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Among the numerous demographic parameters that influence population size, unbiased estimates of pre-fledging survival remain difficult to obtain for precocial birds. In this study, we used capture–mark–recapture modeling to estimate pre-fledging survival in a population of temperate-nesting Canada geese *Branta canadensis maxima* that has undergone an exponential increase over the last two decades. We examined whether pre-fledging survival was affected by relative hatch date, initial brood size, mother age, and weather conditions at hatching. Between 2005 and 2014, 8679 goslings were marked with web-tags at hatching at two adjacent sites. A total of 3922 of these birds were initially recaptured and banded before fledging while 338 were recaptured and banded in subsequent years as after-hatching year birds. Multistate models with joint live and dead encounters were used to estimate pre-fledging survival and evaluate the effects of rearing sites, gosling characteristics, and weather conditions at hatching. Pre-fledging survival of Canada geese varied between 0.45 (95% CI: 0.41–0.50) and 0.75 (0.62–0.84) among years and sites with an overall mean of 0.62 (0.54–0.68). Survival rates were lower for late hatched birds and tended to increase with initial brood size and mother age. Weather conditions at hatching did not affect pre-fledging survival. Significant effect of hatch date on pre-fledging survival has often been described in geese nesting in highly seasonal environments (e.g. the arctic) but our findings of such a relationship in temperate-nesting Canada geese indicate that a selection pressure on the timing of breeding can also occur at more stable temperate latitudes.

Keywords: brood survival, capture–marking–recapture

Reproductive output of birds is affected by breeding propensity, clutch size, hatching success and pre-fledging survival. These fecundity components are often influenced by environmental conditions and can sometimes contribute more to variation in population dynamics than changes in adult survival (Koons et al. 2014). Although ecologists have explored population dynamics for several decades, some parameters are still difficult to assess accurately. In precocial birds like waterfowl, unbiased estimation of pre-fledging survival is particularly challenging. Survival rates are usually based on either a comparison of mean brood size through the rearing period, a comparison of the total number of young in a specific area through time, a change in mean brood size of marked adults or a change in mean brood size of marked young (Eberhardt et al. 1989a). Each of these methods has its own biases and can provide divergent estimates but those based on marked individuals provide the most reliable estimates (Stolley et al. 1999). Recent advances in modeling of capture–marking–recapture (CMR) data have provided the foundation for developing robust estimation methods for pre-fledging survival (Nicolai and Sedinger 2012).

Another challenge to understand population dynamics of precocial birds is to identify factors that influence pre-fledging survival. Causes of mortality generally include predation, starvation and hypothermia but the relative effects of these factors remain difficult to assess (Prop et al. 1984, Gosser and Conover 2000, Bowman et al. 2004). For precocial species like geese, the suitability of a rearing site can be affected by the quality and quantity of food resources, the presence of predators, the level of human disturbance, and the distance from natal sites (Hanson and Eberhardt 1971, Aubin et al. 1993, Hill et al. 2003, Lake et al. 2008, Dunton and Combs 2010). Low temperatures, heavy rains and strong winds prevailing during the first few days after hatching can reduce juvenile survival because they are not yet endothermic and have reduced fat reserves as shown for different goose species (Sedinger 1986, Sedinger et al. 1997). Goslings hatched just before the peak of resource abundance or quality can benefit from better feeding conditions enhancing their growth and survival (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994, Fondell et al. 2008). Larger families may also have an advantage over smaller ones and so,

they can feed and rest for longer periods, which can influence gosling growth and survival (Black and Owen 1983, Loonen et al. 1999; but see Sedinger et al. 2017). Finally, maternal experience, which typically increases with age, may play a role in juvenile growth and survival (Rockwell et al. 1993, Herzog 2002). Rockwell et al. (1993) found that brood survival in snow geese *Anser caerulescens* increased with mother's age up to six years old due possibly to their increasing knowledge about the best rearing sites and then declined due to senescence.

A temperate-nesting population of Canada geese *Branta canadensis maxima* became established in the early 1990s in a suburban area of southern Quebec and has grown exponentially since (Pannetier Lebeuf and Giroux 2014). The birds nest on a series of islands located at two contiguous sites along the Saint Lawrence River and the young are reared along the shorelines of islands and the mainland. Our first objective was to estimate pre-fledging survival of Canada geese using a robust CMR method. We then looked at the effects of gosling characteristics and weather conditions at hatching and predicted that survival should be higher for goslings hatched earlier, in larger families, and with middle-aged mothers. Finally, we predicted that survival should be lower for young that faced cold, windy and rainy conditions shortly after hatching.

Material and methods

Study area

The study was conducted along the St. Lawrence River, approximately 15 km northeast of Montreal, Quebec, Canada (45°40′N, 73°27′W). Canada geese nest on six large islands located near Varennes (total area: 98 ha) and on 18 smaller ones near Repentigny (total area: 123 ha). The Varennes and Repentigny sites are contiguous and encompassed approximately 11 km of the river. Islands are characterized by areas of open vegetation consisting of herbaceous vegetation, shrubs, and small trees (Pannetier Lebeuf and Giroux 2014). Nests are initiated between late March and mid-May, with first nests usually hatching in early May and the last ones in mid-June. Rearing takes place along the river shorelines. Families remain within the study area until they disperse to nearby locations in late summer (Beaumont et al. 2013). Rearing habitats include marshes and wet meadows as well as recreational, agricultural and residential lands along the St. Lawrence River.

Capture, marking and reencounters

Each year between 2005 and 2014, three systematic nest searches were carried out at regular intervals from early April to mid-May on each island of the Varennes and Repentigny sites (considered as the two natal sites). Nest location was recorded with a GPS unit and the number of eggs and parent's identity (if parents were already marked with a neck band), were noted. For nests found during laying, initiation date was calculated by backdating the discovery date considering a laying interval of 1.5 days (Cooper 1978). For nests found during incubation, the age of the embryos was estimated by flotation and the initiation date was based on the number of eggs laid and the incubation stage (Walter and Rusch 1997). In both cases, hatch date was estimated assuming a 28-day incubation period (Cooper 1978). Nests were visited on the expected hatch date or the following days if hatch had not yet occurred to mark newly hatched goslings in the right web with unique numbered web-tags (Alliston 1975). The day after hatching, a visit was made to determine the number of young that left the nests. All goslings were marked in 93% of the 1878 nests found on the islands. In half of the other nests with partial marking, all young but one were marked.

In late June or early July of each year, flocks of molting adults and pre-fledged juveniles were driven towards corral nets set along the shoreline by people on foot and in boats. The banding operations lasted 7–10 days each year and included 10–22 catches per year for a total of 151 catches split between the Varennes (n = 70) and Repentigny (n = 81) sites. The period of banding operations was adjusted each year to capture juveniles that were approximately 40–50 days old. The site where pre-fledged juveniles were recaptured was considered the rearing site. All geese were aged as local (pre-fledged juveniles) or after-hatching year (yearlings and adults) based on plumage, sexed by cloacal examination, and checked for the presence or apparent loss of web-tags (hole or tear in the right webbing). Unbanded birds were fitted with a United States Geological Survey aluminum leg band while a subsample of yearlings and adults (females with brood patches, birds with web-tags, and some randomly chosen males) also received an orange plastic neck-collar with a unique alphanumeric white code to allow visual identification at a distance. Groups of geese were released simultaneously after each banding drive to reduce the probability of family breakup. Band recovery data were obtained from the Bird Banding Laboratory (BBL) while recovered unbanded geese with web-tags were either reported through the BBL or directly to us.

Pre-fledging survival

General modeling approach

We extended the general approach based on double marking developed by Nicolai and Sedinger (2012) to estimate pre-fledging survival. We used a joint live-dead encounter multi-state model that allowed us to follow individuals through time and as a function of different states such as age and brood-rearing locations. Models based on joint live and dead encounters also allow estimation of true survival, an improvement over those relying solely on live encounters in which survival and site fidelity are confounded in the estimate of apparent survival. Multi-state models with joint live and dead encounters implemented in program MARK 8.0 (White and Burnham 1999) were thus used to estimate: 1) true survival (S_i^{ab}) defined as the probability that an animal alive in state a at time i was alive and in state b at time $i+1$, 2) recapture probability (p_i^b), which is the probability that a marked animal alive in state b at time i was recaptured at time i, 3) transition probability (ψ_i^{ab}), which is the conditional probability that an animal in state a at time i moved to state b at time $i+1$, given that the animal was alive at time $i+1$, and 4) recovery probability (r_i^b) defined as the probability

that a bird died in state b at time 1 and that its web-tag and/or band was recovered and reported. It was necessary to distinguish between birds only marked with a web-tag and those that had been recaptured and fitted with a leg band because of the differences in marker retention, recapture probabilities, and recovery probabilities between the two marker types. Individuals also could not transition between the web-tagged group to the leg banded one without being physically recaptured, and then fitted with a metal leg band. To force the transition from web-tagged to leg banded, we treated recaptured web-tagged birds as a loss on capture and immediately released them back as banded individuals from the same location (Reed et al. 2005). For the rest of their life they were considered as banded birds. Web-tagged individuals continued to remain in the web-tagged group until they were later recaptured (in which case they underwent the same process as above) or recovered. Double-marked (web-tag and band) individuals allowed us to model web-tag loss rate, assuming a band retention rate of 1.0 (Pilotte et al. 2014), and enabled us to produce parameter estimates that were not biased by marker loss. Each year was divided into two periods: the pre-fledging period from hatch to fledging which lasted 1.5 months and the post-fledging period which lasted 10.5 months. The modeling approach is described in details in Supplementary material Appendix 1 (Table A1–A9 and Fig. A1–A4).

Transition states

The states considered in our models included: age class (pre-fledged juveniles [a_0], post-fledged juveniles [a_1], yearlings [a_2], and adults [a_3]), time ($t_{0.5}$, t_1, t_2, …, t_{10}), marker type (web-tag or band), location (Varennes or Repentigny) and the status of the web-tag in double-marked individuals (present or lost) for a total of 18 states.

We determined brood movement probabilities between Varennes and Repentigny for birds caught just before fledging. Preliminary analyses indicated that dispersal rates were low and we therefore used the natal site as a proxy for the rearing site for all birds including those caught after their first summer. This conclusion is consistent with the studies of Eberhardt et al. (1989b) and Zicus (1981) who showed that most Canada goose families used only one rearing area until the young fledged.

The loss of web-tags was modeled from double-marked individuals as a function of age of the web-tag. We modeled web-tag loss using a 3-age class model (1, 2 and 3+ years old) and constrained loss probability to be a linear function of age of the web-tag. Age-specific web-tag loss probabilities were assumed to be the same across all cohorts.

Starting model and model selection

The starting model's structure integrated knowledge of the demographic patterns identified in a previous study of this population for post-fledged juveniles, yearlings, and adults (Pilotte et al. 2014). The model structure was constructed by considering:

1) full interaction between year (t) and location (l) for pre-fledging survival [$Sa_0(t \times l)$] and additive effect of year and age classes (a) for post-fledged juvenile, yearling, and adult survival [$Sa_1(a+t)$; $Sa_2(a+t)$; $Sa_3(a+t)$];

2) additive effect of year and age classes with an interaction among locations for post-fledged juvenile, yearling and adult recapture [$p((a+t) \times l)$];

3) full interactions among year, age classes, and locations for transitions of web-tagged individuals [$\psi(t \times a \times l)$], constant in time but varying by age and location for transitions representing web-tag loss, and

4) constant for all age classes and equal recovery for post-fledged juveniles, yearlings, and adults [$ra_0(.), ra_1(.) = ra_2(.) = ra_3(.)$]. Pilotte et al. (2014) showed that recovery probabilities were similar for all three age classes.

All parameters in this model were estimable except for the last survival and recapture events for post-fledging juvenile, yearling, and adult age classes.

Based on this starting model, a set of 36 reduced candidate models was developed (see Supplementary material Appendix 1 Table A10 and Table A11 for a description of all models tested and associated model selection). Time intervals between web-tagging and banding and between the banding and the next hatching event were fixed in MARK at 1.5 and 10.5 months, respectively. Model selection was based on Akaike's information criterion corrected for small sample size relative to the number of parameters (AICc). Goodness of fit tests for multistate data (WBWA, 3G.SR, 3G.Sm and M.ITEC tests) were conducted with program U-Care (see Choquet et al. 2005 for more details).

Effects of weather conditions and gosling characteristics

Weather variables at hatching (temperature, precipitation and wind) and gosling characteristics including initial brood size, relative hatch date, and mother age were added as individual covariates to the three best models. Minimum temperature (°C) and total precipitation (mm) were obtained for each day of the rearing period from the Rivière-des-Prairies station while wind speed (km h⁻¹) was obtained from the Varennes station, both stations being located less than 3 km from the study area (<http://climat.meteo.gc.ca/historical_data/search_historic_data_f.html>). The mean for the first four days of life of each gosling (hatch date + next three days) was computed for each variable. Initial brood size was the number of young leaving the nest where at least one young was marked. Relative hatch date of goslings was calculated as the number of days between the observed hatch date and the median hatch date for each cohort. The effect of mother age on pre-fledging survival was estimated for a subsample of individuals whose mother's age was known and had been fit with a neck-collar to allow identification at distance. A few females had been banded before 2005 as part of another banding program and were therefore more than 10 years old at the time of our study.

Two new sets of models incorporating individual covariates were tested. The first set considered all individuals and included a model with the interaction hatch date × brood size. The second set was based on a subsample of individuals whose mother age was known. To be sure that top models for this subsample were the same as for the whole sample, we also ran a subset of models with the subsample of juveniles with known-aged mothers without covariates and found

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that the top models remained in the same relative order as for the whole sample (Supplementary material Appendix 1 Table A11). Models were selected using AIC_c and regression coefficients (β) estimates were used to evaluate the effect of covariates on pre-fledging survival. Because of the limitations of our data in relation to the models' complexity, especially for the subsample of goslings with known-aged mothers, we limited the set of candidate models by omitting interactions between location and covariates but kept interactions between time and covariates. These limitations also prevented us from testing interactions between mother age and other covariates such as hatch date and brood size.

Results

From 2005 to 2014, 8678 goslings were fitted with a web-tag at hatching (6709 at Varennes and 1969 at Repentigny), representing 1878 broods. A total of 3922 were recaptured and banded at fledging and 338 thereafter as birds from one to six years old. In addition, 880 banded individuals were recaptured at least once for a total of 1319 recaptures. Finally, 966 banded geese were reported dead to the BBL while 28 unbanded geese with web-tags were reported to us or through the BBL. The subsample of individuals with known-aged mothers contained 2805 marked goslings from 611 broods, with 1407 individuals recaptured and banded at fledging.

Pre-fledging survival

The starting model fit the data well, as there were no differences between the observed and expected state of reencounter among individuals previously encountered (WBWA test p-value = 0.975 and 0.844), no differences between newly marked and previously marked individuals in the probability of being later reencountered in state x (3G. SR test p-value = 0.831 and 0.894), no differences between

observed and expected time and state of first reencounter between newly and previously marked individuals encountered at occasion i in state x and seen again at least once (3G.Sm test p-value = 0.878 and 0.673 for web-tagged and banded birds, respectively). The probability of being reencountered in the different states at time $i+1$ between animals in a given state at occasion i (M.ITEC) could not be computed. Overall, there was no overdispersion in the data ($\hat{c} = 1.0$; n = 8,678). The best-approximating model indicated that pre-fledging survival probability varied among years and natal sites ($w_i = 0.73$; Table 1). The second-best model, which did not include interactions between years and natal sites, and the third best model, which did not include an effect of natal site, had less support ($w_i = 0.18$, $\Delta AICc = 2.78$ and $w_i = 0.08$, $\Delta AICc = 4.27$, respectively). These three models accounted for 99% of the AICc weight (see Supplementary material Appendix 1 Table A10 for full model selection). Model-averaged estimates of pre-fledging survival varied between 0.45 (0.40–0.50) and 0.75 (0.62–0.84) over the 10-year period (Fig. 1) for an overall mean of 0.62 (0.54–0.68). Mean pre-fledging survival was 0.60 (0.55–0.65) and 0.63 (0.54–0.71) for Varennes and Repentigny, respectively, with the maximum difference between these two sites recorded in 2011 ($\Delta S_{a0} = 0.21$). The top three models included movement probabilities between Varennes and Repentigny that were equal across all age classes but varied among years and encounter sites (see Supplementary material Appendix 1 Table A12 for parameter estimates from the best model).

Web-tag loss and pre-fledging dispersal

The annual loss rate of web-tags was 0.023 (95% CI 0.014–0.039) during the first year, 0.021 (0.011–0.040) during the second year, and 0.071 (0.051–0.104) thereafter. The loss of web-tags during the pre-fledging period could not be evaluated because there were no double-marked individuals in that period. It was nevertheless considered

Table 1. Top model selection of pre-fledging survival of Canada geese in southern Quebec, 2005–2014.

Survival (Sa_0)	Survival ($Sa_1a_2a_3$)	Recapture ($p\ a_1a_2a_3$)	Transition ($\psi a_0 = a_1 = a_2 = a_3$)	Recovery (r)	ΔAICc	AICc weight (w_i)	K	Deviance	Description
$Sa_0(t \times l)$	$S(a+t)$	$p((a+t) \times l)$	$\psi(t \times l)$	$ra_0(.),a_1 = a_2 = a_3(.)$	0	0.73	135	35104.31	Survival dependent of time and location with full interactions
$Sa_0(t+l)$			$\psi(t \times l)$		2.78	0.18	126	35125.43	Survival dependent of time and location
$Sa_0(t)$			$\psi(t \times l)$		4.27	0.08	125	35128.94	Survival dependent of time
$Sa_0(l \times$ decline Clogit)			$\psi(t \times l)$		7.99	0.01	124	35189.78	Survival declining or stable through time
$Sa_0(l \times$ decline)			$\psi(t \times l)$		39.50	0.00	119	35231.49	Survival declining through time
$Sa_0(l)$			$\psi(t \times l)$		68.24	0.00	117	35264.28	Survival dependent of location
$Sa_0(.)$			$\psi(t \times l)$		70.01	0.00	116	35267.30	Survival constant through time and location

*Only top models are presented and only pre-fledged survival and transition for all age classes varied. a_0 = pre-fledged juvenile; a_1 = post-fledged juvenile; a_2 = yearling; a_3 = adult; t = time; l = location; a = age class; . = constant. Clogit = cumulative logit link. The + between variables indicates an additive effect and the × an interaction. K = number of estimable parameters. Akaike's information criterion (AICc) was for $\hat{c} = 1.0$.
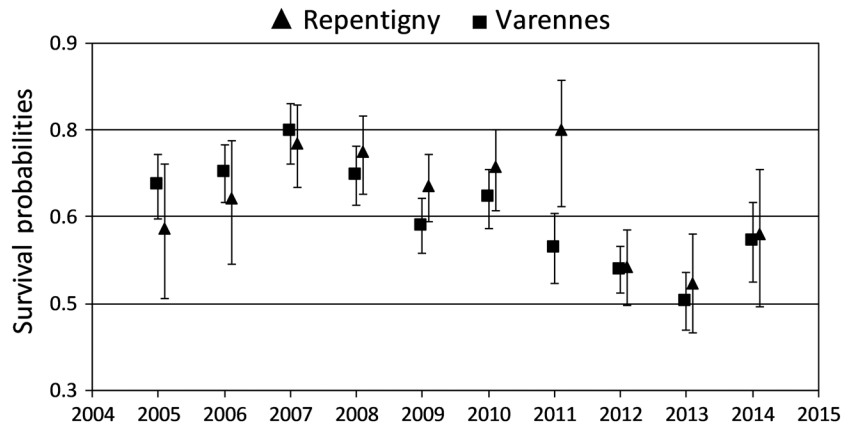
Figure 1. Estimates and 95% CIs of annual pre-fledging survival probabilities of Canada geese at Varennes and Repentigny, 2005–2014.

negligible since only 12 (0.3%) goslings were caught over the course of the study with apparent web-tag loss.

The probability that a juvenile hatched at Varennes stayed at that site during rearing varied between 0.59 (0.77–0.85) and 0.99 (0.96–1.00) among years while it varied between 0.74 (0.61–0.84) and 0.99 (0.93–1.00) for juveniles hatched at Repentigny. The use of the natal site as a proxy for the rearing site was therefore well justified.

Effects of weather conditions and gosling characteristics

The best approximating model included an effect of the relative hatch date and brood size ($w_i = 1.00$). Models which included only brood size, temperature, precipitation or wind speed had no support ($w_i = 0.00$; Table 2). Pre-fledging survival was higher for juveniles that hatched earlier in eight of the 10 years and was significant in 2007 ($\beta = -0.39$ [−0.67– −0.11]), 2009 ($\beta = -0.32$, [−0.57– −0.06]), and 2011 ($\beta = -0.46$, [−0.73– −0.18]; Fig. 2). Pre-fledging survival also increased with initial brood size in five of 10 years but was not significant in any years (range: $\beta = -0.16$ [−0.41–0.09] to $\beta = 0.28$ [0.00–0.56]; Fig. 3).

The model depicting a linear relationship of mother age on pre-fledging survival performed better than the model with a quadratic relationship ($\Delta AICc = 5.25$) and had a similar AICc than the model without covariates ($\Delta AICc = 0.28$; Table 3). Pre-fledging survival increased with mother age in seven of 10 years and was significant in

2010 ($\beta = 0.49$ [0.09–0.90]), 2012 ($\beta = 0.34$, [0.08–0.60]), and 2013 ($\beta = 0.27$, [0.01–0.55]; Fig. 4).

Discussion

Pre-fledging survival of temperate nesting Canada geese

Our study is among the first to use CMR analytical techniques to produce accurate estimates of true pre-fledging survival for a precocial bird species. The use of double marking, live recaptures and dead recoveries in a multistate framework increased the robustness of the estimates and allowed testing the effects of different factors on true survival, avoiding biases related to emigration from the study area (Burnham 1993, Catchpole et al. 1998). In addition to this approach, we also attempted to use a simplified structure model that restricted states to a combination of location and presence/absence of a web tag and considered the presence of a leg band as an individual time-varying covariate switching from 0 to 1 when banded. Time and age were then included in the parameter index matrix. This alternative approach did not significantly reduce computer time and the estimates obtained from the models were comparable to our initial estimates. Nevertheless, such complex models require large data set and may have convergence issues. The use of simplified modeling, such as the use of equal and constant recoveries for post-fledging juveniles, yearlings, and adults

Table 2. Model selection of the effect of hatch date, brood size, temperature, precipitation, and wind on pre-fledging survival rate of Canada geese in southern Quebec, 2005–2014.

Survival (Sa_0)	Model[*] Covariates added to Sa_0	$\Delta AICc$	AICc weight	K	Deviance
$Sa_0(t \times l)$	Hatch date × Brood size	0.00	1.00	156	34994.83
$Sa_0(t \times l)$	Hatch date	28.43	0.00	146	35043.66
$Sa_0(t \times l)$	Temperature	71.40	0.00	146	35086.65
$Sa_0(t \times l)$	Precipitations	111.84	0.00	146	35127.09
$Sa_0(t \times l)$		121.72	0.00	135	35159.41
$Sa_0(t \times l)$	Wind	134.32	0.00	146	35149.57
$Sa_0(t \times l)$	Brood size	154.76	0.00	146	35170.05

[*]Only top models are presented. a_0 = pre-fledged juvenile; t = time; l = location. The × between variables indicate an interaction. K = number of estimable parameters. All models have full interaction except between location and covariate(s) for pre-fledging survival. Akaike's information criterion (AICc) was for ĉ of 1.
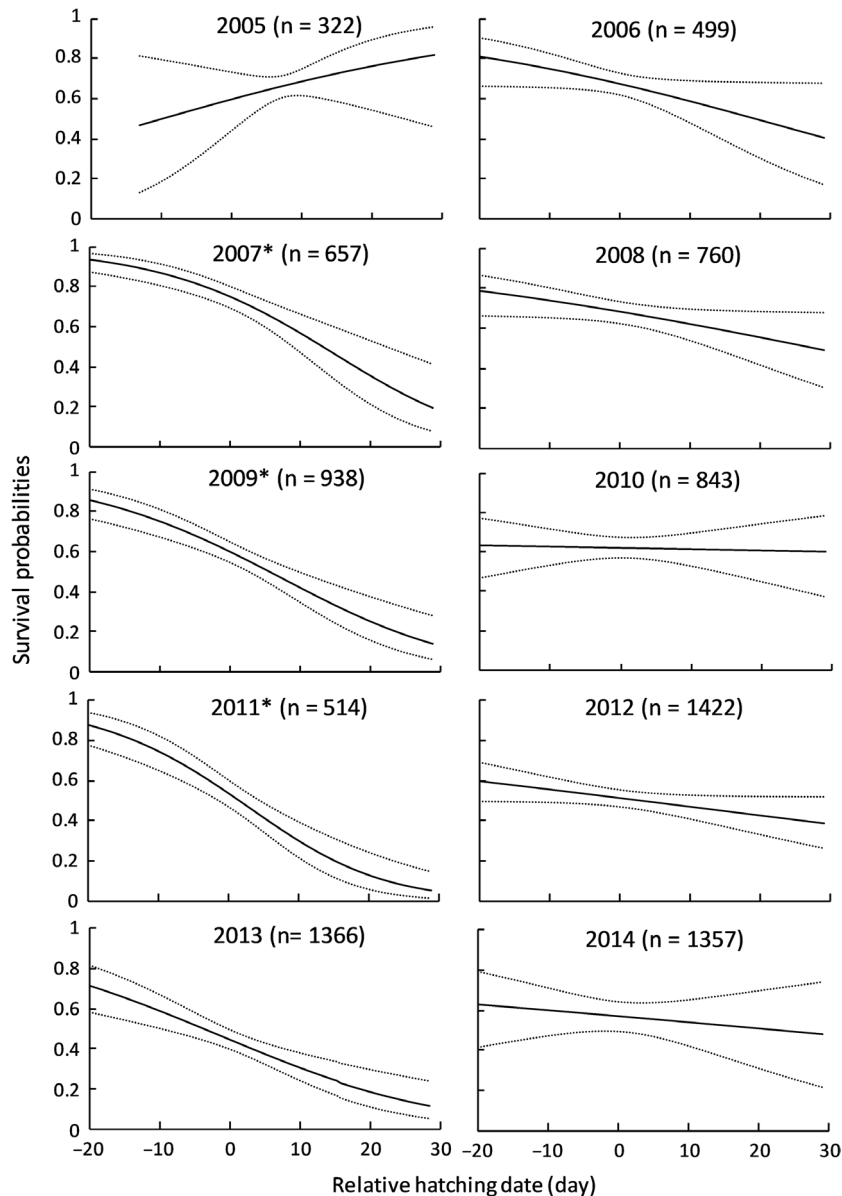
Figure 2. Survival probabilities and 95% CIs (dashed lines) of pre-fledged juvenile Canada geese in relation to their relative hatch date (day) in southern Quebec, 2005-2014. Relative hatch date was defined as the number of days from the median hatch date of each cohort. Years followed by an asterisk indicate a significant effect (β 95% CI excluding 0) and the number of goslings is presented in parentheses.

could possibly lead to potential bias. Another potential issue in assessing pre-fledging survival over several years is pseudo-replication arising from marking siblings hatched in the same nests and tracking the same breeding females during more than one year. This issue would affect variance and lead to overdispersion in the data. However, our goodness of fit tests on our starting model indicated that overdispersion was not a problem and that model assumptions were respected. Therefore, we believe that using data from brood mates did not cause significant estimation issues in our analyses.

Beston et al. (2016) acknowledged the difficulty of measuring pre-fledging survival in Canada geese. Based on total and partial brood loss of marked young and females, pre-fledging survival was estimated between 0.32 and 0.52 in New Jersey and Pennsylvania, respectively (Jacobs and Dunn 2004, Guerena 2012) while Conover (1998) reported pre-fledging survival of 0.75 in Connecticut based on the proportion of successfully fledged birds. Using these three published studies, Beston et al. (2016) estimated mean pre-fledging survival rate of 0.43 and 0.67 for rural and urban resident goose populations, respectively. Our estimates of true survival based on a 10-year study ranged between 0.45 and 0.76 among years and sites with an overall mean of 0.62. These values can be used to improve future population modelling of temperate nesting Canada geese.

We know little about the causes of mortality of goslings in southern Quebec. Only nine carcasses were found during our entire study, none providing evident clues of mortality causes. However, all these dead goslings were less than 14 days-old which is consistent with several studies that found that mortality occurs during the early stages of brood rearing (Brakhage 1965, Zicus 1981,
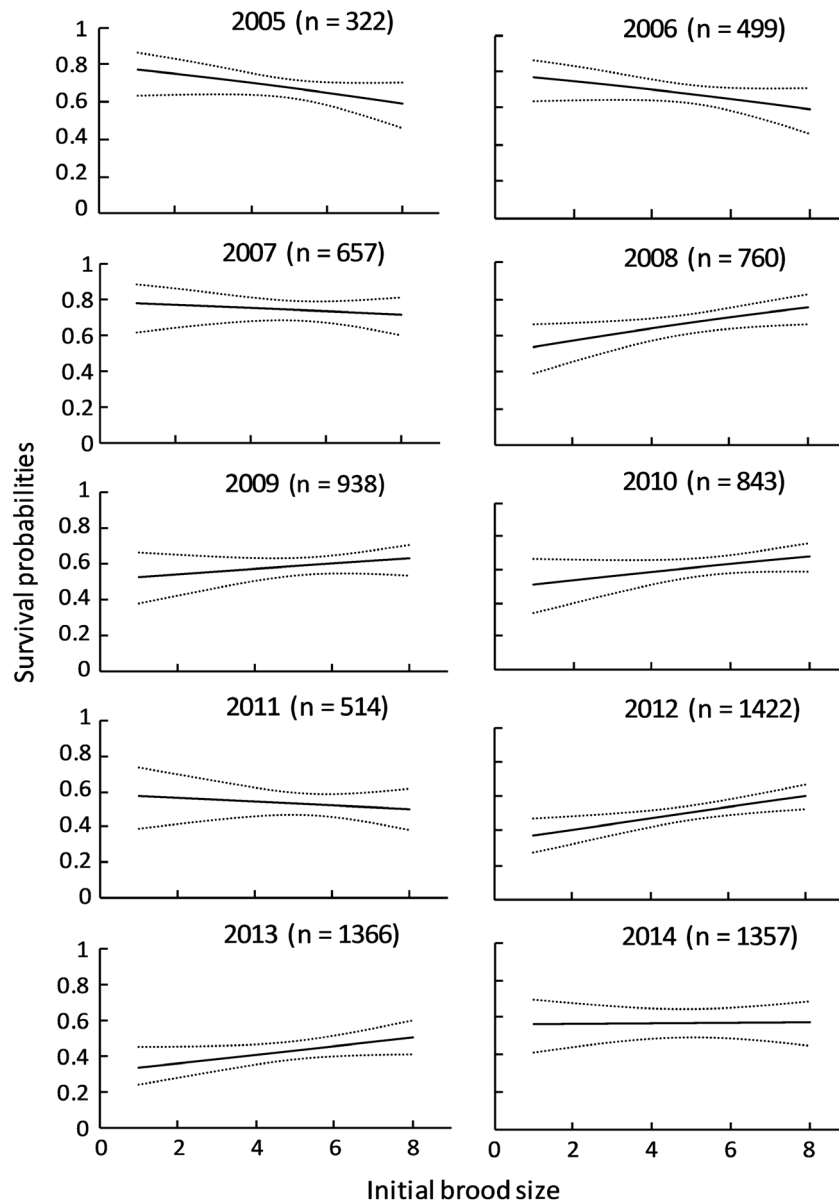
Figure 3. Survival probabilities and 95% CIs (dashed lines) of pre-fledged juvenile Canada geese in relation to the initial brood size of their family in southern Quebec, 2005–2014. Initial brood size is defined as the number of goslings leaving the nest. Number of goslings is presented in parentheses.

Eberhardt et al. 1989b, Flint et al. 1995). One mortality cause commonly mentioned is predation, but measuring predation remains difficult (Prop et al. 1984, Gosser and Conover 2000, Bowman et al. 2004). Potential predators like red fox *Vulpes vulpes*, American mink *Neovison vison*, northern pike *Esox lucius* and peregrine falcon *Falco*

peregrinus are common throughout our study area but no predation event on broods was witnessed during our study. On a few occasions, however, we observed boaters harassing groups of geese with watercrafts which may induce family breakups and result in the death of young goslings.

Table 3. Model selection of the effect of mother age on pre-fledging survival rate of Canada geese in southern Quebec, 2005–2014.

Survival (Sa_0)	Model[*] Covariates added to Sa_0	ΔAICc	AICc weight	K	Deviance
$Sa_0(t \times l)$		0	0.52	135	10142.88
$Sa_0(t \times l)$	Mother age	0.28	0.45	145	10121.75
$Sa_0(t \times l)$	Mother age^2	5.53	0.03	155	10128.46

[*]a_0 = pre-fledged juvenile; t = time; l = location. The × between variables indicate an interaction. Mother age^2 represent a quadratic relation. K = number of estimable parameters. All models have full interaction except between location and covariate(s) for pre-fledging survival. Akaike's information criterion (AICc) was for ĉ of 1. n = 2805.
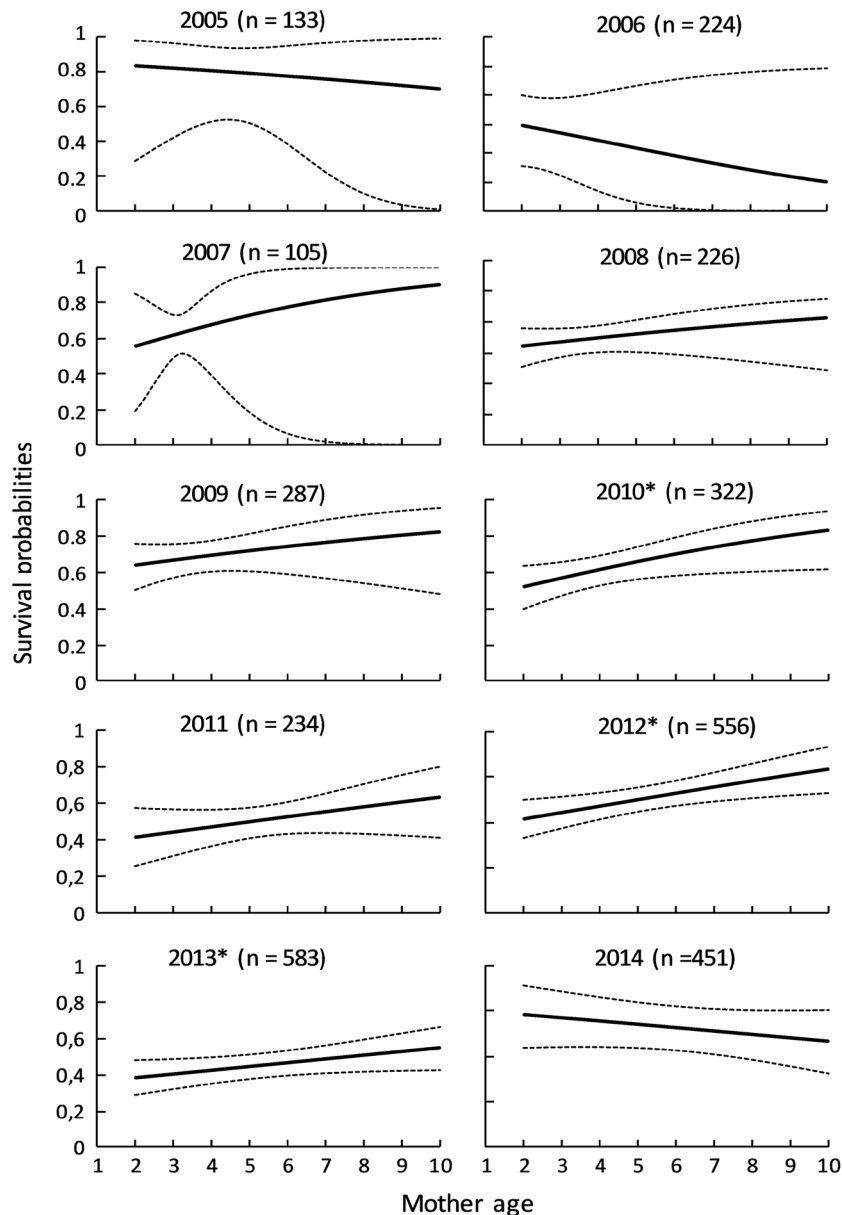
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Figure 4. Survival probabilities and 95% CIs of pre-fledged juvenile Canada geese in relation to the age of their mother in southern Quebec, 2008–2014. Mother age classes from 10 to 15 were pooled because of small sample size. Years followed by an asterisk indicate a significant effect (β 95% CI excluding 0) and the number of goslings is presented in parentheses.

Overall, pre-fledging survival was slightly higher at Repentigny than at Varennes. Feeding site quality and quantity and human disturbances could explain differences between these two sites. Nest density on the islands was higher and increased faster at Varennes than Repentigny (Pannetier Lebeuf and Giroux 2014). Koons et al. (2014) submitted the hypothesis that pre-fledging survival was the most sensitive vital rate to density dependence over the whole life cycle of a waterfowl species. Further investigation is still needed to identify the mechanisms involved.

Effects of weather conditions and gosling characteristics

A few studies have established a link between weather and survival of young Anatidae (Makepeace and Patterson 1980,

Schmutz et al. 2001, Fondell et al. 2008). However, neither temperature, precipitation nor wind influenced pre-fledging survival of Canada geese in our study. Weather conditions in temperate regions like southern Quebec are likely not severe enough to induce hypothermia that will cause mortality of few day-old goslings.

Several studies have shown that early hatching can improve pre-fledging survival of different goose species breeding in highly seasonal environments like subarctic or arctic regions (Sedinger and Raveling 1986, Francis et al. 1992, Brook et al. 2015). One proposed mechanism is that geese try to match gosling hatch to optimal rearing conditions and the quicker they can initiate nests after snowmelt, the better the brood rearing conditions (Sedinger and Raveling 1986). This synchrony constraint, however, may not be as important at more stable temperate latitudes as

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in our study area. Another possible mechanism is a seasonal decline of food resources on brood rearing areas associated with intensive grazing (Sedinger and Raveling 1986). However, food availability in a semi-urban area like ours should not be as limited as what can be found at northern latitudes because of the greater primary production observed in temperate regions (Running et al. 2004) and the use of anthropogenic habitats by geese for foraging (Doiron 2006). Nevertheless, we cannot discard the possibility of a decline in food quality due to an increase of secondary compounds and fibre content as the season progresses (Sedinger and Raveling 1986, Gadallah and Jefferies 1995). Unfortunately, we lack data on both the quality and quantity of forage resources in our study area. Further investigation is needed to explain the effect of hatch date on survival and to evaluate the possible link with food resources.

In geese, aggressive behavior can occur at an individual level (lone gosling-adult) or at a group level (family-family) during rearing. Lepage et al. (1998) showed that pre-fledging survival of goslings in snow geese increased in enlarged broods and decreased in reduced broods compared to controls. The main hypothesis is that larger broods are socially dominant over smaller ones and lone pairs, which provides greater access to rearing areas with high food quality and adequate protection (Prop et al. 1984, Lepage et al. 1998, Loonen et al. 1999). However, other studies found no relationship between brood size and family dominance and assumed that dominance of one family over another was more related to the aggressiveness of the parents (Mulder et al. 1995). Using a manipulation experiment, Sedinger et al. (2017) found a negative effect of brood size on pre-fledging survival and speculated that it could be due to an increased predation rate on larger brood size. Our results showed that pre-fledging survival tended to increase with initial brood size in some years, but the relationship was not significant. Gosling adoption is a common phenomenon in temperate nesting Canada geese and brood size can therefore change during the rearing period (Eadie et al. 1988, Choudhury et al. 1993). In southern Quebec, Doiron (2006) reported adoption rates of up to 50% of goslings. Adoption appears to occur shortly after hatching and may result from accidental brood mixing during aggressive interactions among families when parent–offspring recognition is not yet fully developed (Choudhury et al. 1993, Kalmbach et al. 2005). Because most mortality occurs during the early stage of brood rearing, the effect of brood size on pre-fledging survival is therefore difficult to assess in our population.

The effect of mother age on pre-fledging survival was better explained by a linear than a quadratic relationship. It is possible that our population sample did not have enough old females to detect an effect of senescence and a concomitant decline of pre-fledging survival as reported by Rockwell et al. (1993). Nevertheless, the best model showed that pre-fledging survival increased with mother age in most years supporting the results of Raveling (1981) who hypothesized that older females improve their skill in agonistic behavior, have a better body condition and have a greater knowledge of rearing sites. Several studies on geese have shown that age and breeding experience can affect fertility, breeding

propensity, clutch size and nest initiation date (Hofman 1982, Hamann and Cooke 1987, Lepage et al. 2000, Sedinger et al. 2001). We were unable to test these relationships directly but found an interaction between hatch date and brood size on pre-fledging survival, which supports the idea that these two factors have an influence on each other and act in synergy on pre-fledging survival. Furthermore, Clermont et al. (2018) showed that older females nest earlier than younger females in this population, supporting the idea that mother age, hatch date, and brood size are linked and may influence pre-fledging survival.

In this paper, we showed that innovative and advanced CMR analytical techniques can be used to produce accurate estimates of true pre-fledging survival rates of a precocial bird species. We also found a significant effect of hatch date on pre-fledging survival, which has been ususally observed in geese nesting in highly seasonal environments (e.g. the arctic). Our results thus indicate that a selection pressure on the timing of breeding can also occur at more stable temperate latitudes.

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Supplementary material (available online as Appendix wlb-00391 at <www.wildlifebiology.org/appendix/wlb.00391>). Appendix 1.