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HIGHLIGHTED STUDENT RESEARCH

Density-dependent winter survival of immatures in an irruptive raptor with pulsed breeding

Rebecca A. McCabe[1] · Jean-François Therrien[2] · Karen Wiebe[3] · Gilles Gauthier[4] · David Brinker[5] · Scott Weidensaul[6] · Donald Reid[7] · Frank I. Doyle[8] · Karl-Otto Jacobsen[9] · Tomas Aarvak[10] · Ingar Jostein Øien[10] · Roar Solheim[11] · Guy Fitzgerald[12] · Norman Smith[13] · Kirk Bates[14] · Mark Fuller[14] · Erica Miller[15] · Kyle H. Elliott[1]

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Abstract

Highly mobile predators can show strong numerical responses to pulsed resources, sometimes resulting in irruptions where large numbers of young invade landscapes at a continental scale. High production of young in irruption years may have a strong influence on the population dynamics unless immature survival is reduced compared to non-irruption years. This could occur if subordinate individuals (mainly immatures) are forced into suboptimal habitats due to density-dependent effects in irruption years. To test whether irruptive individuals had lower survival than non-irruptive ones, we combined necropsy results ($N = 365$) with telemetry ($N = 185$) from more than 20 years to record timing and causes of mortality in snowy owls (*Bubo scandiacus*), which irrupt into eastern North America during winter following high breeding output caused by lemming peaks in the Arctic. Mortality was more than four times higher in irruption years than non-irruption years, but only for immatures, and occurred disproportionately in early winter for immatures, but not adults. Mortality was also higher in eastern North America, where owl abundance fluctuates considerably between years, compared to core winter regions of the Arctic and Prairies where populations are more stable. Most mortality was not due to starvation, but rather associated with human activity, especially vehicle collisions. We conclude that immature snowy owls that irrupt into eastern North America are limited by density-dependent factors, such as increased competition forcing individuals to occupy risky human-altered habitats. For highly mobile, irruptive animals, resource pulses may have a limited impact on population dynamics due to low subsequent survival of breeding output during the nonbreeding season.

Keywords Biologging · *Bubo scandiacus* · Irruptions · Mortality · Necropsy

Introduction

Population dynamics of predators at high latitudes are often tied to pulsed resources (e.g. microtine rodents that fluctuate on 3–5 year cycles) with a large number of offspring produced during prey peaks and low numbers or even none during crashes of prey (Elton 1942; Gilg et al. 2006; Therrien et al. 2014a). However, reproductive boom-and-bust cycles of predators may be attenuated because their numerical response to high densities of prey can operate at a large spatial scale as individuals can move large distances to find alternative food (Lack 1968; Therrien et al. 2014b). Winter irruptions of northern latitude predators sometimes occur during years when poor food availability is widespread on their breeding ground, and these individuals are typically in poor body condition and have high mortality (e.g. lack-of-food hypothesis; Cheveau et al. 2004). In other cases,

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By combining 20 years of telemetry and necropsy data from snowy owls in North America, the authors demonstrate that survival during irruption years is influenced by density-dependent factors resulting from the high abundance of first-year owls on the wintering landscape. This research sheds light on our understanding of pulsed resources and cautions against overestimating the role of 'boom' years on long-term population growth for highly mobile, irruptive species.

✉ Rebecca A. McCabe
rebeccamccabe2@gmail.com

Extended author information available on the last page of the article

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irruptions occur when a high reproductive output during a prey peak increases the pool of migrants in the population (mainly juveniles), which are in relatively good condition but are pushed farther south in winter (e.g. breeding-success hypothesis; Robillard et al. 2016; Curk et al. 2018). A key question is whether such species are affected by density-dependent mortality on the wintering grounds during irruption years. If the highest quality wintering habitats become saturated or defended by the dominant sex- or age- class (Boxall 1979; Evans 1980), a lack-of-food in alternative habitats may cause a decrease in body condition and an increase in mortality during the winter season. The potential consequences of irruptive movements on demographic parameters are important for bridging the gap between individual movements and predicting population dynamics in irruptive species.

As a species reaches higher population densities and lower-quality habitats are increasingly used due to saturation in higher-quality habitats, decreased survival in low-quality habitats can affect the overall population growth in a density-dependent manner (e.g. buffer effect; Brown 1969; Gill et al. 2001; Newton 2004). For example, American redstarts (*Setophaga ruticilla*) wintering in low-quality scrub habitats in Jamaica lost body mass throughout the winter period and had lower annual survival compared to redstarts wintering in high-quality mangrove habitats (Marra and Holmes 2001). Sources of mortality for animals involve natural and anthropogenic risks and the interactions between them (Newton 1998). Individuals moving southwards from northern environments during irruptions will encounter a human-altered landscape with new risks that immatures may have not encountered previously (Sergio et al. 2004; Schaub et al. 2010; Grilo et al. 2014). Under the 'doomed surplus' hypothesis (Errington 1946), subordinate individuals (immatures) may be forced out of saturated, high-quality habitats by dominant individuals (adults) and thus experience higher 'natural' mortality due to reduced food availability (Newton 1998). If the suboptimal, low-quality habitats have been altered by human activity, mortality of immatures may be linked to human-related causes, such as collisions with vehicles or electrocution.

The snowy owl (*Bubo scandiacus*) is an irruptive species exhibiting large winter fluctuations in population abundance, especially in eastern North America (Smith 1997; Robillard et al. 2016). Winter irruptions occur during peak lemming years in the Arctic when high numbers of young produced during the summer disperse and move farther south during the nonbreeding season, while dominant individuals (i.e. adults and immature females) usually remain closer to their breeding area in the Arctic (Kerlinger and Lein 1986; Doyle et al. 2017; Robillard et al. 2018). Specifically, the winter abundance in temperate North America is correlated with lemming abundance on the Arctic breeding grounds during the previous summer (Robillard et al. 2016), and more than 80% of individuals observed in irruption years are immature (Smith 1997; Santonja et al. 2018). Immature raptors in their first year are inexperienced at hunting, eluding predators, and avoiding bad weather (Squires and Reynolds 1997; Bennetts et al. 1999; Roth et al. 2005). Thus, we anticipated that immature owls would have high mortality, especially in irruptive years, due to density-dependent effects, many of them becoming a 'doomed surplus'.

We examined differences in survival and sources of mortality among sex and age classes in wintering snowy owls based on combined necropsy data from owls found dead ($N = 365$) and known or apparent mortality rate from telemetry-tracked snowy owls ($N = 185$). Our approach harnessed the advantage of the large sample size of necropsy birds with accuracy of data available from telemetry-tracked birds, which was unbiased by discoverability of carcasses. We predicted that immature birds, due to their inexperience and presumed subordinate social status, should have lower overwinter survival compared to adults. Irrespective of age or sex, owls maintain smaller home ranges on the Prairies (a region where the habitat is more homogeneous and presumably offers a higher and more stable food supply; referred to as 'optimal habitats') than in eastern North America where they are more irruptive and nomadic, moving across heterogeneous habitats with greater human populations (referred to as 'suboptimal habitats') (McCabe et al. 2021). Thus, we predicted that adult birds wintering in the Arctic (e.g. a region which can also provide good habitat for owls in winter) or the Prairies would have higher survival compared to adults wintering in regions with more heterogeneous habitats (e.g. eastern North America).

We predicted that if urbanized habitats are the lowest quality for owls, and if the subordinate individuals are forced into these areas, then anthropogenic causes of mortality (especially vehicle collisions) would be higher among immature than adult owls. Finally, if immature birds during irruption years are influenced by density-dependent factors resulting from the high abundance of owls on the wintering landscape (i.e. explained by the breeding-success hypothesis; Robillard et al. 2016), we expected survival to be lower in irruption years than non-irruption years for immature birds, but not for adults. As snowy owls were recently listed as "vulnerable" (IUCN 2020), a greater understanding of the species' demography is a priority.

Materials and methods

Study area and data collection

We studied wintering snowy owls in the USA and Canada from 2000 to 2020. We used geographic/habitat regions

defined by the North American Bird Conservation Initiative (see Bird Studies Canada and NABCI 2014) to classify wintering populations. At the continental scale, owls were divided into two groups: Arctic, those that wintered in the Arctic Plains and Mountains, and temperate, those that wintered south of the Arctic Plains and Mountains. We further divided the temperate region into two groups based on human population density, which is higher in the eastern USA and Canada than on the Prairies (Bhaduri et al. 2007). Thus, we defined the 'Prairies' region to include the Prairie Potholes, Prairie Hardwood Transition, Eastern Tallgrass, and Badlands and Prairies, whereas the 'eastern North America' region incorporated the Boreal Hardwood Transition, Boreal Softwood and Taiga Shields, Lower Great Lakes, Appalachian Mountains, New England/Mid-Atlantic Coast, and Atlantic Northern Forest.

We tracked snowy owls using wildlife telemetry trackers (~30 g satellite transmitters ($N=97$): Microwave Telemetry Inc., MD, USA, North Star Science and Technology, VA, USA, and GeoTrack Inc., NC, USA; ~40 g GPS–GSM transmitters ($N=88$): Cellular Tracking Technologies, NJ, USA), fitted with a backpack harness of tubular Teflon™ or Spectra™ (Steenhof et al. 2006). The complete tracking device weighed less than 3% of an individual owl's total body mass. Birds were trapped in the Canadian Arctic during the breeding season (June–July) and in southern Canada (i.e. Saskatchewan and Quebec) and northern USA (i.e. from North Dakota in the west to states along the Atlantic Coast) during the winter period (November–April). In the Arctic, only adult females were trapped using bow nets at nests, approximately one week after young hatched (Therrien et al. 2012). During the winter period, owls were trapped using live lure-animals in either bal-chatri traps or bow nets (Bloom et al. 2007). We used plumage characteristics and molt patterns to assess sex and age for each individual (Seidensticker et al. 2011; Solheim 2012), and classified immatures as being <12 months old and adults as ≥ 12 months. GSM transmitters recorded one GPS location (± 3 m) at 30- to 60-min intervals during the winter period and downloaded the data via the Global System for Mobile Communications networks whereas satellite transmitters relied on the ARGOS system and transmitted locations following fixed schedules (described in Therrien et al. 2014b; Heggøy et al. 2017).

Survival analysis

To estimate survival during the winter period, we recorded the number of days the individual appeared to be alive, starting with the capture date, and proceeding until the end of the winter period. We defined the winter period using the earliest date of tagging, 24 November (day 0), as the start date, and the average initiation date of spring migration for snowy owls in North America (Brown et al. 2021), 10 April (day 138), as the end date, giving a 4.5 month-long period. Because we were interested specifically in the winter season, individuals that were alive by the end of the winter period were censored (Therneau and Grambsch 2013). If the transmitter stopped transmitting (e.g. transmitter malfunction, battery failure, owl permanently outside of cell tower range) during the winter period, then the individual was censored on the last known date of transmission. We detected or confirmed mortality by as follows: (a) locating the carcass in the field whenever possible, and determining cause-specific mortality via necropsy reports, or (b) estimating date of mortality from the transmitter activity sensor which can indicate death based on temperature and activity level. If owls were tracked for more than one winter, a new entry was made for each winter season an owl was alive.

Necropsy assessments of Snowy Owl carcasses from eastern North America

Carcasses reported to wildlife agencies across eastern North America between 2013 and 2020 were analyzed to compare mortalities with telemetry-tracked owls. Necropsies of non-telemetry-tracked owls were performed by veterinarians at the Faculté de médecine vétérinaire of the Université de Montréal and University of Pennsylvania's New Bolton Center. All necropsies occurred within 48 h after the time of death, or a carcass was immediately frozen and the necropsy was conducted at a later date. The date of mortality is considered to be the date the carcass was found and the cause of death was determined by gross necropsy findings supported by histopathology, toxicology, radiography, and microbiology findings. Only owls that died between 1 November and 30 April were included in this analysis.

Statistical analyses

Statistical tests were conducted in R (R Core Team 2018), with the Cox proportional hazard regression and Kaplan–Meier curve generated in the package 'survival' (Therneau 2020). We used the non-parametric Kaplan–Meier estimator (Kaplan and Meier 1958) to compute overall winter survival curves and the proportion of individuals who survived until the end of the winter period (138 days). The Kaplan–Meier analysis allows the use of censored data as well as staggered entry of animals during the course of a study (Pollock et al. 1989). To examine the relationship between winter survival and categorical covariates (i.e. age, sex, winter regions, irruptions), we built separate Cox proportional hazards regression models (Therneau and Grambsch 2013). For each model, we used likelihood ratio tests (LRT) to determine the model's overall statistical significance and the Wald test (z-value) to determine P-values for each covariate: (a) continental winter region

(Arctic or temperate), (b) temperate winter region (Prairies or eastern North America), (c) age (adults or immatures), (d) sex (males or females), and (e) irruption vs. non-irruption years in eastern North America.

Prior to running the irruption vs. non-irruption survival analysis, we first had to determine which years were considered irruptions. To determine years of winter irruptions in eastern North America, we used Christmas Bird Count (CBC) abundance data (National Audubon Society 2020) from 1999 to 2019 for states and provinces that are within the eastern North America Bird Conservation Regions described above (USA: Connecticut, Delaware, District of Columbia, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, Virginia, West Virginia, and Wisconsin; Canada: New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Québec). CBC is a well-known citizen-science database that gathers annual 1-day birding records between 14 December and 5 January across North America (Sauer and Link 2002; Dunn et al. 2005) and has been previously used to assess snowy owl winter abundance (Robillard et al. 2016; Santonja et al. 2018; Curk et al. 2018). We did not correct for observation effort because a previous study (Robillard et al. 2016) found no relationship between the number of snowy owls censused during the annual CBC and observation effort. Following Krebs et al. (2002), we defined peak years as those years in which the abundance is higher in one year than in the preceding or following year. Within the study period, six winter irruptions occurred in eastern North America (2001–2002, 2005–2006, 2008–2009, 2011–2012, 2013–2014, and 2017–2018; Fig. 1). All other years were categorized as non-irruption years. We tested for an interaction between sex and irruption and between age and irruption as we expected a lower survival of immatures in irruption years than in non-irruption years but not in adults according to the breeding-success hypothesis. We used separate χ^2 tests to assess the relationship between causes of deaths of necropsied owls across all winter months (1 Nov–30 Apr) for sex and age classes.

Results

Survival rates and hazard factors for telemetry-tracked owls

In total, 185 snowy owls were affixed with transmitters between 2000 and 2020, 38 (21%) were identified as immature females, 38 (21%) as immature males, 76 (41%) as adult females, and 33 (18%) as adult males. Of these, 34 were captured and tagged in the Arctic (i.e. Nunavut and Yukon; all adult females) during the breeding season and the other 151 were captured and tagged in temperate regions during the nonbreeding season. During the winter period, 18 (9.9%) of the 185 owls died. Of the 18 confirmed deaths, 12 occurred in eastern North America (8 immatures and 4 adults), 5 in the Prairies (2 immatures and 3 adults), and 1 in the Arctic (1 adult). Known proximal causes of death of telemetry-tracked owls included automobile and plane collisions, electrocution, disease or parasites, and death from inclement weather (Table 1).

For adult females, the winter survival estimate was slightly lower for those wintering in temperate regions (93%) than for those wintering in the Arctic (98%) but the difference was not significant (Table 2). For all owls wintering in temperate regions (sex and age classes pooled), winter survival estimate was significantly higher for those wintering on the Prairies (94%) than those wintering in eastern North America (81%; Fig. 2a; Table 2).

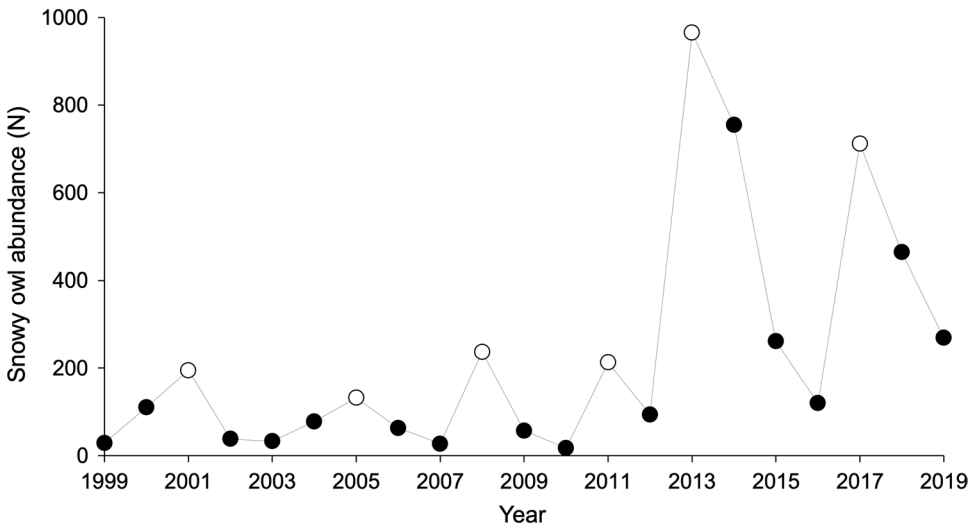

Fig. 1 Annual variation of snowy owl winter abundance at Christmas Bird Count sites in temperate eastern North America. Peak years (white circles) where abundance is higher in one year than in the preceding or following year (black circles) are classified as irruptions

Table 1 Causes of death of snowy owls wintering in the USA and Canada

Cause of death	Telemetry-tracked owls ($N=18$)	Necropsied owls ($N=365$)
Natural	4 (22.2%)	87 (23.8%)
Emaciated	0	59 (16.2%)
Disease or parasites	1 (5.6%)	23 (6.3%)
Inclement weather[a]	3 (16.7%)	2 (0.5%)
Predation	0	3 (0.8%)
Anthropogenic	9 (50%)	151 (41.4%)
Automobile collision	4 (22.2%)	64 (17.5%)
Airplane collision	2 (11.1%)	31 (8.5%)
Other collisions	1 (5.6%)	28 (7.7%)
Electrocution	1 (5.6%)	12 (3.3%)
Ingested poison or toxin	1 (5.6%)	3 (0.8%)
Trapped in man-made structures	0	7 (1.9%)
Gunshot	0	6 (1.6%)
Unknown	5 (27.8%)	127 (34.8%)

Of the Telemetry-tracked owls between 2000 and 2020, one confirmed death occurred in the Arctic, and the other deaths occurred in temperate North America (eastern North America: $N=12$; Prairies: $N=5$). Necropsied owls were collected and analyzed in northeastern USA and Canada from 2013 to 2020. Proportions of the total samples of telemetry-tracked owls and necropsied owls in each category are in parentheses

[a]Owl died from hypothermia or was found dead after a winter storm

As predicted, immatures wintering in temperate regions (Prairies and eastern North America regions pooled) had a lower winter survival estimate (68%) than adults (95%) also wintering in temperate regions (Fig. 2b; Table 2). Immatures had a higher probability of mortality at the beginning of winter compared to the end, whereas mortality was low and constant over the winter for adults (Fig. 3). We found no significant differences in winter survival estimates between the sexes in temperate regions (Table 2).

Among owls wintering in eastern North America, survival was not affected by an interaction between 'sex and irruption' (Table 2), but we detected a strong interaction between 'age and irruption' (Table 2) so we examined the effect of irruption for age classes separately. Winter survival estimate of immatures tended to be lower during irruption years (52%) than during non-irruption years (100%; $\chi^2=3.74$, df = 1, $P=0.06$; Fig. 4). In contrast, winter survival estimate of adults was similar between irruption (100%) and non-irruption years (90%; $\chi^2=0.71$, df = 1, $P=0.39$).

Causes of death for necropsied owls

Of the 365 owls turned in for necropsies in eastern USA and Canada from 2013 to 2020, 73 (20%) were identified as immature females, 102 (28%) as immature males, 72 (20%) as adult females, 53 (15%) as adult males, 4 (1%) as unknown adults, 3 (1%) as unknown immatures, 14 (4%) as unknown females, 22 (6%) as unknown males, and 22 (6%) as unknown. Cause of death or injury was undetermined for 33% of the owls that either were found dead or died shortly after being found. For necropsied owls, anthropogenic mortality was almost two times greater than natural mortality (i.e. 41% to 24%, respectively). Of the known causes of death, the most common natural source was emaciation and

Table 2 Results of the survival analyses based on the Cox model for winter regions, age, sex, and interactions between age and irruptions and sex and irruptions, of telemetry-tracked snowy owls in North America

Model	Regression coefficient[a]	Hazard ratio[b]	95% CI	Wald z	*P* value	Test summary
Continental winter region (Arctic = 1 vs. temperate = 2)	1.232	3.427	0.399–29.43	1.123	0.262	N = 144, # of events = 6, df = 1, LRT = 1.6, $P=0.26$
Temperate winter region (Prairies = 1 vs. eastern North America = 2)	1.165	3.205	1.213–8.465	2.350	0.019*	N = 252, # of events = 17, df = 1, LRT = 5.6, $P=0.02$*
Age (Immature = 1 vs. Adult = 2)	-1.823	0.162	0.058–0.454	-3.459	0.001*	N = 259, # of events = 17, df = 1, LRT = 12.1, $P<0.001$*
Sex (Male = 1 vs. Female = 2)	0.340	1.405	0.534–3.692	0.689	0.491	N = 259, # of events = 17, df = 1, LRT = 0.5, $P=0.50$
Irruption: Age (eastern North America owls only)	-0.794	0.452	0.232–0.880	-2.338	0.019*	N = 93, # of events = 10, df = 1, LRT = 7.68, $P=0.006$*
Irruption: Sex (eastern North America owls only)	-0.416	0.660	0.346–1.258	-1.264	0.206	N = 93, # of events = 10, df = 1, LRT = 1.81, $P=0.20$

[a]A positive sign means the hazard or risk of death is higher for subjects with higher values of that variable

[b]The hazard ratio is given for the second group in each of the model (i.e. encoded as numeric vector 2) relative to the first group (i.e. numeric vector 1 is reference level)

*Statistical significance at the $P<0.05$ level

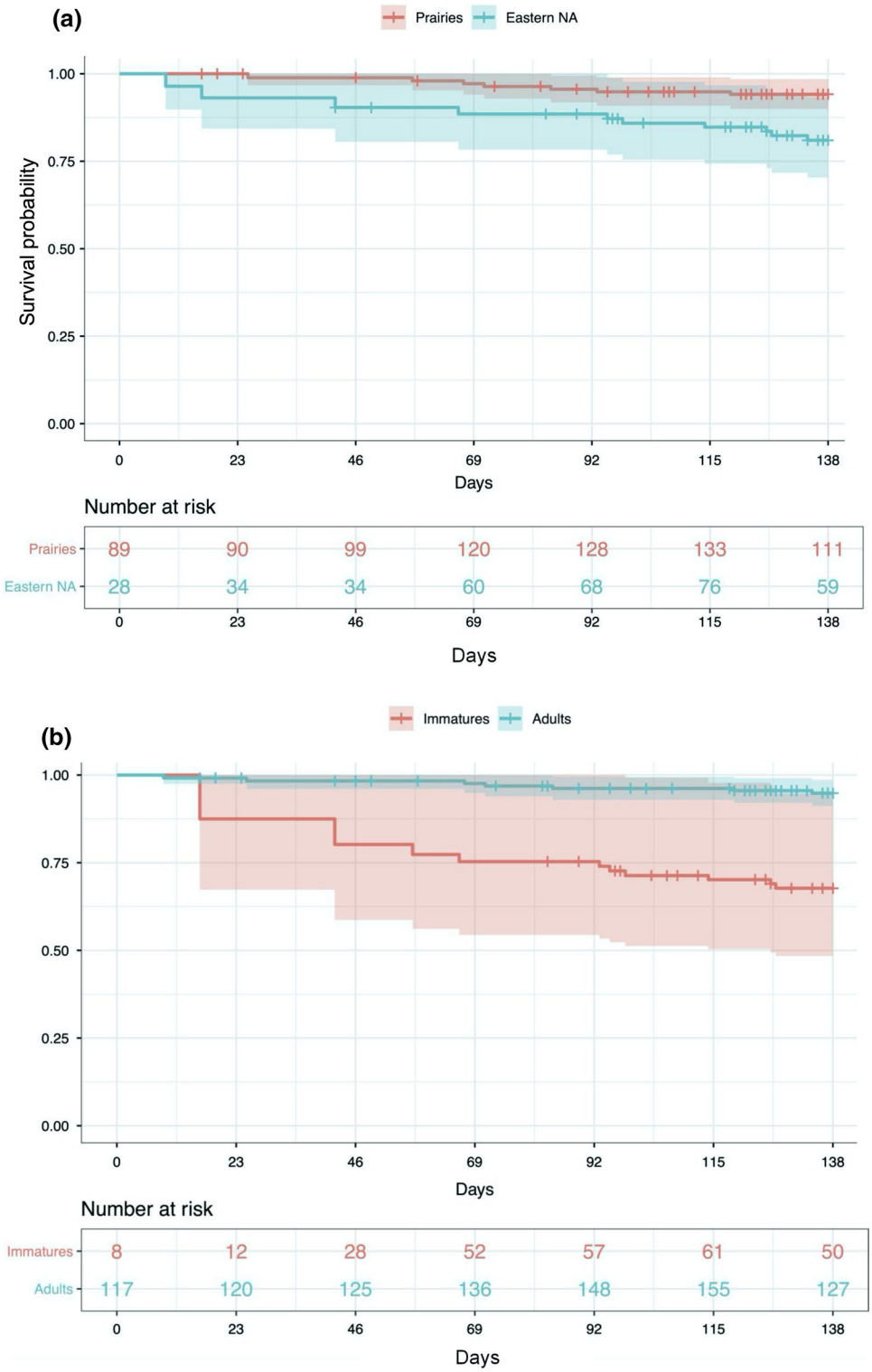

Fig. 2 Kaplan–Meier survival curves of snowy owls during winter (24 November to 10 April) in temperate North America. Survival is computed from telemetry-tracked snowy owls by (**a**) wintering region and (**b**) age. For each curve there is a 95% confidence interval and tick marks are for censored observations (tag failure without apparent mortality)

the most common anthropogenic source was automobile collisions (Table 1).

We found an association between sex (ages pooled) and the number of owls turned in for necropsy throughout the winter period ($\chi^2 = 20.64$, df = 5, $P < 0.001$; $N = 336$), with a greater number of reported deaths for males at the beginning of winter compared to the end (Fig. 5a). We also found an association between age (sexes pooled) and the number of owls turned in for necropsy throughout the winter period ($\chi^2 = 49.05$, df = 5, $P < 0.001$; $N = 307$), with a greater number of deaths reported for immatures owls at the beginning of winter compared to the end (Fig. 5b).

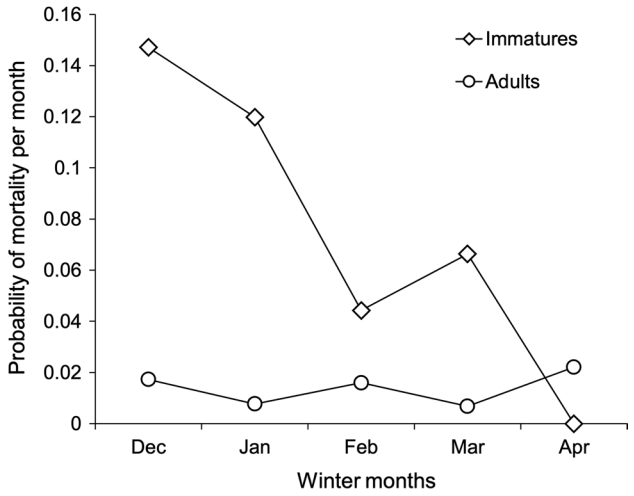

Fig. 3 Monthly probability of mortality for telemetry-tracked snowy owls wintering in temperate North America. We excluded November (i.e. tracking period started on 24 November) due to few individuals in the study at that time, and we only included the first 10 days of April (i.e. tracking period ended on 10 April) when calculating monthly probability

Discussion

As predicted, (1) survival was lower in immatures than adults; (2) survival was lower in birds wintering in suboptimal habitats (irruptive range, i.e. eastern North America) than birds wintering in optimal habitats (core range, i.e. Prairies and Arctic); and (3) mortality was primarily due to human-related causes. However, in contrast to classic predator–prey cycles where predator fitness is high during the years of prey peak and declines during the prey crash (Brand and Keith 1979; O'Donoghue et al. 1998), the irruptive pattern of highly mobile owls apparently meant that a high proportion of the breeding output during prey peaks was 'doomed' to die during the subsequent non-breeding season. Indeed, survival probability of immatures in our study decreased by almost 50% during irruptive years. Similarly, during southern irruptions of northern hawk owls (*Surnia ulula*), winter mortality was largely human-induced or linked to predation from great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), and fishers (*Pekania pennanti*) (Duncan and Harris 1997; Dale 2017). Nonetheless, without knowing subsequent survival during spring migration and breeding propensity it is impossible to know the exact effect of this high mortality on population dynamics. Due to their high mobility, many northern raptors move large distances to match breeding to peaks in small-mammal population cycles, sometimes doubling breeding output through a linear functional response to microtine rodents (Korpimäki and Norrdahl 1991; Korpimäki and Wiehn 1998). Similar irruptive movements occur in many northern bird species (e.g. winter finches, waxwings; Kennard 1976; Koenig and Knops 2001; Dunn 2019). Low survival of immatures during irruptive years implies that the numerical response on

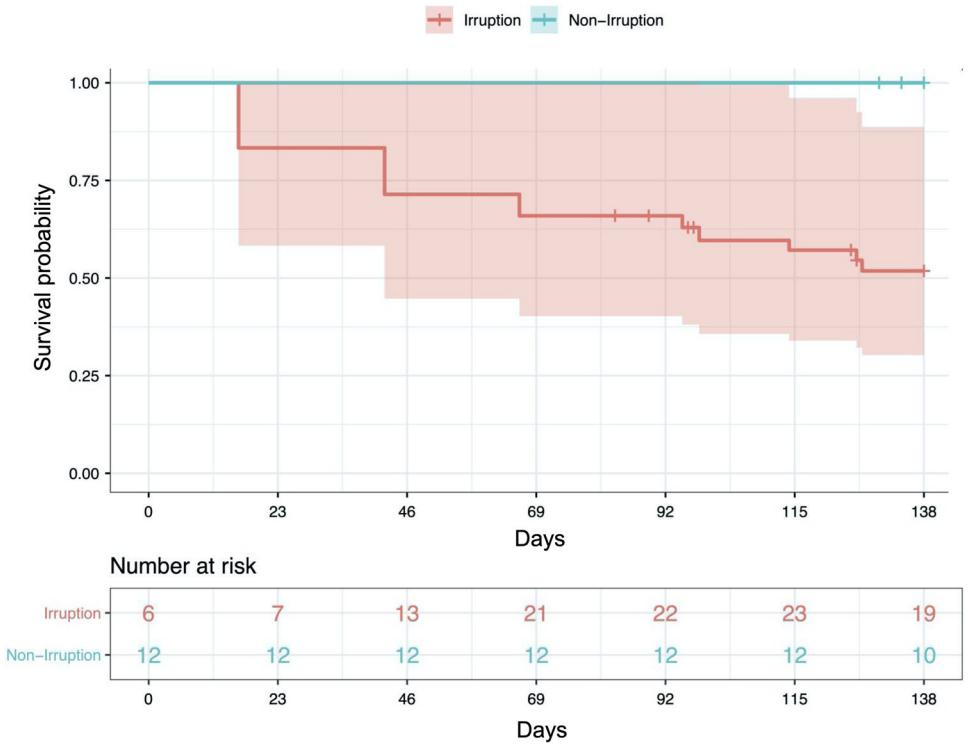

Fig. 4 Kaplan–Meier survival curves of immature (< 12 months old) snowy owls during winter (24 November to 10 April) in eastern North America. Survival is computed from telemetry-tracked owls in irruption years (6 years) and non-irruption years (14 years). For each curve there is a 95% confidence interval and tick marks for censored observations (tag failure without apparent mortality)

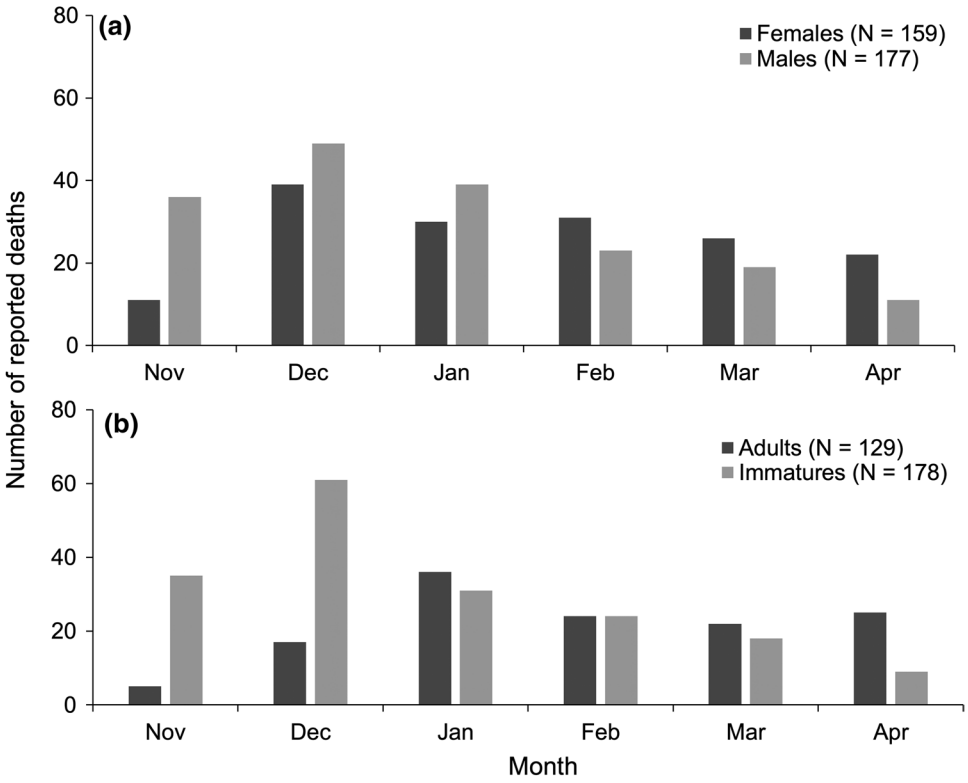

Fig. 5 Reported deaths of known (**a**) sex and (**b**) age classes of snowy owl carcasses ($N = 365$) turned in for necropsies to veterinary facilities during winter in eastern North America from 2013–2020

the breeding grounds likely has an attenuated demographic impact compared with predators with limited mobility in response to northern resource pulses (i.e. foxes, resident birds of prey such as tawny owls [*Strix aluco*] and Ural owls [*Strix uralensis*]; Korpimäki and Sulkava 1987; Roth 2003; Karell et al. 2009).

Most of the owls in our study died from human-related causes. The 'doomed surplus' was originally conceived as individuals that could be harvested as they would otherwise die from natural, compensatory mechanisms (e.g. Boyce et al. 1999), and human-related causes of death are often not considered to be density-dependent (Newton 1998). However, if human-related causes of death are more prevalent in suboptimal habitats used by immatures, then this source of mortality could become density-dependent. Wintering owls died of many anthropogenic and natural causes, but collisions with automobiles was the highest source of known mortality for both necropsied and telemetry-tracked owls. Interestingly, although carcasses might be expected to be disproportionately found near where humans are active, the rate of natural mortality was similar (22.3% vs. 23.8%) between necropsied carcasses and telemetry-tracked owls, implying that our estimates from carcasses are unlikely to be strongly biased. Similar to our findings, Kerlinger and Lein (1988) reported that the most common source of mortality for snowy owls wintering in Alberta, Canada were collisions (66%) and other anthropogenic mortalities (20%), compared to 14% natural mortality (i.e. starvation).

Snowy owls demonstrated the classic trend of lower survival in immatures than adults, with immature mortality declining through their first winter (Martin 1995; Martín et al. 2007). A number of raptor studies have reported annual survival estimates, including for snowy owls (Therrien et al. 2012; Heggøy et al. 2017). However, few have assessed sex-, age-, region, or time-specific variation in survival at the seasonal level (Newton et al. 2016). Survival rates of telemetry-tracked owls differed according to age, but not sex, for owls wintering in temperate regions. Some studies provided age-specific survival analyses of telemetry-tracked raptors, albeit mainly for annual survival (Klaassen et al. 2014). For example, McIntyre et al. (2006) reported the risk of mortality for juvenile golden eagles (*Aquila chrysaetos*) was greatest during the first migration and early in their first winter, with starvation and dehydration, likely due to hunting inexperience, being the highest cause of mortality. In addition, other studies reported lower survival in immatures compared to adults for various raptor species (e.g. Bowman et al. 1995; Bennetts et al. 1999; Tenan et al. 2012). Age- and season-specific survival estimates were calculated by Roth et al. (2005) for sharp-shinned hawks (*Accipiter striatus*) and Cooper's hawks (*A. cooperii*), and adult survivorship was also greater for adults (75.4%) than immatures (9.4%) by the end of the winter period. The age-specific survival estimates combined with the lower survival rate in irruptive than in non-irruptive years, may indicate a mechanism

for population control for snowy owls and other highly dispersive, and irruptive species as detailed below.

The high mortality of immatures in early winter may be related to their inexperience as hunters, or inexperience in avoiding dangers in human-dominated areas. Their inexperience, coupled with a low body condition post-migration, may entice them to higher risk, suboptimal habitats. For example, airports are known to be attractive for many raptor species as they provide open, undeveloped land that often contain small-mammal populations (Baker and Brooks 1981). However, raptor–aircraft collisions are frequent in North America and often lethal (Dolbeer et al. 2015). Such high-risk habitats in human-dominated areas, which also include overhead power lines, highways and roads, may not be recognized by inexperienced immature owls when they arrive on the wintering grounds. Therrien et al. (2017) reported age-related differences in habitat types used by snowy owls in eastern North America, and found that juvenile owls wintered in developed areas more than adults, suggesting the potential for increased exposure to contaminants (Miller et al. 2015) and human disturbance. Interestingly, other studies of migratory birds have reported that mortality rates of immatures and adults do not differ much once immatures have survived a period of high risk immediately post-fledging such as the initial migration (e.g. Menu et al. 2005; Grüebler et al. 2014; Zúñiga et al. 2017). Moreover, Curk et al. (2018) reported an improvement of body condition of immature snowy owls throughout the winter season (i.e. from 1 October to 1 April) in both irruptive and non-irruptive winter ranges. This suggests that, over time, immatures may be able to find and settle in areas with an abundant food supply or improve their foraging skills, which could allow individuals to maintain a positive energy balance and explain why monthly survival probability increases throughout the winter (Newton 2006).

Our study supports the idea that density-dependent, compensatory winter mortality of immatures may play an important role in regulating the population dynamics of snowy owls in North America. The high mortality in irruption years may be linked to the boom-and-bust breeding strategy of snowy owls that lay large clutches (e.g. 5–10 eggs, $\bar{x} = 7.0 \pm 2.1$ eggs; Potapov and Sale 2012; Holt et al. 2020) during years when the abundance of small mammals in the Arctic tundra is high (i.e. 'boom' years) (Robillard et al. 2016). This breeding strategy yields an abundance of immature owls at the end of the breeding season during peak years but apparently also leads to high rates of mortality in their first winter due to density-dependent effects. In contrast, during years of low breeding output due to the lack of prey on the breeding grounds (i.e. non-irruptive years), the few young produced apparently survive better during the winter. In the end, these opposing mechanisms may even out the number of young that will eventually recruit in the population between 'boom' and 'bust' years. It is thus possible that the high production of young in 'boom' years may not drive population growth in the long term due to a low recruitment of those young in subsequent years. A key point is whether anthropogenic mortality is entirely compensatory or has an additive component. If the latter, then the high anthropogenic mortality could be contributing to global declines as fewer birds recruit, diminishing the numerical response (Sinclair and Pech 1996; Péron 2013). Tawny owls show a similar numerical response during the breeding season, albeit a resident owl with short natal dispersal, with high fecundity during vole peaks driven by new recruits breeding in those years, yet that fecundity has relatively little importance for overall tawny owl population dynamics compared with adult survival (Karell et al. 2009).

In conclusion, our findings caution against overestimating the role of 'boom' years on long-term population growth of species relying on pulsed resources. Indeed, production of young in 'bust' years may not be negligible on the population level, because, even if fewer young are produced, they may be more likely to survive the winter period and eventually recruit. In an increasingly human-altered landscape, compensatory, density-dependent anthropogenic mortality appears to stabilize population fluctuations in snowy owls.

Author contribution statement

RAM, JFT, and KHE conceived the study. RAM, JFT, KW, GG, DB, SW, NS, KB, MF, TA, IJO, KOJ, RS, FID, DR, GF, and EM participated in data collection. RAM analyzed the data and wrote the manuscript. All authors contributed to revisions of the manuscript.

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Data availability All datasets used in this study are available upon request from the authors.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Authors and Affiliations

Rebecca A. McCabe[1] · Jean-François Therrien[2] · Karen Wiebe[3] · Gilles Gauthier[4] · David Brinker[5] · Scott Weidensaul[6] · Donald Reid[7] · Frank I. Doyle[8] · Karl-Otto Jacobsen[9] · Tomas Aarvak[10] · Ingar Jostein Øien[10] · Roar Solheim[11] · Guy Fitzgerald[12] · Norman Smith[13] · Kirk Bates[14] · Mark Fuller[14] · Erica Miller[15] · Kyle H. Elliott[1]

1 Department of Natural Resource Sciences, McGill University, 21111 Lakeshore, Ste-Anne-de-Bellevue, QC, Canada

2 Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, Orwigsburg, PA, USA

3 Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

4 Department of Biology and Centre d'études Nordiques, Université Laval, Québec, QC, Canada

5 Maryland Department of Natural Resources, Annapolis, MD, USA

6 Ned Smith Center for Nature and Art, Millersburg, PA, USA

7 Wildlife Conservation Society Canada, Whitehorse, YT, Canada

8 Department of Biology, University of British Columbia Okanagan, Kelowna, BC, Canada

9 Department of Arctic Ecology, Norwegian Institute for Nature Research, Tromsø, Norway

10 Norwegian Ornithological Society/BirdLife Norway, Trondheim, Norway

11 Natural History Museum, University of Agder, Kristiansand S, Norway

12 Faculté de Médecine Vétérinaire, Université de Montréal, Saint-Hyacinthe, QC, Canada

13 Massachusetts Audubon, Milton, MA, USA

14 Boise State University, Raptor Research Center, Boise, ID, USA

15 Wildlife Futures Program, Department of Pathobiology, School of Veterinary Medicine, University of Pennsylvania, Kennett Square, PA, USA