

Climatic conditions during outward migration affect apparent survival of an arctic top predator, the peregrine falcon *Falco peregrinus*

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In long-lived species, population growth rate is highly sensitive to changes in adult survival. Despite the growing concerns regarding recent climate changes, few studies have investigated the effect of climatic conditions on survival in long-lived wildlife that are either resident or breed in the Arctic. In this study, we evaluated the effect of climate across the annual life cycle (breeding, outward migration, wintering, and inward migration) on apparent annual survival of arctic-breeding peregrine falcons. From 1982 to 2008, peregrine falcons breeding near Rankin Inlet, Nunavut, Canada were monitored, in part, to assess apparent annual survival (the product of true survival and site fidelity) using re-observations of marked individuals. Our study indicated that apparent annual survival of adult peregrine falcons was correlated with indices of climatic conditions during outward migration (i.e. flight from the Arctic breeding grounds). These climatic indices (fall NAO of the current year and fall NAO with a lag of one year) explained 35% of the temporal variation in apparent annual survival of peregrine falcons. Our results suggest that this top-predator is vulnerable to weather-related environmental conditions encountered during fall migration.

In long-lived species, adult survivorship is one of the most important life history traits to consider when studying population dynamics, as slight changes in annual adult survival can lead to far-reaching consequences at the population level (Gaillard et al. 2000, Saether and Bakke 2000). Factors that affect adult survivorship in wild populations can be biotic (e.g. interactions within and/or between species) or abiotic (mediated through climatic factors). Although the study of climate effects on animal populations is not new (Elton 1924), it remains a central topic in ecology particularly within the context of climate change (Post et al. 2009). The Intergovernmental Panel on Climate Change reported that Earth's polar regions are warming rapidly, yet very little is known about the consequences of climate change on animal populations at high latitudes (Anisimov et al. 2007). This is especially true for birds species (Gaston et al. 2005 on Brünnich's guillemots; Dickey et al. 2008 on snow geese) as most studies on the effects of climate change on animal populations have been conducted in temperate regions (Møller et al. 2006a). In addition, studies of climate effects in wild populations are taxonomically biased. In birds, most studies on climate effects concern passerines (reviewed by Møller et al. 2006b) and to a lesser extent, seabirds (Barbraud and Weimerskirch 2001, Durant et al. 2004, Gaston et al. 2005,

Jenouvrier et al. 2005, Sandvik et al. 2005, Le Bohec et al. 2008) and waterfowl (Skinner et al. 1998, Sorenson et al. 1998, Dickey et al. 2008).

Raptorial species are seldom studied in relation to climatic conditions (Jaksic et al. 1997, Sergio 2003, Wichmann et al. 2003, Kim et al. 2008) and the influence of climate on raptor populations remains poorly understood, especially in the Arctic. Most raptor species are generally long-lived, often exhibit strong breeding-site fidelity and are, therefore, good candidate species for mark-resighting studies. However, they generally occur at low densities (Newton 1997), which can make long-term monitoring of raptor populations difficult. Despite this drawback, long-term monitoring of raptors is essential in order to improve our understanding of the effects of fluctuating climatic conditions. In addition, gaining insight into the effects of climate on long distance migrants is challenging. It is extremely difficult to characterize the effect of local environmental conditions (including weather) across geographic regions and multiple life history stages, notwithstanding the importance of pinpointing periods and locations where individuals are most vulnerable. This is particularly true when the effects of climate change on long distance migrants are most likely different in time and space across the annual life cycle. In this

context, global climatic indices can be used to integrate information on the effects of climate over several months (Stenseth et al. 2003, Hallett et al. 2004) and geographical regions (see Hurrell et al. 2001 for an example on the North Atlantic Oscillation).

We investigated the effect of climate on adult apparent survival of a population of arctic-nesting peregrine falcons *Falco peregrinus tundrius* breeding in north western Hudson Bay, Nunavut, Canada, using a unique long-term dataset spanning over 27 yr. We tested for associations between apparent annual survival of adult falcons measured on the breeding grounds and climatic conditions at several stages of an annual life history cycle using global indices during outward migration, wintering and inward migration, and local weather variables during the breeding season. This approach allowed us to identify periods during the annual cycle in which weather exerted the strongest effect on adult apparent survival. Although the associations are limited to correlations, this approach is a first step in forecasting the impact of climate change on animal populations (Root and Schneider 1995). Climate effects on apparent survival can be direct, through an increase of thermoregulation costs and a decrease in foraging success (Sergio 2003), and indirect (through food chains) leading to time-lags between climatic conditions and their effect on predators (Jaksic et al. 1997, Ottersen et al. 2001, Sandvik et al. 2005). Therefore, we considered climatic conditions in current as well as previous years.

Migration is energetically expensive and may lead to greater mortality particularly when combined with harsh environmental conditions (Newton 2007). We therefore predicted that any negative effects of harsh climatic conditions on peregrine falcon apparent survival rates should be pronounced during migration.

Material and methods

Study area and study species

The study population was encompassed within a 455 km² study area in north-western Hudson Bay (62°49'N, 92°05'W) near the hamlet of Rankin Inlet, Nunavut, Canada (Fig. 1). This population represents the highest known density of breeding peregrine falcons in the Arctic and the second highest density recorded worldwide (Court et al. 1989).

As with other long-distance migrants, the annual cycle of arctic-nesting peregrine falcons is comprised of 4 distinct periods. The summer breeding season extends approximately from late-May through mid-September, followed by an outward migration to wintering grounds in South America, which is usually completed by early December (Franke unpubl.). Birds depart from their wintering territories by mid-April. Within the study area, breeding pairs generally arrive after 20 May, and time their arrival to coincide with the start of the Arctic thaw and onset of summer productivity, which usually occurs in the first weeks of June. On the breeding grounds, passerines, shorebirds and small mammals comprise the bulk of the diet. Doves, songbirds, and shorebirds likely form the greater part of the diet during migration and on the wintering grounds (White et al. 2002).

From 1982 to 2008, a full census of the study area was conducted at least twice each year (except 2000 and 2001, when resighting effort was null or extremely low). If nest sites were occupied by unmarked individuals, effort was made to trap and mark these birds with a unique alphanumeric color-coded leg band and a United States Fish and Wildlife metal ring. When sites were occupied by

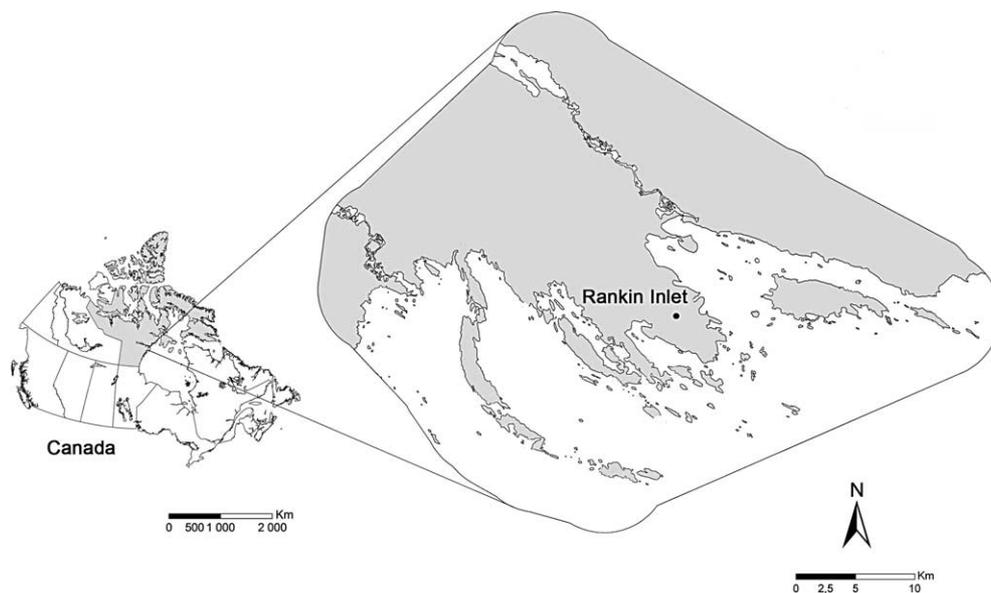


Figure 1. Rankin Inlet study area.

previously marked individuals, alphanumeric bands were read using a Questar Field Model telescope (75×).

Selection of climatic variables

The North Atlantic Oscillation (NAO) and Southern Oscillation Index (SOI) are well known global indices of climate and can represent weather over several months and large geographic scales (Hurrell 1995, Holmgren et al. 2001, Ottersen et al. 2001, Stenseth et al. 2003). Both are associated with climatic conditions encountered during inward migration to Arctic breeding grounds and outward migration from the Arctic to destinations in Austral South America. Table 1 lists the variables used and the rationale for including them in this study. We obtained daily values of NAO and SOI from the Climate Prediction Center of the National Weather Service (<www.cpc.ncep.noaa.gov>). On the breeding grounds, local climatic conditions were recorded hourly at the Environment Canada airport weather station situated centrally within the study area. Mean temperature and precipitation for the entire breeding period (June through August) were used in the analyses. We excluded the use of NAO over the period May–September as the phenomenon is known to be relatively weak in the Arctic during summer months (Hurrell et al. 2003).

Estimation of apparent survival

Between 1982 and 2008, 110 adult male and 154 adult female peregrines were captured and marked. Only the capture–resighting histories ($n = 566$ encounters) of adult peregrines were included for analysis. We included the capture–resighting histories of known-age recruits, but limited the encounter history to include only those years in which they were first sighted as adults. We performed apparent survival (the product of true survival and permanent emigration from the breeding grounds) analyses based on modeling of capture–mark–resighting (CMR) data with software M-Surge (Choquet et al. 2004). The first step in CMR apparent survival analyses was to assess goodness-of-fit (GOF) of the most general model (model with time-dependent apparent survival and resighting rates, generally referred as the Cormack–Jolly–Seber, or CJS model). Generally, lack of fit indicates that the data do not fulfill the “iii” (independence of fate and identity among individuals) assumption (Lebreton et al. 1992). GOF was performed using software U-CARE (Choquet et al. 2005) and indicated a good fit between the CJS model and our data ($\chi^2 = 73.5$, $p > 0.99$). Outputs for GOF were similar when considering each sex separately. Akaike’s information criteria corrected for small sample size (AICc) and AICc-weights (w_i , which measure the relative likelihood that a given model is the best among a set of candidate models) were used to perform model selection (Burnham and Anderson 2002).

We initially queried if annual rates of survival and resighting rates were time or sex-dependent. Little or no resighting effort was undertaken in 2000 and 2001. We thus fixed the resighting rate to 0 in 2000 and 2001, and consequently fixed apparent survival rates equal in years 1999/2000, 2000/2001 and 2001/2002 because apparent

Table 1. Climatic variables that potentially affect apparent survival of arctic-nesting peregrine falcons according to different time periods of their annual cycle.

Climate index	Model variable	Life history stage
Inward SOI	average SOI over the period of April–May	Inward Arctic migration
Inward NAO	average NAO over the period of April–May	Inward Arctic migration
Breeding temperature	average monthly temperature over the period May–September	Arctic breeding season
Breeding precipitation	total precipitation over the period May–September	Arctic breeding season
Outward NAO	average NAO over the period of October–November	Outward Austral migration
Outward SOI	average SOI over the period of October–November	Outward Austral migration
Wintering SOI	average SOI over the period of December–March	South American wintering

survival for these three years could not be estimated separately. We then considered the climatic covariates (see details below) to determine whether temporal variation in apparent survival rate could be explained by climate variability. For each of these models, we calculated a ‘pseudo- R^2 ’ to quantify the proportion of temporal variance in apparent survival explained by each covariate (Schemper 1990). This proportion was calculated as:

$$\frac{Dev_{(x)} - Dev_{(\phi)}}{Dev_{(t)} - Dev_{(\phi)}} \quad (1)$$

where $Dev_{(x)}$ represents the deviance of the model where apparent survival was a linear function of X, $Dev_{(\phi)}$ represents the deviance of the model where apparent survival was constant, and $Dev_{(t)}$ represents the deviance of the model where apparent survival was time-dependent.

Results

Time and sex effects on resighting and apparent survival rates

Recapture probability over the entire study (1982 to 2008) averaged 0.53 ± 0.03 , and showed substantial annual variations (Table 2). Females had higher recapture rates than males (0.59 ± 0.03 versus 0.43 ± 0.04 on average). An additive effect of sex was preferred to an interaction between year and sex (Table 2), indicating that recapture rates of both males and females varied in parallel over time.

Apparent survival rates of male and female peregrine falcons were identical (i.e. adding a sex effect did not decrease AICc values; Table 2) and averaged 0.73 ± 0.02 over the study period. From 1982 to 2008, apparent annual survival estimates varied from 0.49 (between summers 1983 and 1984, and summers 1992 and 1993) to 1. Apparent survival of peregrine falcons breeding near Rankin Inlet did not exhibit any clear trend during the study period (i.e. models including a linear trend in survival rates did not decrease AICc).

Table 2. Time and sex effects on survival (ϕ) and recapture (p) probabilities in peregrine falcons breeding at Rankin Inlet, Nunavut, Canada (data from 1982 to 2008, $n=110$ males and 154 females). Symbol 't' indicates inter-annual variations in ϕ or p ; 's' indicates constant ϕ or p ; 's' indicates sex differences in ϕ or p . Symbol '+' indicates additive effect.

Model	np ^s	Deviance	AICc	Δ AICc ^s	wi [†]
$\phi_t p_t^{s+}$	26	1191.78	1246.39	0.00	0.68
$\phi_s p_t^{s+}$	27	1191.213	1248.02	1.63	0.30
$\phi_t p_t$	25	1201.19	1253.60	7.21	0.02
$\phi_t p_t^s$	3	1311.65	1317.69	71.30	0.00
$\phi_s p_t^s$	49	1153.93	1261.42	15.03	0.00
$\phi_t p_t^{s+}$	51	1165.72	1278.04	31.66	0.00
$\phi_t^s p_t^{s+}$	52	1164.37	1279.18	32.73	0.00
$\phi_t^s p_t^s$	75	1144.39	1317.65	71.26	0.00
$\phi_t^s p_t$	74	1153.38	1323.99	77.60	0.00
$\phi_t^s p_t^s$	97	1105.25	1339.87	93.48	0.00
$\phi_t^s p_t^s$	52	1228.36	1343.11	96.72	0.00
$\phi_t^s p_t$	51	1236.61	1348.93	102.54	0.00

^s number of parameters.

^s: difference between the AICc of a given model and the lowest AICc.

[†] AICc weight.

Climate effects on apparent survival rates

Apparent survival rates of adult peregrine falcons were unaffected by either local summer temperature or precipitation (pseudo- $R^2 \leq 1\%$; Appendix 1). Inward NAO and SOI, and Winter SOI had little effect on survivorship and explained only 6% of annual variation (Appendix 1). Results were similar when time lags of 1 to 3 yr were considered (Appendix 1). Neither Winter SOI nor Inward SOI explained any variation in peregrine apparent survival. However, on its own Winter SOI $t-1$ explained 10% of annual variation in apparent survival, and led to slightly lower AICc values when compared to the constant apparent survival model (Table 3).

Outward NAO in the current year (Outward NAO_t) and Outward NAO with a time lag of 1 year (Outward NAO_{t-1}) were the environmental covariates among those we tested that best explained peregrine falcon apparent survival (Table 3). Outward NAO_t was positively related (slope of 0.407, SE = 0.016) to apparent survival of adult peregrine falcons (Fig. 2a), and on its own explained 14% of the variation in

apparent survival (Table 3). Conversely, Outward NAO_{t-1} was negatively associated (slope of -0.410 , SE = 0.019) with peregrine falcon apparent survival (Fig. 2b), and by itself explained 11% of the variation in apparent survival (Table 3). However, the combined effects of Outward NAO_t and Outward NAO_{t-1} explained 35% of the variation in apparent survival (Table 2). When including both Outward NAO_t and Outward NAO_{t-1}, Winter SOI $t-1$ no longer explained falcon survival (Table 3).

Discussion

We found within season and time-lagged effects of climate on apparent survival of Arctic nesting peregrine falcons. Although our approach is limited to the examination of correlations, we nevertheless suggest that the patterns reported here provide further insight into potential relationships that exist between climate and apparent survival of long distant migrants. In the context of this study, it appears that apparent survival of adult peregrine falcons was unaffected by local weather conditions on the breeding grounds, and was less affected by environmental conditions encountered during wintering or inward migration when those life history stages are compared to outward migration.

Although our analysis indicated that apparent survival remained constant over time, we caution against interpreting this finding to argue strictly that survival did not vary among years, but rather that standard errors around annual survival estimates are large due to relatively small sample sizes. In addition, AIC selection preferred a time-constant model despite sufficient variation in estimates of annual apparent survival to seek the environmental correlates examined in this study. We suggest that the high number of years in the study (28) is likely responsible for this initially counterintuitive result. In other words, models that included annual estimates of survival incorporated many more parameters compared to the constant survival models, and thus the AIC value of the time varying models increased considerably.

Our estimates of apparent annual survival for highly migratory peregrines falcons (0.73 ± 0.02 for both sexes) breeding near Rankin Inlet, Nunavut, Canada between

Table 3. Climate effects on peregrine falcon apparent survival rates, Rankin Inlet, Nunavut, Canada (data from 1982 to 2008, $n=110$ males and 154 females). Resighting rates were modeled as p_t^{s+} (Table 2). Only 10 most parsimonious models are presented; complete model selection is presented in Appendix 1.

Model	np ^s	Deviance	AICc	Δ AICc ^s	wi [†]	Pseudo- R^{2*}
Outward NAO _t +Outward NAO _{t-1}	28	1182.73	1241.76	0.00	0.20	0.35
Outward NAO _t +Outward NAO _{t-1} +Winter SOI _{t-1}	29	1182.64	1243.89	2.13	0.07	0.35
Outward NAO _t +Outward NAO _{t-1} + Inward SOI _{t-2}	29	1182.67	1243.91	2.16	0.07	0.35
Outward NAO _t +Winter SOI _{t-1}	28	1185.50	1244.52	2.76	0.05	0.24
Outward NAO _t +Inward SOI _{t-2}	28	1188.08	1247.10	5.34	0.01	0.14
Outward NAO _t	27	1188.10	1244.91	3.16	0.04	0.14
Outward NAO _{t-1}	27	1188.83	1245.64	3.88	0.03	0.11
Winter SOI _{t-1}	27	1189.25	1246.06	4.31	0.02	0.10
Inward SOI _{t-2}	27	1189.43	1246.24	4.48	0.02	0.09
Constant	26	1191.79	1246.39	4.64	0.02	0.00

^s: number of parameters.

^s: difference between the AICc of a given model and the lowest AICc.

[†]: AICc weight.

^{*}: proportion of temporal variations in apparent survival explained by the covariate considered (see Material and methods for details).

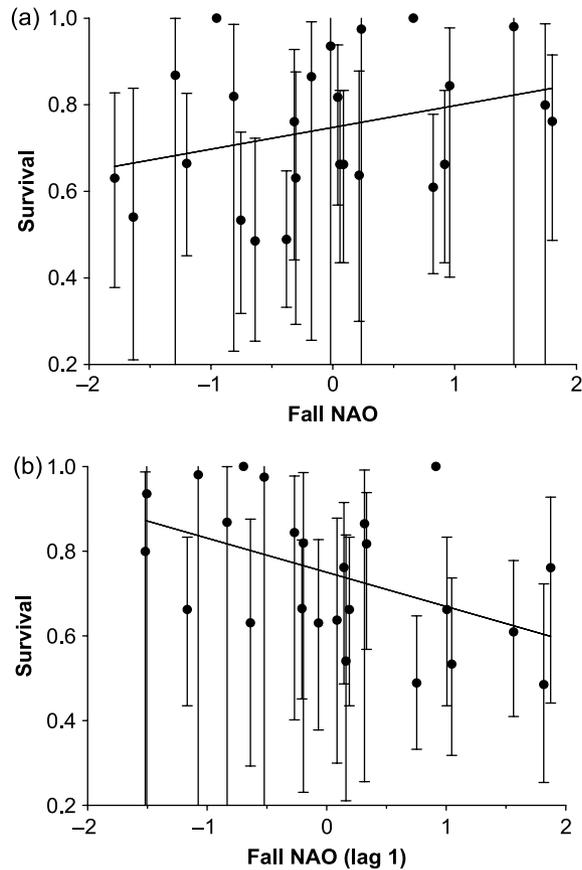


Figure 2. Annual survival (\pm 95% confidence intervals) in relation to Outward NAO (no time lag: graph (a) time lag of 1 year: graph (b)) in peregrine falcons breeding at Rankin Inlet, Nunavut, Canada, from 1982 to 2008 ($n = 264$ falcons).

1982 and 2008 are lower than those reported in other studies that have examined marked adult peregrines on their breeding territories. Mearns and Newton (1984) used turn over analysis to calculate apparent survival (0.91) for female peregrine falcons breeding in a non-migratory population in Scotland. Gould and Fuller (1995) calculated apparent survival rates of highly migratory female peregrine falcons breeding in Greenland between 1983 and 1991 using mark-resighting modeling (0.78 ± 0.03), and Tordoff and Redig (1997) reported apparent survival estimates for males (0.79) and females (0.93) breeding in the midwest United States between 1987 and 1995 using turn over analysis. Kauffman et al. (2003) reported that survival for non-migratory adult falcons in California between 1977 and 1999 was 0.85 ± 0.03 . Newton (2003) pointed out that the estimates of apparent survival calculated during the 1980s often coincided with increasing population growth after the all time lows recorded in the 1970s, and implied that higher estimates of apparent survival may have been a consequence of reduced density dependent mortality. Regardless, the non-migratory populations in Scotland and California had the highest estimate of survival, and the lowest estimate was calculated for the highly migratory population breeding in Greenland. Although several other differences undoubtedly exist among resident and migratory populations, the inherent risks associated with migration are consistent

with lower apparent survival calculated for the Rankin Inlet population.

Peregrine falcons initiated their outward migration from our study area in the third week of September and satellite data suggest that their outward migration has progressed significantly by the third week in October with most birds poised to cross or having crossed the Gulf of Mexico (Franke unpubl.). Moreover, satellite tracking has revealed that peregrines were more inclined to cross water-bodies such as the Gulf of Mexico and/or the Caribbean Sea during outward migration while northern routes rarely included water crossing (Fuller et al. 1998, McGrady et al. 2006). A greater number of storms (including hurricanes) tend to enter the Gulf of Mexico or make landfall on the eastern United States seaboard under meteorological conditions that lead to positive NAO values (Scott et al. 2003). Based on these general patterns, one would expect adult survivorship to be negatively related to Fall NAO values, rather than the positive association reported in this study. However, the North East Trade Winds tend also to be stronger under positive NAO conditions (Wanner et al. 2001), and we suggest that despite greater frequency and severity of storms, including a higher likelihood of encountering a hurricane, the increase in the NE Trade Winds improved overall conditions during migration and could thus increase the likelihood of safely crossing large expanses of water between Florida and Cuba, Louisiana and the Yucatan, Haiti and Colombia, and the Panama Gulf, for example.

In addition to the positive effect of NAO values on falcon apparent survival in the current year, we observed a negative effect of NAO values during September and October of the previous year. Other studies (Jaksic et al. 1997, Ottersen et al. 2001) have suggested that lag effects, like the one evident in this study, are most likely mediated through the food chain, and can indirectly influence predator apparent survival through abundance and distribution of prey. In this study, partitioning of environmental effects according to the falcons' life cycle is appropriate for the unlagged effects, but it is improper for the lagged effects as the relationship is dependent entirely on the manner in which prey species were influenced by NAO. Regardless, environmental conditions associated with years with high NAO values could have led to poor prey conditions that resulted in low reproduction or survival and, as a consequence, low prey abundance in next year. Consequently, the succession of a low NAO in year $t - 1$ and a high NAO in year t would represent the best conditions for peregrines (in year t), i.e. the ones associated with high food availability and good weather conditions in year t . Although it is well established that time lags associated with climate indices can have significant effects on adult survivorship in seabirds (Barbraud and Weimerskirch 2001, Frederiksen et al. 2004, Sandvik et al. 2005, Le Bohec et al. 2008), it is currently unclear how or when this effect might manifest itself in peregrines. The negative effect of NAO values during September and October in year $(t - 1)$ may indeed reduce abundance and/or distribution of prey. However, despite our results, we caution against assuming that the effect on peregrine survival necessarily occurs the following fall. For example, conditions in year $(t - 1)$ that lead to poor survival of avian prey and therefore smaller breeding

populations in year_(t) can potentially lower the abundance of avian prey on the winter grounds and therefore reduce survival of peregrines in the interval between year_(t) and year_(t+1). In other words, although a lagged Fall NAO remains a key model variable, its main effect on the peregrines themselves could be during winter.

Historically research has focused on birds on the breeding grounds. Even for a well studied raptor of near cosmopolitan distribution, knowledge of peregrine migration and wintering ecology is lacking. This lack of information from a time period that represents the majority of the year when falcons may face ecological challenges that potentially increases mortality can serve to undermine established conservation and management actions. Although the specific causal mechanisms influencing apparent survival in our study population remain unknown, our results reinforce the view that migration is a key life history stage. Therefore, climatic events affecting peregrine falcons perhaps through foraging and orienting could ultimately influence their apparent survival (Newton 2007). Potential consequences associated with climate change on animals remain poorly understood (Saether et al. 2006). However, the manner in which animal populations respond to climate variation is an important component required to predict effects of global climate change. By investigating the effects of local and broad scale weather effects on demography we gain awareness of potential pinch points that may exist across different life history stages of an annual cycle, particularly for long-lived migrants that may be particularly susceptible to climatic variability (Timmermann et al. 1999).

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Appendix 1. Environmental effects on peregrine falcon apparent annual survival rates, Rankin Inlet, Nunavut, Canada (data from 1982 to 2008, n = 110 males and 154 females). Resighting rates were modeled as p_i^{s+} (Table 2). An additive sex effect on resighting was included in all models.

Model	np [§]	Deviance	AICc	Δ AICc [§]	w _i [†]	Pseudo-R ^{2‡}
Outward NAO+Outward NAO _{t-1}	28	1182.733	1241.757	0.000	0.201	0.35
Outward NAO+Outward NAO _{t-1} +Winter SOI _{t-1}	29	1182.64	1243.886	2.129	0.069	0.35
Outward NAO+Outward NAO _{t-1} + Inward SOI _{t-1}	29	1182.667	1243.913	2.156	0.068	0.35
Outward NAO+Winter SOI _{t-1}	28	1185.497	1244.521	2.764	0.050	0.24
Outward NAO+Inward SOI _{t-2}	28	1188.076	1247.100	5.343	0.014	0.14
Outward NAO	27	1188.102	1244.912	3.155	0.042	0.14
Outward NAO _{t-1}	27	1188.831	1245.641	3.884	0.029	0.11
Winter SOI _{t-1}	27	1189.252	1246.062	4.305	0.023	0.10
Inward SOI _{t-2}	27	1189.425	1246.235	4.478	0.021	0.09
Constant	26	1191.787	1246.392	4.635	0.020	0.00
Outward SOI _{t-2}	27	1189.839	1246.649	4.892	0.017	0.07
Inward SOI _{t-1}	27	1189.866	1246.676	4.919	0.017	0.07
Inward SOI _{t-3}	27	1189.942	1246.752	4.995	0.017	0.07
Inward NAO	27	1190.303	1247.113	5.356	0.014	0.06
linear trend	27	1190.491	1247.301	5.544	0.013	0.05
Inward SOI	27	1190.881	1247.691	5.934	0.010	0.03
Outward SOI _{t-3}	27	1191.264	1248.074	6.317	0.009	0.02
Outward SOI _{t-1}	27	1191.645	1248.455	6.698	0.007	0.01
Outward SOI	27	1191.73	1248.540	6.783	0.007	0.00
Outward NAO _{t-1} +Winter SOI _{t-1}	28	1188.514	1247.538	5.781	0.011	0.13
Winter SOI _{t-3}	27	1191.137	1247.947	6.190	0.009	0.02
Winter SOI	27	1191.21	1248.020	6.263	0.009	0.02
Winter SOI _{t-2}	27	1191.368	1248.178	6.421	0.008	0.02
Outward NAO _{t-3}	27	1191.377	1248.187	6.430	0.008	0.02
Average summer temperature	27	1191.544	1248.354	6.597	0.007	0.01
Outward NAO _{t-2}	27	1191.621	1248.431	6.674	0.007	0.01
Inward NAO _{t-1}	27	1191.633	1248.443	6.686	0.007	0.01
Inward NAO _{t-3}	27	1191.637	1248.447	6.690	0.007	0.01
Inward NAO _{t-2}	27	1191.643	1248.453	6.696	0.007	0.01
Total summer precipitation	27	1191.786	1248.596	6.839	0.007	0.00
Time	50	1165.718	1275.621	33.864	0.000	1.00

[§] number of parameters.

[§]: difference between the AICc of a given model and the lowest AICc.

[†]: AICc weight.

[‡]: proportion of temporal variations in apparent survival explained by the covariate considered (see Introduction for details).

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