Climate change and the demographic demise of a hoarding bird living on the edge

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Population declines along the lower-latitude edge of a species' range may be diagnostic of climate change. We report evidence that climate change has contributed to deteriorating reproductive success in a rapidly declining population of the grey jay (*Perisoreus canadensis*) at the southern edge of its range. This non-migratory bird of boreal and subalpine forest lives on permanent territories, where it hoards enormous amounts of food for winter and then breeds very early, under still-wintery conditions. We hypothesized that warmer autumns have increased the perishability of hoards and compromised subsequent breeding attempts. Our analysis confirmed that warm autumns, especially when followed by cold late winters, have led to delayed breeding and reduced reproductive success. Our findings uniquely show that weather months before the breeding season impact the timing and success of breeding. Warm autumns apparently represent hostile conditions for this species, because it relies on cold storage. Our study population may be especially vulnerable, because it is situated at the southern edge of the range, where the potential for hoard rot is most pronounced. This population's demise may signal a climate-driven range contraction through local extinctions along the trailing edge.

Keywords: climate change; demography; grey jay; *Perisoreus canadensis*; hoarding

1. INTRODUCTION

A number of evidences indicate that climate change has already influenced the phenology and distribution of a great variety of taxa (Walther *et al.* 2005). A recent meta-analysis documented significant poleward shifts in species' geographical ranges averaging 6.1 km per decade and significant advancement of spring events averaging 2.3 days per decade (Parmesan & Lohe 2003). To date, a diagnostic fingerprint that climate change is already having these effects has been documented for 279 species (Parmesan & Lohe 2003). These fingerprints indicate that shifts in phenology, distribution and abundance are overwhelming in the direction predicted by climate change.

In birds, considerable evidences indicate trends towards earlier breeding (e.g. Both *et al.* 2004), which may often be mistimed owing to the decoupling of peak food demands by nestlings and invertebrate food supplies (Visser *et al.* 1998, 2004, 2006; Both *et al.* 2006). This mismatch between spring events may be a common by-product of climate change, but we describe evidence for a novel mechanism underlying the detrimental impacts of climate change on avian breeding. Irrespective of the underlying mechanism, detrimental impacts of climate change have apparently contributed to poleward range shifts in some bird species (e.g. Thomas & Lennon 1999; Hickling *et al.* 2006).

Populations at the lower-latitude edge may be especially vulnerable to climate change. Detailed studies on such populations are needed, because while warming may promote establishment of populations along the higher-latitude edge, it may contribute to extinction of populations along the lower-latitude edge (Parmesan &

Lohe 2003). Poleward shifts in ranges are projected to cause not only the losses of many of these lower-edge populations and the genetic diversity stored in them (Hampe & Petit 2005), but also the commitment of many species to extinction (Thomas *et al.* 2004). Thus, the demise of populations along the lower-latitude edge may signal poleward range shift, reduction in total population size (Shoo *et al.* 2005), loss of evolutionary history and even extinction.

A climate-related decline in a population of grey jays (*Perisoreus canadensis*) at the southern edge of the range is reported here. These non-migratory birds rely on hoarded food, which would seem to buffer them against mistiming caused by warming. However, we reasoned that if cool weather during autumn ordinarily aids preservation of hoards, then warm autumns could create a latent form of food limitation. We test this 'hoard-rot hypothesis', confirming that warm autumns delay and compromise breeding, especially when followed by cold late winters. We also consider the possibility that warm late winters induce advanced breeding, which could backfire when followed by severe weather. We provide minimal support for this 'mistiming hypothesis'. Climate change has apparently contributed to the demise of this trailing-edge population, primarily through detrimental effects of warm autumns.

2. STUDY SPECIES

Grey jays occupy permanent, group-held territories in boreal and subalpine forests of North America (Strickland & Ouellet 1993). Territorial groups comprise a mated pair, which may be accompanied by a non-breeder (a philopatric offspring that evicted its subordinate siblings or an immigrant auxiliary). Nesting occurs extremely early, under wintry conditions, without self-regenerating food

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available at the onset. Clutches are initiated as early as February, when temperatures in our study area remain well below freezing and snow cover approaches the annual maximum. Fledging begins in April, weeks before leaf-out and the return of most migratory birds. The jays depend on stored food for overwinter survival and early breeding. During summer and autumn, they place many thousands of food items in arboreal crevices throughout the territory. Seeds are notably absent from the stored food; apparently perishable items are prominent (e.g. berries, arthropods, fungi and vertebrate flesh). This raises the question of how stored food can last in sufficient quantities until the onset of food-preserving temperatures, particularly during warm autumns.

3. FIELD METHODS AND DATA SOURCES

Our study population is located in Algonquin Provincial Park (APP), Ontario, Canada (45°33' N, 78°38' W). We used data collected during 1980–2006, when as many as 46 territories (occupied and vacant) were monitored annually. Of these, an average of 18.2 occupied territories (range 13–23) was judged to be appropriate for inclusion in our analysis of reproductive timing and success. Other territories were excluded for the following reasons. First, we excluded those territories where jays had access to supplemental food, which tends to advance laying date and increase the number of nestlings. These territories, though, were included in an opportunistic, follow-up analysis to test whether jays in unsupplemented territories were food limited, as assumed by the hoard-rot hypothesis. Second, we excluded those territories lacking extensive tracts of suitable boreal habitat and previously judged to be of low quality. All such territories have gone vacant and remained so.

Through routine nest checks and annual autumn censuses, the following were determined for each territory: date of first egg, clutch size (i.e. maximum number of eggs known to exist in the nest, including during incubation), number of nestlings (i.e. banded approximately 11 days post-hatch) and whether the territory was occupied during autumn. We used climatic data (<http://www.climate.weatheroffice.ec.gc.ca/climateData/>) collected at the Ontario Climate Centre station in Dwight (2460H), specifically records of monthly mean temperature for specified periods as predictors of reproductive timing and success, and also used ice-in date for a lake in APP as a proxy for potential hoard rot during autumn.

4. DATA ANALYSIS

Statistical analyses used SPSS (2005) routines and the tests were two-tailed, unless otherwise specified. We performed time-series analysis using first-order autoregression (Prais–Winsten method). We first evaluated the trends in temperature, reproductive timing (median, owing to skew, first-egg date) and performance (mean clutch size and mean number of nestlings) and the proportion of territories occupied. We then evaluated whether mean temperatures during autumn ($TEMP_{OctNov}$) and late winter ($TEMP_{FebMar}$) were predictive of reproductive timing and success. ($TEMP_{OctNov}$ was not a significant predictor of $TEMP_{FebMar}$; $r^2=0.082$, $p=0.16$, $n=26$.) We reasoned that cool weather during autumn facilitates preservation of

perishable hoards and hence influences timing and success. We also considered that weather during late winter, which includes nest building and sometimes egg laying, should impact timing and perhaps success. We included year as a predictor variable to capture any temporal trends in the response variable not attributable to $TEMP_{OctNov}$ and $TEMP_{FebMar}$ *per se*.

We used information-theoretic model selection (Burnham & Anderson 2002). For each full model (i.e. with $TEMP_{OctNov}$, $TEMP_{FebMar}$ and YEAR as predictors) and all subset models, we calculated the Akaike information criterion with correction for small sample size: $AIC_c = n(\ln[RSS/n]) + 2K + 2K(K+1)/(n-K-1)$, where n is the sample size (years in time-series); RSS, the residual sum of squares; and K , the number of parameters (including α , δ and ϵ). The first term on the right-hand side represents the fit to data, the second term represents the penalty for including K parameters and the third term represents the correction for small sample size. Models were ranked from best to worst based on the ascending AIC_c values. ΔAIC_c was calculated as the difference between each AIC_c value and the smallest value (i.e. for the best model $\Delta AIC_c=0$). We calculated the relative likelihood of each model as $\exp[(-0.5)(\Delta AIC_c)]$. Finally, we calculated weight, w , by dividing each model's relative likelihood by the sum of relative likelihoods. These weights represent information content. The ratio of weights represents relative support (i.e. w_i/w_j represents support for model i versus j). We report ΔAIC_c and w , as well as r^2 .

5. RESULTS AND INTERPRETATION

Analysis revealed some evidence for a noisy warming trend over the past three decades near our study area. Air temperature throughout the year (mean of mean monthly temperatures) increased, on an average, by about 0.4 °C per decade ($\beta=0.045$, $r^2=0.15$, $p=0.021$, one-tailed) since 1975. Mean temperature increased at similar rates during autumn and late winter, the periods we reasoned would have the greatest impact on jays. The trend was significant for autumn ($TEMP_{OctNov}$: $\beta=0.047$, $r^2=0.10$, $p=0.048$, one-tailed), but not for late winter ($TEMP_{FebMar}$: $\beta=0.037$, $r^2=0.02$, $p=0.22$, one-tailed). Corresponding trends during the interval (1979–2004) matching our time-series of jay data were positive ($\beta>0.022$, but $ps>0.16$). Overall, we detected some evidence for local warming, with considerable interannual variation.

Our study population shrank, as revealed by the declining rates of territorial occupancy (figure 1; $\beta=-0.022$, $r^2=0.63$, $p=2.4\times 10^{-6}$; exponential decay model provides better fit: $r^2=0.84$). New vacancies outnumbered reoccupations in 20 out of 26 years (binomial $p=0.0012$, accounting for one tie). The trend in territorial occupancy rate has not improved ($\beta=-0.004$, $r^2=0.03$, $p=0.42$). Having documented this decline, we next evaluate the influence of climate.

Jays advanced their breeding season by about 3.1 days per decade on an average (figure 2a; $\beta=-0.309$, $r^2=0.20$, $p=0.024$). Reproductive performance declined significantly, as indexed by both mean clutch size ($\beta=-0.021$, $r^2=0.20$, $p=0.026$) and mean number of nestlings (figure 2b; $\beta=-0.018$, $r^2=0.16$, $p=0.045$). Having established these trends, we then evaluated whether temperature during autumn ($TEMP_{OctNov}$) and late winter

Figure 1. Proportion of territories occupied by grey jays during 1981–2006 (calculated as number of territories occupied during breeding season of year t divided by number of territories monitored during year t). Fitted curve is based on exponential decay model ($y = 3 \times 10^{30} e^{-0.035x}$, $r^2 = 0.84$).

(TEMP_{FebMar}) could account for variability in timing and performance. In doing so, we test whether breeding was delayed and less successful following warmer autumns, as predicted by the hoard-rot hypothesis.

Both TEMP_{FebMar} and TEMP_{OctNov} were important predictors of timing (median first-egg date), with year included in the model (table 1). Females initiated egg laying earlier during warmer late winters ($\beta = -1.93$, $p = 0.0008$), following colder autumns ($\beta = 1.66$, $p = 0.042$), and in recent years ($\beta = -0.35$, $p = 0.0005$). The next best model included TEMP_{FebMar} and YEAR. This model received approximately 30 times more support than the model including TEMP_{OctNov} and YEAR (i.e. based on the ratio of w_i s = 0.319/0.010). Thus, timing of breeding was apparently influenced by temperature during both autumn and late winter, with late winter having a stronger influence.

In our analysis of reproductive performance as indexed by mean clutch size, TEMP_{OctNov} was the only predictor included in all the 'good' models ($\Delta AIC_c < 2$). The best model indicated that clutches were larger following colder autumns ($\beta = -0.11$, $p = 0.007$), during warmer late winters ($\beta = 0.052$, $p = 0.059$), and earlier in the time-series ($\beta = -0.018$, $p = 0.020$). Two exceptional cases may be attributable to climatic anomalies. In 2001, the smallest mean clutch size corresponded with the second earliest median first-egg date; February was the rainiest since 1980, with the highest total precipitation. In 1992, the very small mean clutch size corresponded with second earliest median first-egg date, apparently owing to cold weather in March (second coldest). More typically, we could reliably predict mean clutch size based on TEMP_{OctNov}, TEMP_{FebMar} and YEAR.

In our analysis of reproductive performance as indexed by mean number of nestlings, TEMP_{OctNov} was the only temperature variable included in the good models. This variable, by itself, was not a very significant predictor ($\beta = -0.12$, $p = 0.08$) of lower reproductive performance following warmer autumns.

Figure 2. Temporal trends in (a) median first-egg date and (b) mean number of nestlings. Fitted lines are based on first-order autoregressive model.

Figure 3 provides further evidence that reproductive success has been compromised by warm autumns. The proportion of mated pairs producing at least one nestling tended to be low following warm autumns (two-dimensional Kolmogorov–Smirnov test (Garvey *et al.* 1998): $D = 0.135$, $p = 0.017$, $x = -4.90$, $y = 0.12$), where ice-in date for a local lake indexes hoard-rot potential. Reproductive success was low (negative residual) in 10 out of 11 years when the preceding ice-in had been late (positive residual), i.e. there was a 91% chance of low success when the opportunity for hoard rot had been high in the preceding autumn. No similar pattern emerged for a separate set of territories, where jays had access to supplemental food throughout winter ($D = 0.056$, $p = 0.81$, $x = -2.51$, $y = 0.13$; mean $n = 4.1$ territories per year). In these supplemented territories, breeding attempts were just as likely to succeed following warm (six cases) versus cold autumns (five cases). Thus, jays in supplemented territories, with chronic access to superabundant food, were apparently buffered against deleterious impacts of warm autumns.

Two final analyses provide additional support for our assumption that food limitation could cause delayed and less successful breeding. Median first-egg date was later in unsupplemented than in supplemented territories in every year but one (binomial $p = 7.7 \times 10^{-7}$; mean $n = 4.0$ territories). Likewise, in a preponderance of years (22 of 25), mean clutch size was smaller in unsupplemented than in supplemented territories ($p = 7.8 \times 10^{-5}$). These results

Table 1. Models of reproductive timing and success, with mean temperature during two periods and year as predictors (for clarity α , δ and ϵ are not listed). (Models ordered from best to worst according to ΔAIC_c , ΔAIC_c , weight w and r^2 (based on autoregression) are shown. Italics indicate 'good' models (i.e. $\Delta\text{AIC}_c < 2$).)

dependent variable	model	ΔAIC_c	w	r^2
median first-egg date	$\text{TEMP}_{\text{FebMar}} + \text{YEAR} + \text{TEMP}_{\text{OctNov}}$	0	0.572	0.590
	$\text{TEMP}_{\text{FebMar}} + \text{YEAR}$	1.167	0.319	0.455
	$\text{TEMP}_{\text{FebMar}}$	5.318	0.040	0.179
	YEAR	5.399	0.038	0.203
	$\text{TEMP}_{\text{FebMar}} + \text{TEMP}_{\text{OctNov}}$	7.24	0.015	0.218
	$\text{YEAR} + \text{TEMP}_{\text{OctNov}}$	8.07	0.010	0.215
	$\text{TEMP}_{\text{OctNov}}$	9.886	0.004	0.009
mean clutch size	$\text{TEMP}_{\text{OctNov}} + \text{YEAR} + \text{TEMP}_{\text{FebMar}}$	0	0.354	0.471
	$\text{TEMP}_{\text{OctNov}} + \text{YEAR}$	0.766	0.241	0.362
	$\text{TEMP}_{\text{OctNov}} + \text{TEMP}_{\text{FebMar}}$	1.507	0.167	0.322
	$\text{TEMP}_{\text{OctNov}}$	1.816	0.143	0.220
	YEAR	3.643	0.057	0.197
	$\text{YEAR} + \text{TEMP}_{\text{FebMar}}$	5.256	0.026	0.242
	$\text{TEMP}_{\text{FebMar}}$	6.733	0.012	0.051
mean number of nestlings	YEAR	0	0.346	0.164
	$\text{YEAR} + \text{TEMP}_{\text{OctNov}}$	0.849	0.226	0.231
	$\text{TEMP}_{\text{OctNov}}$	0.976	0.212	0.122
	$\text{YEAR} + \text{TEMP}_{\text{FebMar}}$	3.153	0.071	0.165
	$\text{TEMP}_{\text{OctNov}} + \text{TEMP}_{\text{FebMar}}$	3.628	0.056	0.143
	$\text{TEMP}_{\text{OctNov}} + \text{YEAR} + \text{TEMP}_{\text{FebMar}}$	4.024	0.046	0.240
	$\text{TEMP}_{\text{FebMar}}$	4.19	0.042	5.0×10^{-5}

suggest that jays are food limited in the breeding season, despite having hoarded enormous amounts of food. Our findings suggest that jays have been especially food limited following warmer autumns in recent years and that the observed population decline can be provisionally attributed to climate change.

6. DISCUSSION

Our long-term study of a grey jay population situated at the southern edge of the range has revealed trends towards earlier breeding, declining reproductive performance and increasing rates of territorial vacancy. Our results suggest that warmer autumns in recent years have driven reductions in reproductive success. Following such autumns, jays have typically delayed breeding and produced fewer young ones. This result would be puzzling if observed for other birds, because warm autumns represent benign conditions for them. Superficially, delayed onset of winter may seem favourable even for grey jays, because it should lengthen the window of opportunity for food storage and hence increase the total accumulated hoard. For this species, however, warm autumns are apparently hostile, because this species relies on natural refrigeration to preserve its hoards. The grey jay is unusual among hoarders, because it relies on perishable food rather than on long-lasting seeds. Following delayed onset of hoard-preserving temperatures in some recent autumns, grey jays have delayed their breeding and suffered reduced success, consistent with our hoard-rot hypothesis.

A second way by which climate change might adversely affect reproductive success is through warmer late winters inducing jays to nest earlier. This apparently adaptive shift could backfire, particularly if it exposed nesting jays to major snowstorms and freezing rain. Our results provide little support for this mistiming hypothesis. In 2001, jays bred very early and unsuccessfully, apparently because

Figure 3. Relationship between relative (residual) ice-in date during autumn and relative (residual) proportion of mated pairs producing at least one nestling in the next breeding season. Residuals are based on first-order autoregressive models (year regressed on each variable separately).

wintry conditions prevailed early in the nesting season. More typically, warm late winters were favourable for breeding, particularly when they followed warm autumns. Our findings suggest that cold weather during late winter can exacerbate the food limitation created by late onset of winter, again in keeping with our hoard-rot hypothesis.

Our analysis focused on two fitness components, clutch size and number of nestlings. These components show declining trends, but why? Beyond the direct effect of increasing food limitation for experienced breeders, we implicate an Allee effect (Stephens & Sutherland 1999), where frequency of first-year breeders has increased as population density has fallen, and poor reproductive

success in these inexperienced breeders has accelerated the demographic demise. In saturated populations, grey jays rarely breed as yearlings. But, in our declining population, yearlings are increasingly the only individuals locally available to fill vacancies. The proportion of mated pairs where at least one member was a yearling has increased from zero since 1980 ($r_s = 0.42$, $p = 0.034$, $n = 26$), and such pairs have been less successful than other pairs in producing even a single nestling (medians 0% versus 66.7%; means 29.5% versus 67.0%; Wilcoxon signed-ranks exact test $p = 0.010$, $n = 13$ years). These inexperienced breeders may be especially prone to food limitation caused by warm autumns. They may compensate by divesting, sometimes even deserting the nest. While such adjustments may be adaptive, they would still tend to accelerate population decline.

To conclude, warm autumns in recent years have arguably increased the perishability of stored food, leading to delayed and less successful breeding and apparently to the ongoing decline of our study population. Causal attribution awaits future work in which we plan to: (i) test the hoard-rot hypothesis experimentally; (ii) perform path analysis to evaluate causal linkages among climate, fitness components including recruitment and survival, and population performance; and (iii) evaluate whether other populations along the southern edge of the range are undergoing similar declines, indicative of range contraction. While ample evidence indicates that increasingly warm weather in spring may induce premature breeding in birds (e.g. Both *et al.* 2006), our findings reveal a novel connection between climate change and avian reproduction. Warm weather during autumn, months before the breeding season, apparently creates hostile conditions for the grey jay, a hoarder that relies on cold storage and so may be especially prone to extinction along the southern edge of its range.

We thank M. Strickland-Pageot, R. Tozer, D. Tozer, D. Hanes, G. Hanes, R. Hawkins, B. Crins, K. Clute, M. Runtz, S. Strickland, L.-M. Strickland and others for their help in the field; L. Campbell, J. Vucetich, I. Hamilton and the Waite Lab for comments on the manuscript; and R. Tozer for the ice-in data. T.A.W. was supported by the NSF grant 0351037 and LIDGP grant, OSU Office of Research.

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