Latitudinal gradients in some, but not all, avian life history traits extend into the Arctic

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Latitudinal variation in avian life history strategies is well documented. Clutch size and nest success tend to increase with latitude, whereas longevity and developmental periods have been argued to decrease with latitude. However, these patterns are largely based on interspecific comparisons of species breeding at tropical and temperate latitudes. We compared the life history of Yellow Warblers *Setophaga petechia* breeding in arctic habitat at the northern extent of their range, in Inuvik, NWT (68°N), Canada, with those breeding in temperate habitat in Revelstoke, BC (50°N), and use data from 21 populations spanning 0–68°N to evaluate latitudinal trends in life history traits from tropical to arctic habitats. Females breeding in Inuvik laid first clutches that were slightly (although not significantly) larger and had higher nest success, which resulted in higher annual productivity compared with their low- latitude counterparts. Apparent adult survival rates were only marginally lower in Inuvik than in Revelstoke, whereas incubation and nestling periods in the arctic were similar to our temperate site. When comparing life history traits across the Yellow Warbler breeding range, we observed increases in clutch sizes and nest success with increasing latitude that appeared to be associated with declines in adult survival, though this relationship was weakened by the addition of our arctic site. We detected more moderate declines in incubation and nestling periods with increasing latitude. As we observed latitudinal variation in some life history traits, but not a consistent transition of traits associated with a shift from a slow to fast life history from tropical to arctic latitudes, our study suggests that the expectation for a general shift in life history traits may be over-simplified.

Keywords: latitude, passerine, reproduction, slow–fast continuum, survival, trade-off, Yellow Warbler.

Life history theory predicts that species with the ability to breed in a variety of habitats will evolve different strategies that optimize the trade-off between survival and reproduction under different environmental conditions (Stearns 1976, Berven & Gill 1983, Ricklefs & Wikelski 2002). Avian life history strategies appear to follow a continuum from slow life history strategies (characterized by late maturation, low fecundity and high survival) at one extreme, to fast life history strategies (characterized by early maturation, high fecundity and low survival) at the other (Saether & Bakke 2000, Ricklefs

& Wikelski 2002). Comparisons within and across species show that trait values associated with slow life histories tend to be more common for species inhabiting the southern hemisphere (Rowley & Russell 1991, Yom-Tov *et al.* 1994, Green & Cockburn 1999), whereas shifts toward faster life histories are observed with increasing latitude in the northern hemisphere. Clutch size and reproductive success tend to increase with latitude, whereas survival and developmental periods tend to decline with latitude (Cody 1966, Ricklefs 1969, Koenig 1986, Briskie 1995, Martin 1996, 2002, Robinson *et al.* 2008, Salgado-Ortiz *et al.* 2008).

Theories regarding avian life history evolution have been based largely on data from north-

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temperate systems (Martin 2004). Comparative studies that include data from birds that breed in the arctic are less common. Migrants that breed in the arctic may benefit from longer foraging periods and lower nest predation rates (Hussel 1972, Jetz et al. 2008, McKinnon et al. 2010, Rose & Lyon 2013) that increase productivity. However, shorter breeding seasons should favour greater investment in early clutches and shorter nesting cycles (Spencer & Steinhoff 1968). Finally, migration is costly and the distance travelled may be negatively correlated with adult survival (Sillett & Holmes 2002, Wikelski et al. 2003). Collectively, conditions in arctic habitat may therefore select for faster life histories characterized by high investment in early clutches, faster development rates and shorter lifespans. Although some studies suggest that arctic birds have shifted life history traits towards faster life-styles (Hussel 1972, Jetz et al. 2008), most arctic-breeding birds that have been studied tend to have narrow breeding distributions and/or tend to belong to taxonomic groups that exhibit high survival, high parental investment and care, and relatively long life spans, such as Arctic Terns Sterna paradisaea (Hatch 2002) and Common Murres Uria aalge (Ainley et al. 2002).

Comparative life history studies of species with broad breeding distributions that extend from tropical to arctic habitats provide an opportunity to evaluate changes in reproductive and demographic parameters along the latitudinal gradient. We describe the life history of Yellow Warblers Setophaga petechia breeding in Inuvik, NWT (68°N), Canada, at the northern extent of their range and compare it with a second population breeding 2000 km to the south in Revelstoke, BC (50°N, Drake et al. 2014), and other populations breeding across a latitudinal gradient from 0 to 68°N, to examine whether latitudinal trends in life history traits, that are apparent from tropical to temperate habitats (Salgado-Oritz et al. 2008), extend into the Arctic. We predicted that if (1) Yellow Warblers in the arctic benefit from greater food abundance and lower predation pressure, but the greater migration distance incurs a cost, and (2) low temperatures in the arctic delay the onset of breeding and limit re-nesting potential, then Yellow Warblers breeding in Inuvik would lay larger clutch sizes and fledge more young but have lower adult survival and shorter developmental periods compared to Yellow Warblers at lower latitudes. We also expected greater seasonal and annual variability in clutch sizes and development periods, nest success and productivity for Yellow Warblers in Inuvik due to the greater variability in weather conditions (Green & Cockburn 1999, Martin et al. 2009, Skagen & Adams 2012) and elevated costs of fledging late in the season (Murphy 1986, Young 1994).

METHODS

We collected detailed data on the breeding biology and demography of Yellow Warblers (aestevia group) near Inuvik, NWT (68°N, 133°W), and Revelstoke, BC (50°N, 118°W). In Inuvik, adults and nestlings were banded starting in 2009 and continuing through to 2011. Resight surveys for returned individuals were conducted from 2010 to 2012. In Revelstoke, adults and nestlings were banded from 2004 to 2016; resighting surveys were conducted from 2005 to 2017 (although 2007 was a year of less extensive monitoring). During 2009–2011, we tracked banded individuals at both sites and monitored male arrival, pair formation, clutch initiation, clutch sizes, incubation periods and nest fate. We monitored nestling periods in 2010 in Revelstoke, and in 2011 in Inuvik.

Study species

The Yellow Warbler complex comprises more than 40 subspecies divided into three main groups that vary in appearance and lifestyle. Migratory subspecies belong to the aestevia group that breed across most of North America. Breeding populations have been linked with their respective wintering grounds using band records, genetic markers and results from stable isotope analysis. North-western populations winter primarily in Mexico and Central America, and north-eastern populations winter mostly in Central America and the northern portion of South America (Boulet et al. 2006). Sedentary subspecies belong to the petechia (Golden Warbler) and erithachorides (Mangrove Warbler) groups. Golden Warblers are residents of the south-eastern USA and the Caribbean Islands. Mangrove Warblers are residents of Central America and northern South America. Migratory and sedentary Yellow Warblers may initiate one to five nesting attempts per season, but rarely fledge more than one brood (Lowther et al. 1999).

Study site characteristics

Yellow Warblers in Inuvik were monitored at one 20-ha site adjacent to the East Channel of the Mackenzie River. This low-elevation site (< 170 m) is located in riverside riparian habitat dominated by willow shrubs (*Salix* spp.) and is prone to seasonal flooding. Yellow Warblers in Revelstoke were monitored at three sites of 30–39 ha located in riparian habitat in the drawdown zone of the Arrow Lakes reservoir system. These sites are located at relatively low elevations (< 440 m) and varied in terms of their vegetation, ranging from plots dominated by mature stands of Black Cottonwood *Populus balsamifers* to riverside riparian habitat dominated by cottonwoods and willow shrubs (*Salix* spp.) and to dispersed willow patches (Quinlan & Green 2012). Like Inuvik, these sites are also prone to seasonal flooding.

Daily temperatures during the breeding season (first clutch initiation to latest active nest date) in Inuvik were lower and more variable compared with Revelstoke (Table 1). Males typically started arriving on the breeding grounds near the end of May in Inuvik, and after the third week of May in Revelstoke. However, the average range of male arrival days in Inuvik was approximately half of the range observed in Revelstoke (Table 1). On average, females in Inuvik initiated their first nests 6 days later compared with females in Revelstoke and the average breeding season length in Inuvik was 8 days shorter compared with Revelstoke (Table 1).

Field methods

We conducted systematic searches of our sites every 1–2 days beginning in mid-May in Inuvik and early May in Revelstoke to determine when adults arrived on the breeding grounds. We attempted to catch and band all breeding adults on our sites. Males were caught in mist-nets using call-playback upon arrival; females were caught with their mate upon arrival or near active nests later in the season. Individuals were sexed based on plumage (Pyle 1997). Adults were fitted with one metal and three colour bands to allow individuals/pairs to be monitored for the entire breeding season. Nests were found by following females carrying nest material or returning to active nests. Once located, nests were monitored every 3 days (range 1–4) to record nest stage (construction, laying, incubation and nestling), clutch/brood size, age of young, parental activity and nest fate (success or cause of nest failure). To ensure that we obtained precise hatch dates, nests were checked more frequently after day 8 of the incubation period. Nestlings were banded with one metal band 7 days following hatch day. In 2010 (Revelstoke) and 2011 (Inuvik) we intensified monitoring efforts to obtain more precise fledging dates in order to determine nestling periods. During these years, nests were checked each day following banding until nests were empty.

Characterization of breeding parameters

Clutch initiation dates were either directly observed for nests found during construction or laying, or were determined for nests with known hatch dates by backdating initiation dates for nests found during the incubation or nestling period (assuming a laying rate of 1 egg/day, Lowther *et al.* 1999). The breeding season was defined as the period between the first clutch initiation and the latest active nest date. Only complete clutches were included in our estimate of clutch size. We limited these clutches only to first nesting attempts that were not parasitized by Brown-headed Cowbirds *Molothrus ater* and which contained the same number of eggs on consecutive nest checks during the incubation period, or clutches that were observed during the laying period and at least once during the incubation period. Incubation periods were measured from and including the date of the penultimate egg to hatch day, and only nests with known clutch initiation dates, complete clutches and those that were successfully hatched were included in our estimates of incubation periods. Our estimates of incubation periods included first and replacement clutches (Inuvik: 19 replacement clutches, total nests = 87; Revelstoke: nine replacement clutches, total nests = 39). Nestling periods were measured from and including the day of hatch to the day of fledging and were estimated using only nests for which fledging events were directly observed. Our estimates of nestling periods included first and replacement clutches (Inuvik: four replacement clutches, total nests = 23; Revelstoke: four replacement clutches, total nests = 17). First and replacement clutches were included in our analysis of nest survival (Inuvik: 26 replacement clutches, total nests = 163; Revelstoke: 48 replacement clutches, total nests = 124).

Table 1. Daily temperatures, male arrival dates, clutch initiation dates and breeding season lengths in Inuvik, NT (68°N) and Revelstoke, BC (50°N) during 2009–2011.

	Mean daily temperature (°C)	Range in daily temperatures (°C)	Mean male arrival date (Julian)	Range in male arrival dates (Julian)	Mean Julian clutch initiation date (1st nest attempts)	Breeding season length (1st clutch initiation date to latest active nest date)
Inuvik						
2009	10.0 ± 0.5 (39)	3.3–16.5	154.0 ± 0.4 (35)	150–161	165.3 ± 0.6 (43)	38
2010	12.4 ± 0.5 (53)	5.6–21.8	149.6 ± 0.8 (23)	146–161	160.3 ± 0.7 (54)	53
2011	12.6 ± 0.8 (50)	−1.5 to 25.4	149.6 ± 1.0 (32)	142–162	166.3 ± 0.8 (52)	50
Overall	11.8 ± 0.4 (142)	2.5–21.2	151.3 ± 0.5 (90)	146–161	164.0 ± 0.5 (149)	47
Revelstoke						
2009	17.7 ± 0.3 (44)	13.4–21.5	140.7 ± 1.1 (25)	130–157	153.3 ± 0.4 (26)	43
2010	17.6 ± 0.4 (69)	9.9–24.3	139.1 ± 1.4 (22)	127–159	161.2 ± 1.4 (32)	69
2011	16.1 ± 0.3 (54)	12.1–22.2	146.5 ± 2.1 (23)	136–167	158.3 ± 1.3 (18)	52
Overall	17.1 ± 0.2 (167)	11.8–22.7	142.1 ± 1.0 (70)	131–161	157.8 ± 0.8 (76)	55

Daily temperatures were derived from Environment and Climate Change Canada (Inuvik: Station AWOS; Revelstoke: Station Revelstoke A; Environment and Climate Change Canada 2011). Means ± se, sample size in parentheses.

Nests parasitized by Brown-headed Cowbirds (which occurred in Revelstoke only) were removed from analyses of clutch size, incubation and nestling periods, but were used to determine clutch initiation dates, nest survival and annual productivity. Annual productivity was estimated based on the number of fledglings produced per female per season.

Latitudinal variation in life history traits of Yellow Warblers

We conducted a literature review to locate data on breeding and demography for additional breeding populations of Yellow Warblers across their range. Keyword searches ('Yellow Warbler', '*Dendroica petechia*' and '*Setophaga petechia*' in conjunction with 'breeding biology', 'demography' and 'life history') were conducted using Web of Science (Thomson Reuters 2011) and Google Scholar (Google 2012). We collated data for 21 populations of Yellow Warblers breeding over a 68° latitudinal gradient. We verified that published estimates were calculated using consistent methodology and, if necessary, adjusted estimates accordingly. We recalculated our estimates of nest survival using the classic Mayfield method (Mayfield 1975) to allow for comparison with other studies. We initially restricted our analysis of latitudinal variation in breeding traits to published estimates for which the methodology was clearly explained and for which sample sizes were greater than at least 10. In the few cases where studies did not provide enough information to determine

how estimates of life history traits were derived, we assumed that the most common method (based on other published studies) was used (clutch size: $n = 3$ studies, incubation period: $n = 3$, nestling period: $n = 3$, nest success: $n = 5$, % nests depredated: $n = 1$). Including these data points did not change our findings or interpretation of the results.

Statistical analyses

Variation in breeding traits between Inuvik and Revelstoke

Initial models examining variation in clutch size and incubation periods included site, year, date-of-first-egg and a squared date-of-first-egg term, as well as interaction terms between the main effects. Models examining variation in nestling periods did not include a year term, as we only collected precise data on nestling period for 1 year for each site. Dates-of-first-egg were standardized for each year and site by subtracting the first date by which at least 10% of first nests had been initiated. We used linear models to explore variation in incubation and nestling periods, and generalized linear models with Poisson distributions to evaluate variations in clutch size. We compared nested models; interaction terms and/or the squared date-of-first-egg terms were dropped from full models if analyses showed they were non-significant.

Daily nest survival and annual productivity

We examined site differences and annual and seasonal variation in daily nest survival probabilities

using the logistic exposure method (Shaffer 2004). We observed a three-way interaction between site, year and date terms during our preliminary analysis of factors influencing daily nest survival probabilities; we therefore used a univariate model to explore site differences, and then explored annual and seasonal variation in daily nest survival probabilities for each site separately. Exposure periods were determined using the 'Last Active B' method as described in Manolis *et al.* (2000). Hurdle models (which combine analyses of failure/success and the number of young fledged/successful nest) were used to examine site differences and annual variation in productivity. These models have two components: a hurdle component for zero counts (binomial response), and a truncated count component for positive counts (Zeileis *et al.* 2008).

Adult survivorship

Apparent adult survival probabilities for Yellow Warblers in Inuvik and Revelstoke were estimated using methods described by Lebreton *et al.* (1992) and were derived in the program MARK version 5.1 (White & Burnham 1999). Apparent adult survival was defined as the probability of an adult surviving and returning to the study site (adult survival φ) adjusted by the resighting probability for banded individuals (*p*). The Inuvik dataset (2009–2012) contained 242 individuals (119 females and 123 males) that contributed 138 between-year recaptures for a total of 380 encounter histories. The Revelstoke dataset (2004–2017) contained 494 individuals (250 females, 244 males) that contributed 330 between-year recaptures for a total of 824 encounter histories. Global models for both study sites allowed adult survival to vary as a function of sex and year. Global models allowed resighting probabilities to vary as a function of sex in Inuvik, and to vary with sex and between years with extensive monitoring (2005–2006 and 2008–2017) and the year with less extensive monitoring (2007) in Revelstoke. Preliminary analyses of the Revelstoke dataset indicated that there was no evidence of a temporal trend, and that our comparison of survival estimates between the two sites was not confounded by such a trend. We did not include age-related terms in our recapture models so that our data could be compared with other published survival estimates of Yellow Warblers. The goodness-of-fit for the global model was evaluated by estimating the variance inflation factor ($\hat{c}$) using the median

procedure implemented in program MARK (White & Burnham 1999, Cooch & White 2009). Our models fit the data relatively well; $\hat{c}$ was estimated to be 1.75 for Inuvik and 1.20 for Revelstoke (Burnham & Anderson 2002). We used a stepwise procedure in our survival analysis to minimize the number of candidate models. First, we determined the best model structure for the recapture rate. We then examined variation in survival using a candidate model set that included all combinations of the terms sex, time, all possible interactions, and a model with constant survival over time (denoted as '.') to serve as a null model (Cooch & White 2009). We used Akaike's information criterion corrected for small sample sizes (AICc) to rank competing models in the two datasets.

Latitudinal variation in breeding traits

Finally, linear models were used to examine latitudinal variation in clutch size, development periods, nest success and nest depredation rates of Yellow Warblers. We compared estimates of apparent survival in Inuvik and Revelstoke to all published estimates of annual apparent survival. We were unable to compare our estimates of annual productivity with those of other studies, because the vast majority of studies only provide estimates of fledglings per nesting attempt, and not per breeding female.

Means are reported ± se. All statistical analyses were completed in R (R Development Core Team, 2018).

RESULTS

Variation in breeding traits between Inuvik and Revelstoke

Female Yellow Warblers laid first clutches that were approximately half an egg larger in Inuvik than in Revelstoke, although this difference was not statistically significant (Inuvik: 4.81 ± 0.06 eggs, *n* = 100; Revelstoke: 4.33 ± 0.09 eggs, *n* = 52; Tables 2 and 3). First clutches did not vary among years or with dates-of-first-egg at either site (Table 3). Daily nest survival rates were higher in Inuvik (0.961 ± 0.01, *n* = 163) than in Revelstoke (0.952 ± 0.001, *n* = 124; $\chi^2_1 = 12.87$, *p* < 0.001, *n* = 287), and consequently nest success was higher in Inuvik (Tables 2 and 3). Nest depredation rates were approximately 20% lower in Inuvik

than in Revelstoke (Table 2). Observed rates of abandonment were similar at the two sites (Inuvik: 9%, Revelstoke: 10%).

Daily nest survival probabilities in Inuvik varied annually and seasonally. Daily nest survival probabilities in Inuvik were lower in 2011 than in 2009 and 2010 (Tables 2 and 3). In 2011, daily nest survival probabilities in Inuvik were lowest at the beginning of the season (June 1) and then rose sharply over a period of approximately 10 days and remained high as the season progressed (range 0.40–1.00). The full model included a squared date-of-first-egg term, indicating a non-linear trend of daily nest survival probability with date in 2011. Daily nest survival probabilities in Inuvik did not appear to vary with date-of-first-egg in 2009 or 2010 (Table 3). We did not detect seasonal or annual variation in daily nest survival probabilities in Revelstoke (Table 3).

Females in Inuvik produced more fledglings than females in Revelstoke (Inuvik: 2.96 ± 0.17, $n = 148$; Revelstoke: 1.91 ± 0.29, $n = 93$) as a consequence of being less likely to experience complete breeding failure and, if successful, of producing more fledglings over the course of the breeding season (Tables 2 and 3). During 2009–2011, 29% of female breeders failed to produce any fledglings in Inuvik, compared with 46% in Revelstoke. Female breeders that were successful produced an average of 4.17 ± 0.11 ($n = 105$) fledglings in Inuvik, and 3.49 ± 0.15 ($n = 51$) fledglings in Revelstoke. While annual productivity showed some variation among years in Inuvik, this variation was not significant for Inuvik or Revelstoke (Tables 2 and 3).

Incubation periods did not differ between Inuvik and Revelstoke. We observed a slight overall seasonal decline in incubation periods ($\beta = -0.02 \pm 0.01$); however, only Inuvik showed annual variability. Incubation periods in Inuvik were longer in 2009 than in 2010 and 2011 (Tables 2 and 3). Nestling periods were similar at the two sites and did not appear to vary throughout the breeding season at either site (Tables 2 and 3).

Adult survival in Inuvik and Revelstoke

Resighting probabilities did not vary with sex in Inuvik, but resighting probabilities of males were higher than those of females in Revelstoke (Tables 4 and 5). The top model estimated the resighting probability in Inuvik to be 0.92 ± 0.06.

Table 2. Breeding parameters of Yellow Warblers breeding in Inuvik, NT (68°N), and Revelstoke, BC (50°N), during 2009–2011.

	Clutch size (first attempt)	Incubation period (days)	Nestling period (days)	Daily nest survival probabilities	Nest success	% Nest depredation	Productivity (fledglings/female)
Inuvik							
2009	4.84 ± 0.11 (25)	12.05 ± 0.15 (18)	–	0.976 ± 0.005 (38)	0.55	32	3.37 ± 0.32 (41)
2010	4.91 ± 0.07 (35)	11.05 ± 0.10 (34)	–	0.977 ± 0.001 (64)	0.57	22	3.23 ± 0.27 (56)
2011	4.70 ± 0.10 (40)	10.66 ± 0.20 (35)	9.22 ± 0.18 (23)	0.937 ± 0.013 (61)	0.21	27	2.33 ± 0.30 (51)
Overall	4.81 ± 0.06 (100)	11.10 ± 0.11 (87)	9.22 ± 0.18 (23)	0.961 ± 0.005 (163)	0.38	27	2.96 ± 0.17(148)
Revelstoke							
2009	4.47 ± 0.11 (21)	10.94 ± 0.18 (17)	–	0.959 ± 0.000 (39)	0.37	48	1.86 ± 0.32 (35)
2010	4.35 ± 0.15 (20)	11.08 ± 0.23 (12)	9.29 ± 0.17 (17)	0.953 ± 0.000 (42)	0.32	47	1.97 ± 0.36 (30)
2011	4.00 ± 0.19 (11)	11.20 ± 0.29 (10)	–	0.944 ± 0.000 (43)	0.25	48	1.93 ± 0.37 (28)
Overall	4.33 ± 0.09 (52)	11.05 ± 0.13 (39)	9.29 ± 0.17 (17)	0.952 ± 0.001 (124)	0.31	48	1.91 ± 0.20 (93)

Daily nest survival probabilities (DNS) for each site were derived using logistic exposure models (Shaffer 2004; top model for Inuvik: DNS~year+(date-of-first-egg (dfe) + year × (dfe + dfe²); top model for Revelstoke: DNS~year + dfe). Nest success was calculated over the entire nesting period, including the laying, incubation and nestling intervals (24.18 and 23.68 days for Inuvik and Revelstoke; respectively). Nest predation estimates = % of total active nests that failed due to predation. Our measure of productivity included all nest attempts (failed and successful). Means ± se, sample size in parentheses.

Table 3. Analyses of clutch sizes, incubation and nestling periods, nest survival and productivity (fledglings per female) of Yellow Warblers breeding in Inuvik, NT (68°N), and Revelstoke, BC (50°N), during 2009–2011.

Predictor variable (*df*)	Clutch size (*n* = 152) χ^2 (*P*)	Incubation period (*n* = 126) χ^2 (*P*)	Nestling period (*n* = 40) χ^2 (*P*)	Daily nest survival Inuvik (*n* = 163) χ^2 (*P*)	Daily nest survival Revelstoke (*n* = 124) χ^2 (*P*)	Productivity (*n* = 241) χ^2 (*P*)
Site (1)	2.02 (0.156)	1.45 (0.228)	0.10 (0.756)	–	–	Binomial: 6.87 **(0.009)** Count: 4.65 **(0.031)**
Year (2)	0.19 (0.911)	9.45 **(0.009)**	–	6.82 **(0.033)**	0.79 (0.674)	Binomial: 4.86 (0.089) Count: 0.14 (0.932)
dfe (1)	0.37 (0.544)	3.75 **(0.053)**	0.00 (0.994)	7.36 **(0.007)**	0.05 (0.830)	
dfe+dfe^2 (1)	0.01 (0.913)	0.05 (0.820)	0.00 (0.949)	8.50 **(0.003)**	1.86 (0.172)	–
site × year (2)	0.16 (0.924)	18.99 (**< 0.001**)	–	–	–	Binomial: 2.86 (0.239) Count: 1.41 (0.494)
site × dfe (1)	0.38 (0.535)	0.00 (0.988)	0.00 (0.971)	–	–	–
year × dfe (2)	0.84 (0.656)	1.56 (0.457)	–	7.60 **(0.022)**	0.11 (0.948)	–
site × (dfe + dfe^2) (2)	0.15 (0.697)	2.54 (0.281)	0.26 (0.607)	–	–	–
year × (dfe + dfe^2) (4)	0.20 (0.906)	2.87 (0.580)	–	9.98 **(0.041)**	1.45 (0.836)	–

Dates-of-first-egg (dfe) were standardized by year and site by subtracting the earliest date by which at least 10% of nests had been initiated. Predictor variables were tested by comparing nested models. Interaction terms and the squared date-of-first-egg term (dfe^2) were dropped from full models if they were non-significant. Significant *P*-values are in bold type.

In contrast, in Revelstoke the resighting probability was estimated to be 0.96 ± 0.02 for males and 0.74 ± 0.06 for females.

Two models in the candidate model set examining variation in apparent annual survival in Inuvik received strong support. The top model suggested that males had higher annual apparent survival than females. However, this model received only marginally more support than the second model, in which apparent survival did not vary with sex (Table 4). Weighted model average estimates of apparent survival for adult males ranged from 0.45 to 0.48 during 2009–2012, and from 0.39 to 0.42 for adult females during 2009–2012 (Table 5).

One model in the candidate model set examining variation in apparent annual survival of Yellow Warblers in Revelstoke received strong support. This model included sex (Table 4). The weighted model average estimate of apparent survival was 0.51 for adult males and 0.42 for adult females in Revelstoke (Table 5). These estimates were marginally higher than those observed in Inuvik (weighted model average estimates averaged across years: male 0.47, female 0.41; Table 5).

Latitudinal variation in life history traits

Clutch sizes of Yellow Warbler populations increased with latitude; latitude explained 57% of the variation in clutch size of 16 populations breeding at latitudes ranging from 0 to 68° ($R^2 = 0.59$; $\chi^2_1 = 13.44$, $P < 0.001$, $n = 16$; Fig. 1a). Nest success increased from 26% at 20° latitude to 58% at 68° latitude ($R^2 = 0.40$, $\chi^2_1 = 5.14$, $P = 0.023$, $n = 10$, Fig. 1b). Consistent with this result, nest predation rates showed a steep latitudinal decline from 64% at 20°N to 27% at 68°N, although this relationship was not significant ($R^2 = 0.19$, $\chi^2_1 = 2.81$, $P = 0.094$, $n = 13$; Fig. 1c). Although adult survival rates for Yellow Warblers from the Arctic were slightly lower compared with tropical and temperate habitats (Fig. 1f), our arctic site did not show the expected decline and the decrease in survival from temperate to arctic habitats was smaller than anticipated. As we only had data from five populations across the Yellow Warbler range, we were unable to evaluate latitudinal variation in this trait. We observed a weak latitudinal decline in incubation periods, with those from populations breeding in tropical habitats being approximately 1.5 days longer than for those breeding in arctic habitats ($R^2 = 0.25$, $\chi^2_1 = 3.77$, $P = 0.052$, $n = 13$; 12.7 days at 0°N to 11.10 days at 68°N; Fig. 1d). Finally, nestling periods showed a slightly stronger latitudinal decline from 11 days at 20°N to 9.22 days at 68°N ($R^2 = 0.43$, $\chi^2_1 = 6.15$, $P = 0.013$, $n = 11$; Fig. 1e). Nestling and incubation periods at our arctic site were similar to those at temperate sites and did not show the expected decline.

Table 4. Top ranked models (ΔAICc < 2) describing recapture probabilities and apparent survival (adult survival (φ) adjusted by the resighting probability of banded individuals (*p*)) of Yellow Warblers breeding in Inuvik, NT (68°N, 2009–2012), and Revelstoke, BC (50°N, 2004–2017).

	K	*AICc*	*ΔAICc*	*wi*
Inuvik				
Recapture models				
φ(sex × time) *p*(.)	7	283.3	0.00	0.64
φ(sex × time) *p*(sex)	8	284.4	1.12	0.36
Survival models				
φ(sex) *p*(.)	3	277.0	0.00	0.39
φ(.) *p*(.)	2	277.2	0.22	0.35
Revelstoke				
Recapture models				
φ(sex × time) *p*(sex)	28	1175.7	0.00	0.63
φ(sex × time) *p*(sex + 2007)	29	1177.6	1.89	0.24
Survival models				
φ(sex) *p*(sex)	4	1149.6	0.00	0.89

Models in Inuvik and Revelstoke are ranked based on Aikake's Information Criterion corrected for small sample sizes (AICc). The variance inflation factor (ĉ) was estimated to be 1.75 in Inuvik and 1.2 in Revelstoke. *K* denotes the number of parameters in the model. ΔAICc denotes the change in Akaike's information criterion and *wi* denotes the AICc weights.

DISCUSSION

Historically, avian ecologists have considered that food limitation is a major driver of life history variation (Lack 1947, 1954, 1968, Martin 1987). Martin (1995, 2002), however, argued that nest predation and adult survival may be more important drivers of variation in clutch size, fecundity and incubation period in birds. Others have focused attention on seasonality and the role of breeding season and day length as explanations for variation in life history traits (Lack 1947, Spencer & Steinhoff 1968, Rose & Lyon 2013). Moving from tropical to arctic habitats within their broad breeding range, we observed shifts in a number of life history traits across the broad Yellow Warbler complex; however, some of these shifts were less apparent between temperate and arctic breeding sites. Arctic Yellow Warblers benefitted from low predation rates, which translated into greater nesting success and higher annual productivity compared with those breeding in temperate and tropical habitats. Apparent adult survival, although slightly lower, did not show the expected decline for these birds compared with their temperate counterparts. Similarly, developmental periods showed slight latitudinal declines across the breeding range, although these declines did not extend into the arctic.

Yellow Warbler populations within tropical and temperate latitudes appear to trade off adult survival and fecundity (Salgado-Oritz *et al.* 2008, this study); however, it is less clear whether this trend extends from temperate regions into the arctic. Estimates of apparent adult survival for Yellow Warblers calculated using mark–recapture methods varied from 0.52 to 0.41 in females and from 0.65 to 0.47 in males. We expected Yellow Warblers in the arctic to have lower adult survival rates due to their greater migration distance, as mortality during migration is known to be elevated (Sillett & Holmes 2002) and conditions on migration explain a large proportion of the annual variation in apparent adult survival of Yellow Warblers on the western flyway (Drake *et al.* 2014). Consistent with a latitudinal shift in this trait, the lowest adult survival estimates for males and females across the breeding range were derived from our arctic study. However, these estimates were similar to estimates from two temperate breeding sites in located in Revelstoke, BC, at 50°N (female: 0.42, male: 0.51; this study), and in Montana, USA, at 46°N (female: 0.41, male: 0.49, Cilimburg *et al.* 2002). Thus, when compared with survival estimates across this range, there is only limited support for

Table 5. Weighted model averages for male and female apparent survival (±unconditional standard errors) and 95% confidence intervals for Yellow Warblers breeding in Inuvik, NT (68°N, 2009–2012), and Revelstoke, BC (50°N, 2004–2017). As there was no support of a year effect in Revelstoke, only one estimate was provided for this site.

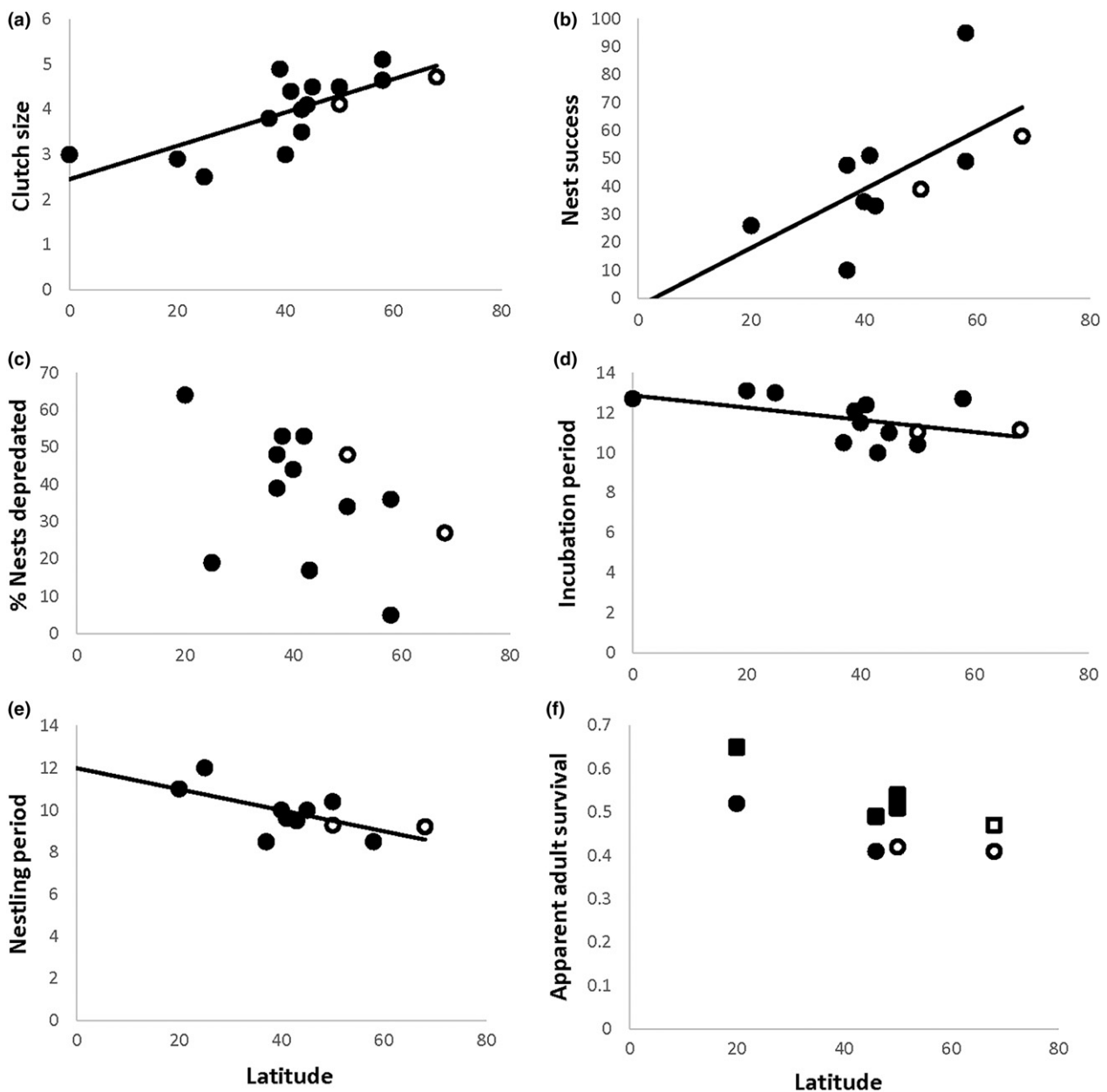| Site	Year	Male	95% CI	Female	95% CI
Inuvik	2009–2010	0.48 ± 0.07	0.35–0.61	0.42 ± 0.07	0.29–0.56
	2010–2011	0.48 ± 0.07	0.35–0.61	0.42 ± 0.07	0.29–0.56
	2011–2012	0.45 ± 0.07	0.32–0.58	0.39 ± 0.07	0.27–0.53
	2009–2012	0.47 ± 0.01	0.45–0.49	0.41 ± 0.01	0.39–0.43
Revelstoke	2004–2017	0.51 ± 0.03	0.46–0.56	0.42 ± 0.04	0.35–0.49

Figure 1. Breeding parameters of Yellow Warblers across a latitudinal gradient. Regression lines are drawn where latitudinal trends are statistically significant. (a) Clutch size. (b) Nest success (Mayfield nest survival probabilities). (c) Predation rates (% of total nests lost to predation). (d) Incubation period. (e) Nestling period. (f) Apparent adult survival rates of males (squares) and females (circles). Data points from this study not filled. Data for other latitudes were derived from Snow (1966) (0°N); Salgado-Oritz *et al.* (2008) (20°N); Prather & Cruz (1995) (25°N); Ortega & Ortega (2000) (37°N); Strusis-Timmer (2009) (37°N); Heath *et al.* (2010) (37°N); Latif *et al.* (2011) (38°N); Wilson & Holberton (2004) (39°N); Humple & Burnett (2010) (40°N); Mitra (1999) (41°N); Heltzel & Earnst (2006) (42°N); Young (1949) (43°N); Schrantz (1943) (43°N); Clark & Robertson (1981) (44°N); Lozano & Lemon (1999) (45°N); Cilimburg *et al.* (2002) (46°N); Goosen (1978) (50°N); Mazerolle *et al.* (2005) (50°N); Briskie (1995) (58°N) and Rogers (1994) (58°N).

declining adult survival rates (or additional migratory costs) between temperate and arctic latitudes.

Overall, we observed higher productivity in the arctic than in lower latitudes because clutches were slightly larger and nests were less likely to be predated. Latitude explained nearly 60% of the variation in the clutch size of Yellow Warblers; females in Inuvik laid clutches that were, on

average, 57% larger than clutches laid by females breeding in the Galapagos. However, compared with our temperate site, clutch sizes were not significantly higher for our arctic site. Clutch size has traditionally been argued to increase with latitude because of increased food availability (Lack 1954, 1968). We did not measure food availability in Inuvik or Revelstoke, but Schekkerman et al. (2003) found no evidence that arthropod abundance was higher in the Siberian arctic (75°N) than in the Netherlands (52°N). Lower nest predation rates in the arctic may select for greater investment in individual nesting attempts (Martin 1995), but predation rates across the breeding range are highly variable (Fig. 1c) and consequently unlikely to be a driver of clutch size in this species. The shorter breeding season could reduce the potential to re-nest (Martin & Wiebe 2004) and favour the production of larger clutches (Spencer & Steinhoff 1968). However, female Yellow Warblers in Inuvik and Revelstoke were both able to initiate up to three nesting attempts in a breeding season, and tend to be single-brooded across their range (Salgado-Oritz et al. 2008; this study). Therefore, the short breeding season experienced by this species in the arctic probably plays a limited role in influencing female investment in clutches. Although we observed marginally larger clutch sizes, significantly greater nest success and productivity and slightly lower adult survival for our arctic-breeding Yellow Warblers, the evidence that arctic-breeding Yellow Warblers trade off survival (as incurred by the costs of a greater migration distance) for fecundity is limited.

Latitudinal gradients in embryonic and nestling development that lead to shorter incubation and nestling periods at temperate than at tropical latitudes have been documented in several species (e.g. Yellow Warblers, Salgado-Oritz et al. 2008; Orange-crowned Warblers Vermivora celata, Sofaer 2012). Negative relationships between developmental periods and latitude could extend into the arctic if short breeding seasons favour fast embryonic and nestling development (Spencer & Steinhoff 1968, Schekkerman et al. 2003), or reduced adult survival favours increased investment in the current breeding attempts (Ricklefs 2000). Short incubation and nestling periods may be facilitated by longer photoperiods that promote embryonic development (Cooper et al. 2011) and increase foraging opportunities, thereby potentially increasing nest attentiveness and parental care, reducing

incubation and nestling periods, respectively (Chalfoun & Martin 2007, Londono et al. 2008, Rose & Lyon 2013).

Data collected as part of this study do not conflict with the Salgado-Oritz et al. (2008) conclusion that developmental periods decline as one moves from the tropics to temperate regions. The relationship between incubation and nestling periods and latitude was, however, weakened by the addition of data from more northern populations. We also found no evidence that incubation and nestling periods were shorter in an arctic population than in a north-temperate population, despite the shorter breeding season, lower adult survival and longer photoperiod.

There are several reasons why the latitudinal gradients in developmental rates may not have extended into the Arctic. First, females in Inuvik (where environmental conditions are relatively harsh) may have been unable or unwilling to maintain high nest attentiveness and incubation temperatures, leading to slower embryonic development rates (Hepp et al. 2006, Ardia et al. 2010). Alternatively, the low nest predation rates may have favoured longer developmental periods that have been associated with the production of higher quality offspring (Martin & Schwabl 2008, Martin et al. 2011). Thus, the effects of season length, adult survival and photoperiod on female behaviour and development rates may have been balanced by the counteracting negative effects of temperature and the benefits of slower development (when predation rates are low), leading to similar trait values for incubation and nestling periods in our two sites.

The low and fluctuating temperatures that characterize arctic habitats are likely to influence breeding phenology, nest success and development rates (Martin & Wiebe 2004), leading to greater temporal variation in the life history traits of Yellow Warblers breeding in the Arctic than at lower latitudes. Yellow Warblers breeding in Inuvik did encounter greater fluctuations in climatic conditions than those breeding in Revelstoke, which was reflected in the greater temporal variation in a number of life history traits at this site.

Seasonal variations in clutch sizes appear more pronounced in habitats with shorter breeding seasons and may relate to decreased survivorship of young fledged late in the season (Young 1994, Farnsworth & Simons 2001). We did not detect seasonal declines in first clutches at Inuvik or Revelstoke but given that first clutches are

initiated over a narrow set of dates early in the breeding season, our ability to detect a seasonal pattern would be weakened. However, we also failed to detect significant seasonal declines in clutch sizes during preliminary analyses that included replacement clutches. In conclusion, we found no evidence that female Yellow Warblers in Inuvik invested relatively more resources in early clutches compared with females in Revelstoke.

Incubation periods varied across years in Inuvik but not in Revelstoke. Incubation periods in Inuvik were longer in 2009, when mean daily temperatures were approximately 2°C lower than in 2010 and 2011. Incubation periods at both sites declined seasonally and were slightly shorter late in the season when it was warmer. This suggests that the ambient temperature influences nest attentiveness and/or nest temperatures and hence incubation periods (Hepp *et al.* 2006, Martin *et al.* 2007, Ardia *et al.* 2010). We observed evidence for annual and seasonal effects on daily nest survival rates in Inuvik, but we did not detect any variation in daily nest survival rates in Revelstoke. Finally, annual productivity appeared more variable in Inuvik than in Revelstoke. Females in Inuvik produced the fewest fledglings in 2011, a year in which the majority of early breeding attempts were abandoned or delayed during a 1 to 2-week period when the daily temperatures dropped from a high of 17 °C to a low of −1.5 °C, and the mean daily temperature was 6°C lower than during the same period in 2009 and 2010.

Previous work has described a general shift in life history traits of Yellow Warblers from tropical to temperate latitudes (Salgado-Oritz *et al.* 2008). Results from this study suggest that while latitudinal variations in some life history traits extend into the arctic, the differences between arctic and temperate-breeding Yellow Warblers are less than expected. Arctic-breeding Yellow Warblers appear to trade off adult survival and productivity, although evidence for this relationship is limited, as increases in clutch size and decreases in adult survival are marginal. Latitudinal gradients in developmental rates were detected but there is little evidence that incubation and nestling periods in the Arctic were shorter than in north temperate regions. Our study indicates that the expectation for a consistent shift in life history traits from tropical to arctic habitats may be over-simplified. Multiple environmental factors probably influence and select for variation in life history traits, and the combined influence of these factors may lead to unexpected trait values. However, the degree to which individual environmental factors influence different traits remains unclear and requires further studies that combine comparative life history observations with experimental evaluation/manipulation of temperature, predation, food availability and photoperiod.

DATA AVAILABILITY

The data that support the findings of this study are available upon request from the corresponding author for anyone wishing to conduct further meta-analyses. The multiple year adult re-sighting data are currently part of a PhD study and will be made available after the work is completed.

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