction is necessary to determine how its use by top predators could scale-up to affect demographic processes within the population, and also to assess potential ecosystem consequences (Lecomte *et al.* 2008; Leroux and Loreau 2008; Killengreen *et al.* 2011; Giroux *et al.* 2012).

### Conclusion

Our study shows how heterogeneous breeding environments can generate proximate (variation in resource use) and ultimate (reproduction) consequences on a population of generalist predators during its breeding season. The results we present here contrast with observations made under a similar context (landscape heterogeneity) but at a larger spatial scale and with different species (Darimont *et al.* 2009; Giroux *et al.* 2012), thus highlighting the importance of fine-scale investigations of spatial variability and a sound understanding of animal life-history.

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## Conflict of Interest

None declared.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix 1.** Species found with the study area, Rankin Inlet, Nunavut.

**Appendix 2.** Stable isotope signatures of prey species found with the study area.

**Appendix 3.** Breeding cycle of peregrine falcons.

**Appendix 4.** Laboratory preparation of falcon and prey tissues for stable isotope analyses.

**Appendix 5.** On the calculation of niche variation metrics.

**Appendix 6.** Results of fitted linear regression.

# Intraspecific Adoption and Double Nest Switching in Peregrine Falcons (*Falco peregrinus*)

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**ABSTRACT.** We describe an observation of post-fledging double nest switching and alloparenting in the Peregrine Falcon (*Falco peregrinus tundrius*). During the summer of 2010, a 36-day-old male Peregrine Falcon that had been marked with leg bands was seen flying from its natal site and was subsequently observed at a neighboring nest site that contained two nestlings. Motion-sensitive camera images indicated that the adopted nestling remained at the neighboring site for several days, during which time it shared the nest ledge with the two resident nestlings and was fed by the adults that occupied the site. The juvenile falcon subsequently returned to its natal site, where it shared the nest ledge with its natural sibling and received care from its natural parents. This note is the first documentation of nest switching in wild Peregrine Falcons.

**Key words:** brood adoption, nest switching, alloparenting, peregrine falcon, avian, Arctic

**RÉSUMÉ.** Nous décrivons l'observation d'un double échange de nids après l'envol et d'alloparents chez le faucon pèlerin (*Falco peregrinus tundrius*). À l'été 2010, nous avons aperçu un faucon pèlerin bagué âgé de 36 jours en train de s'envoler de son site natal, après quoi nous l'avons observé à un site de nidification avoisinant qui comprenait deux oisillons. Les images de caméras détectrices de mouvement ont indiqué que l'oisillon adopté est resté au site avoisinant pendant plusieurs jours. Pendant ce temps-là, il a partagé la corniche avec les deux oisillons résidents et s'est fait nourrir par les adultes qui occupaient le site. Plus tard, le faucon juvénile a regagné son site natal, où il a partagé la corniche avec l'autre membre de sa fratrie et reçu des soins de ses parents naturels. Il s'agit de la première fois qu'un échange de nids a été documenté chez le faucon pèlerin sauvage.

**Mots clés :** adoption de nichée, échange de nids, alloparent, faucon pèlerin, aviaire, Arctique

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## INTRODUCTION

An individual is considered an alloparent when it provides care for young that are not its own (Wilson, 1975). Riedman (1982) reviewed the phenomenon and proposed a suite of mechanisms that may explain its evolution in several taxonomic groups. In birds, several known mechanisms can result in alloparentalism. Among these, brood parasitism (Payne et al., 2001), brood adoption (Howitz, 1986; Simmons, 1992), and brood mixing (Patterson et al., 1982) are best known. Brood adoption and brood mixing are common among precocial and semi-precocial species and usually occur early in the development of the nestlings (Williams, 1994). Alloparental care can also be manifested through replacement of one or both adults after eggs have been laid (Grubb et al., 1988) or through nest switching once young have learned to fly but remain dependent on parental care. Nest switching occurs most often in altricial and semi-altricial species, and adoption usually occurs late in the development of the nestlings, resulting in short periods of

alloparental care (Ferrer, 1993; Redondo et al., 1995). Post-fledging adoption by nest switching has been documented in several avian species, including American Crows (*Corvus brachyrhynchos*; Schaefer and Dinsmore 1992), White Storks (*Ciconia ciconia*; Redondo et al., 1995), and Alpine Swifts (*Apus melba*; Bize and Roulin, 2006). In raptor species, post-fledging nest switching has been documented in Northern Goshawks (*Accipiter gentilis*; Kenward et al., 1993), Egyptian Vultures (*Neophron percnopterus*; Donazar and Ceballos, 1990), Ospreys (*Pandion haliaetus*; Poole, 1989; Gilson and Marzluff, 2000), Eagle Owls (*Bubo bubo*; Penteriani and Delgado, 2008), Spanish Imperial Eagles (*Aquila adalberti*; Ferrer, 1993), and Lesser Kestrels (*Falco naumanni*; Tella et al., 1997). In these studies, nest switching was often attributed to high nesting density (e.g., colonial nesting) or attempts to improve food intake (e.g., subordinate siblings in large broods), or both.

In Peregrine Falcons (*Falco peregrinus*), replacement of adults within a breeding season is well known (Ratcliffe, 1993), and fostering of young into wild nests was widely

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employed in the recovery of the species (Cade, 1980; Craig and Enderson, 2004; Alberta Peregrine Falcon Recovery Team, 2005). To our knowledge, however, no case of post-fledging adoption between wild peregrine nest sites has previously been observed. We present here the first documented observation of nest switching in Peregrine Falcons.

Biologists have monitored a very dense (1 site/12 km<sup>2</sup>) Peregrine Falcon population located near the hamlet of Rankin Inlet, Nunavut, Canada since 1982 (e.g., Franke et al., 2010, 2011). Territorial peregrines have routinely occupied the same general nest site locations each breeding season, with some sites holding pairs either more frequently over the course of the study, or for longer periods, or both. Each location was assigned a unique site identification number that has remained constant through time, despite annual variation in nest ledges on which pairs chose to lay eggs. Since 2008, motion sensitive cameras (RECONYX models PM35T25, PC85, and PC800 Hyperfire) have been employed each breeding season to monitor nest ledges continuously during incubation and nestling rearing. All nestlings received a federal leg band and a unique alphanumeric coded color visual identification band once they reached approximately 25 days of age. Cameras were positioned 1–4 m from the nest, allowing individual identification by reading the alphanumeric code on the leg band.

#### DESCRIPTION OF OBSERVATIONS

On 19 August 2010, at approximately 1730 (see Table 1), we arrived at Site 29 (the natal nest of a 36-day-old male and a 34-day-old female) to conduct routine sampling procedures (mortality check, weight, and nest camera maintenance). The male had previously been banded with identification tag No. 25 A. As the field crew approached the base of the nesting cliff, they saw this male flying from the cliff in the general direction of the neighboring Site 28, located 536 m to the south. After weighing the female nestling and collecting a blood sample, the crew left the site at 1746.

Routine site monitoring conducted during a previous visit (8 August) indicated that the male (25 A) at Site 29 weighed 636 g at 25 days of age. His female sibling was two days younger and weighed 764 g. In comparison, the male at Site 28 weighed 408 g at 24 days of age, and the female weighed 566 g at 25 days of age. In addition, images of all four nestlings collected at 34–36 days of age show 25 A to be much farther advanced in feather development (almost no trace of down on head, nape, and back) than any of the other three nestlings, all of which retained very large patches of down on legs, head, nape, and back.

On 30 August 2010, we retrieved the cameras located at Sites 28 and 29. The images collected at Site 28 from 19 to 30 August showed that 25 A joined two resident nestlings (banded 27 A and 73 E) on their nest ledge within three hours of leaving his natal site on August 19. Less than 11 hours later, photographs taken at Site 28 showed the resident adult female feeding her own nestlings and the now

adopted nestling from Site 29. On 20 and 21 August, the adult female resident at Site 29 delivered prey items on four more occasions. Each time, 25 A was present on the nest ledge with the resident nestlings and competed for a share of the prey item that was delivered. Over the next two days, the camera recorded limited activity on the nest ledge, but the adopted nestling was observed together with an adult on the nest ledge on 23 August, more than three days after flying from its natal site. No further activity was recorded by the camera at Site 28.

From 19 to 23 August, the single remaining female nestling (62 E) at Site 29 was fed multiple times per day and was seen with distended crop several times over the five-day period. In addition, rather than immediately consuming prey delivered to the nest ledge, 62 E cached several items that were delivered during this period. On 24 August in the morning, an adult falcon delivered a prey item to 62 E; within a few seconds, 25 A appeared on the ledge at Site 29 with his sibling after spending nearly five full days away from Site 29, which included at least three days at Site 28. Both 25 A and 62 E were seen together at the nest ledge on two more occasions that day, but 62 E spent the night alone on the nest ledge. The following day, the resident adults made several prey deliveries, which were mostly consumed and cached by 62 E. However, photographs of 25 A indicated that the male was on the nest ledge at least twice that day. Images clearly show that 25 A either consumed or shared prey items that had previously been cached by 62 E. Although little activity was recorded on the nest ledge after this observation, 25 A was observed on the nest ledge four more times between 25 August at 1903 and 28 August at 1117. When the cameras were removed on 30 August 2010, we confirmed the presence of one free-flying juvenile falcon at Site 28 and another at Site 29.

#### DISCUSSION

This note records nest switching and adoption in Peregrine Falcons. Poole (1982) suggested that nest switching may result from attempts by subordinate individuals in large broods to increase their food intake. In this case, 25 A was not likely subordinate to his much less well developed female sibling, nor was food apparently in short supply, given the food caching behavior by 62 E that we observed. Furthermore, 25 A left a site where he was one of only two nestlings to join a site where he was one of three nestlings, where competition for food would likely have been higher. Moreover, the nestlings at Site 29 were about the same age as 25 A, but much less advanced in their development, suggesting that their feeding rate was perhaps lower than that 25 A had experienced at his natal site. Therefore, moving to Site 29 likely did not represent an advantage in this case.

Some authors (Poole, 1982; Donazar and Ceballos, 1990; Kenward et al., 1993) have suggested that the post-fledging nest switching phenomenon is related to high breeding density. The breeding population at Rankin Inlet is recognized

TABLE 1. Detailed activity of the juvenile male Peregrine Falcon (25 A) as recorded by the automatic scouting cameras positioned at Sites 28 and 29.

Date	Time	Site	Events
August 19	1730	29	Field crew arrived at Site 29. HY male (25 A) left natal site
	1746	29	Field crew departed from Site 29
	1953	28	25 A was seen at Site 28 for the first time
August 20	0720	28	Resident female fed 25 A and her own two offspring
	1116	28	Resident female delivered prey and 25 A competed for food with resident nestlings
	1229	28	Resident female delivered prey, and 25 A competed for food with resident nestlings
	1342	28	Resident female delivered prey, and 25 A competed for food with resident nestlings
August 21	1707	28	Resident female delivered prey, and 25 A competed for food with resident nestlings
August 23	0505	28	A resident adult and 25 A were observed together at nest ledge
August 24	0735	29	Resident adult delivered prey to 62 E; 25 A joined 62 E four seconds later
	1229	29	25 A and 62 E were observed together on the nest ledge
	1323	29	25 A left nest ledge
	1336	29	Resident adult delivered a prey item which was consumed by 62 E
	1555	29	25 A returned to the nest ledge but left shortly thereafter
August 25	1628	29	25 A retrieved a prey item previously cached by 62 E on the nest ledge
	1800	29	25 A and 62 E shared a prey item
	1801	29	25 A left the ledge
	1851	29	25 A arrived on the ledge
	1956	29	25 A left the ledge
August 26	1903	29	25 A arrived on the ledge
	1945	29	25 A left the ledge
August 27	1806	29	25 A arrived on the ledge
	1811	29	25 A left the ledge
August 28	0657	29	25 A arrived on the ledge
	0701	29	25 A left the ledge
	1117	29	25 A arrived on the ledge
August 30	1118	29	25 A left the ledge
	1520	29	Cameras were removed

as one of the densest known worldwide for the species (Court et al., 1988). Moreover, the close proximity (536 m) of the two sites in question likely facilitated nest switching. The nest switch co-occurred with a site visit by our field crew, and it is possible that their presence in part accounted for the movement from one site to the other; however, the nestling flew from the cliff before our field crew reached the base of the cliff, and once airborne, it gained altitude. Sherrod (1983) indicated that the nestling period ranged from 35 to 42 days, and Oliphant (2011) indicated that some precocious male nestlings are capable of sustained flight as early as 35 days after hatching. In this particular case, the proximity of the sites, combined with the advanced physical development of 25 A, likely contributed in large part to the switch from natal site to adopted site and back again.

Regardless of the mechanism that caused 25 A to leave his natal site, the fledgling male was adopted without any apparent aggression from either the nestlings or the adults present at the adopting site. In this regard, Judge (1981) suggested that adult Ospreys feed juveniles on the nest regardless of relationship, and Ferrer (1993) observed the same behavior in Spanish Imperial Eagles. Nest switching and adoption have also been documented in several other raptor species and may be more common than we think. Documenting these events requires marking of nestlings and continuous monitoring of nests. Increased use of automatic scouting cameras in raptor studies may increase the number of observations and bring new information regarding this phenomenon.

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## Brood Reduction by Infanticide in Peregrine Falcons

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**ABSTRACT.** This note describes an observation of infanticide in the Peregrine Falcon (*Falco peregrinus tundrius*). During the summer of 2011, a marked adult female and an unmarked adult male produced and hatched two eggs at a known and regularly monitored nest site. Motion-sensitive camera images indicated that the adults attended to the two nestlings and fed them in a manner that resulted in growth and development typical for the nestlings produced in the study population. During a period of intense rainfall, the two nestlings were left unattended for several hours; both nestlings were clearly distressed, and one was close to death. When the visibly wet marked adult female returned to the nest ledge, she killed and partially consumed the smaller and weaker of the two nestlings. The female flew from the nest ledge without feeding the remaining nestling and returned shortly afterward to kill and partially consume the second nestling. This is the first documentation of infanticide in wild Peregrine Falcons.

**Key words:** infanticide, avian, brood reduction, asynchronous hatch, cannibalism, Peregrine Falcon, Arctic, core brood, marginal brood

**RÉSUMÉ.** Cet article décrit une observation d'infanticide chez le faucon pèlerin (*Falco peregrinus tundrius*). À l'été 2011, une femelle adulte baguée et un mâle adulte non bagué ont produit et couvé deux œufs à un site de nidification connu qui fait l'objet d'une surveillance régulière. Les images de caméras à détection de mouvement ont permis de constater que les deux adultes se sont occupés des deux oisillons et les ont nourris au point où ils ont pu grossir et se développer de manière typique aux autres oisillons visés par la population à l'étude. Pendant une période de pluie intense, les deux oisillons ont été laissés à eux-mêmes pendant plusieurs heures. De toute évidence, les deux oisillons étaient en détresse, et l'un d'entre eux se mourait. Lorsque la femelle adulte baguée visiblement trempée a regagné la corniche, elle a tué et consommé partiellement l'oisillon le plus petit et le plus faible. Ensuite, la femelle s'est envolée de la corniche sans nourrir l'autre oisillon, puis elle est revenue peu après pour tuer et consommer partiellement le deuxième oisillon. Il s'agit de la première fois qu'un cas d'infanticide est répertorié chez le faucon pèlerin en liberté.

**Mots clés :** infanticide, avien, réduction de la couvée, éclosion asynchrone, cannibalisme, faucon pèlerin, Arctique, couvée principale, couvée marginale

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### INTRODUCTION

In an examination of the significance of clutch size in birds, Lack (1947) proposed that asynchronous hatch within broods was an evolutionary adaptation to accommodate unpredictable seasonal food supply. The youngest (and usually the smallest) nestlings were predicted to thrive in years when food was plentiful, but were expected to die under environmental conditions associated with low food supply. Mock and Forbes (1995) pointed out that if we assume that the death of offspring within a brood represents an overall decrease in parental fitness, we also presume that the initial number of offspring was optimal. As a result, the

authors proposed the existence of a “core brood” plus one or more offspring that were associated with “overproduction,” which belonged to a “marginal brood.” The value of marginal siblings within broods is clear when food is abundant and survival of the marginal brood results in an overall increase to parental fitness. However, Mock and Forbes (1995) also present other, perhaps less obvious hypotheses to explain how the value of marginal siblings can enhance the survival of the core brood and lead ultimately to increased overall fitness for adult pairs. For example, under poor conditions, marginal offspring may be consumed by or fed to core offspring. In addition, marginal offspring may serve as replacements when core siblings die as a result of

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either extrinsic (e.g., predation) or intrinsic (e.g., congenital disease) causes. In extreme cases, when environmental conditions severely restrict food, parents may kill and consume their young (Forbes, 1991). This note reports an observation of total brood loss by infanticide and cannibalism in wild Peregrine Falcons.

From 2008 to 2012, we routinely used from 2 to 17 motion-sensitive cameras (RECONYX models PM35T25, PC85, and PC800, Hyperfire) installed at a distance of 1–4 m from nests to determine breeding phenology (e.g., lay date, hatch date), breeding behavior (e.g., feeding rate), and causes of mortality (e.g., rain, starvation, predation). Cameras were programmed to capture from one to three images immediately when triggered by motion, after which the camera remained insensitive to movement for 5 to 15 seconds. In addition, cameras were programmed to collect a single time-lapse image every 15 minutes. Memory cards and batteries were replaced every 5 to 10 days for the duration of the breeding season or until the site failed. All observations described here were made from images captured by the RECONYX camera placed on the nest ledge.

The study population of Peregrine Falcons is encompassed within a study area approximately 350 km<sup>2</sup> near the hamlet of Rankin Inlet, Nunavut, Canada. Though the location (62°49' N 92°05' W) is relatively southern for Peregrine Falcons in the Canadian Arctic, its environmental conditions are as severe as any encountered in the range of the species, and more severe than those at many other locations.

#### DESCRIPTION OF OBSERVATIONS

A marked adult female Peregrine Falcon (67 B) and an unmarked adult male were observed at a known nest site on 28 May 2011. The pair subsequently produced and hatched two eggs. The nestlings were weighed on two occasions, at ages of approximately 7 days (198 g and 136 g) and 12 days (348 g and 231 g). Development of both nestlings was consistent with normal growth curves reported for this population (Court et al., 1988).

From sunrise (~0426) to sunset (~2200) on 1 August 2011, both nestlings (aged 15 and 16 days) were fed on six occasions (four passerines, one large eider duckling, and the remains of one previously cached ground squirrel). Both nestlings were observed with fully distended crops throughout the day. In addition, except for a 15-minute period between 0337 and 0352, the adult female had brooded both young throughout the night from 2030 on 1 August until just after sunrise at 0438 the following morning, when she left the nest ledge. She returned approximately 13 minutes later (0451) and fed a single fully intact passerine to both nestlings. She then brooded both young until 0631, when she retrieved a second fully intact passerine and fed it to the nestlings. At 0637, she again left the nest ledge. Images indicate that it began raining at approximately 0717, and both chicks were clearly wet by 0730. The chicks remained alone and huddled together on the nest ledge until 0846

when the rain-soaked female returned to the ledge for a few seconds. The wet nestlings then remained alone and huddled together for almost three hours until the still wet female returned to the ledge briefly (for less than two minutes) at 1141. During this brief visit, the female attempted to feed what appeared to be the desiccated and previously discarded remnants of a ground squirrel to the nestlings. After the failed feeding, the rain-soaked nestlings remained alone on the ledge until 1643 when the female arrived on the nest ledge. Although both nestlings were alive, they had remained unattended for approximately nine hours. Images clearly indicate that both were distressed (wet, huddled, eyes closed, motionless) and show that the smaller of the two was near death. The female (still wet) almost immediately seized the younger of the two, killed it, and began to consume it, but did not appear to feed the remaining nestling, even though the images clearly show that it was begging vigorously. Within minutes (1647), the adult female carried the carcass of the now dead younger nestling away from the cliff and presumably cached the carcass remains. The adult female returned to the nest ledge within two minutes. Using her beak, she seized the second nestling by the neck and simultaneously restrained its body with her talons. The images show clearly that the nestling was alive, likely vocalizing and struggling to free itself, as the adult female held it down and tore a wound into the back of its neck that is consistent with the method that falcons use to kill their prey (Fig. 1). Within one minute of attacking and mortally injuring her nestling, the adult female flew from the nest ledge, carrying the nestling in her talons.

#### DISCUSSION

Several authors have investigated brood reduction and siblicide in raptors (Bechard, 1983; Edwards and Collopy, 1983; Bortolotti, 1986; Simmons, 1988) and other birds (Mock, 1984). Mock (1984) argued that rapid growth of nestlings and the practice of most avian species to swallow food whole was associated with low incidence of cannibalism in birds, but pointed out that Falconiformes are able to tear their food apart and are therefore not limited by gape size. Although brood reduction has been observed in birds of prey (Reese, 1972; Meyburg, 1974; Newton, 1978; Bortolotti et al., 1991), the fate of the carcass often remains unknown, and it is not clear how often cannibalism occurs. Parental infanticide per se has been confirmed more rarely. An example is the report by Korňan and Macek (2011), who observed a case of infanticide in the Golden Eagle (*Aquila chrysaetos*) in which one chick was killed and then fed to the other.

Asynchronous hatch has been documented in the Rankin Inlet Peregrine Falcon population (Court et al., 1988), and the authors argued that age and size differences among nestlings within broods introduced a competitive disadvantage to the youngest brood members. Starvation was cited as the most likely cause of death in 7% (6/85) of nestlings in 45%





FIG. 1. RECONYX motion-sensitive camera image shows resident adult female Peregrine Falcon (color marked "67 B") killing her nestling near Rankin Inlet, Nunavut, on 2 August 2011.

(5/11) of broods. In peregrines, however, neither starvation of nestlings nor outright infanticide has yet been cited as a mechanism associated with active brood reduction.

In the population of Peregrine Falcons breeding at Rankin Inlet, high levels of annual nestling mortality and a long-term decline in productivity are well documented; they are known to have occurred even though organochlorine residues in blood plasma of this population have declined to concentrations below those known to cause reproductive failure (Franke et al., 2010). The authors of that study discussed the possibility that a change in the precipitation regime and the direct effects of rain were the most likely cause of the observed decline in reproductive success. Anctil et al. (in press) subsequently found that the direct effects of rainfall caused 44% of the recorded nestling mortalities and used an experimental approach to show that nestlings protected in a nest box from the direct effects of rain survived at higher rates than those raised on natural ledges. The authors also found that starvation was responsible for a further 17% of deaths; they reported that within a given brood, fourth-hatched nestlings experienced much lower survival than their siblings regardless of treatment (i.e., nest box vs. natural ledge).

These results indicate that nestlings apparently starved in recent years at twice the rate they did in the early 1980s. They could suggest that the indirect effects of rain are an important component that may have contributed to the observed long-term decline in productivity in the Peregrine Falcon population at Rankin Inlet. In this case, it appears that local environmental conditions (cool and wet weather), in association with acute food restriction, may have provided the catalyst for the adult female to quite suddenly switch from activities typically associated with parental care (brooding and feeding) to killing and consuming her offspring. It would seem that the notion of marginal offspring can, in some instances, extend to an entire brood.

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