Experimental manipulation of perceived predation risk alters survival, cause of death, and demographic patterns in juvenile snowshoe hares

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Abstract

Perceived predation risk alters prey behaviour and physiology, but few studies have examined downstream consequences on prey demography in wild populations. Perceived predation risk could alter adult reproductive performance via reduced investment in offspring quality and post-birth care. We manipulated perceived predation risk in snowshoe hare (*Lepus americanus* Erxleben, 1777) by exposing pregnant mothers to chases by a domestic dog (*Canis familiaris* Linnaeus, 1758). Litter size was comparable between risk-augmented and control groups, but treated females had more stillbirths and gave birth to leverets of lower body condition. Leverets from risk-augmented females had 88% higher 40-day mortality rate. Maternally preventable causes of death like starvation or predation by red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)) caused this difference, particularly during the nursing period. Risk-augmented mothers were always more active than controls, but the difference was greatest during the nursing period. We found that perceived predation risk reduces maternal productivity pre- and post-partum, implying downstream consequences to populations. Because our treatment ended before parturition, we can link offspring performance such as survival and behaviour specifically to maternal life-history trade-offs, which has not been shown in a wild mammal.

Key words: cyclic species, maternal effects, population cycles, predation risk, reproductive investment, snowshoe hare

Introduction

In long-lived species that face variable environments, selection should favour individuals who maximize lifetime reproductive success through plastic responses to variation (Allen et al. 2022). For example, parental investment strategies may vary according to conditions at the time of the reproductive event such as relative risk of predation (e.g., Zanette et al. 2011) or nutritional state of the parent (e.g., Lycett et al. 1998). In turn, these constraints can influence parental investment pre-partum such as the number and quality of offspring produced (e.g., Stahlschmidt and Adamo 2015) or post-partum such as rate or quality of offspring protection or provisioning (e.g., Wheatley et al. 2006; Dudeck et al. 2018). It follows that offspring condition and survival should mainly reflect how much parental investment they receive, and if they survive to independence, then their own responses to conditions in the environment (Avril et al. 2012). Variations in parental investment can lead to variation in offspring survival (Zanette et al. 2011), movements (Fisher and Wiebe 2006), activity patterns (Avril et al. 2012; Rödel et al. 2015), and foraging behaviour (Storm and Lima 2010). Thus, the combined effects of parental reproductive investment and resultant offspring performance should be foundational to life-history strategy, but causal examples of such interactions remain rare (e.g., Erlandsson et al. 2017; Dudeck et al. 2018). This may be because of difficulties disentangling the relative contribution of the post-natal environment from pre- and post-partum maternal investment on offspring performance. Studies assessing how parental investment and offspring performance vary according to environmental variation are needed to advance our understanding of reproductive investment and life-history strategy.

Snowshoe hares (*Lepus americanus* Erxleben, 1777; Fig. S1) occur across the boreal forest of North America, where they exhibit 8–11-year population cycles (Krebs et al. 1995). During hare population declines, virtually all hare deaths are due to predation, with terrestrial carnivores being responsible for >70% of mortalities (Hodges et al. 2000). Survivors of the decline exhibit physiological consequences of chronic stress (i.e., as seen by increases in the production of glucocorticoids; Boonstra et al. 1998*a*; Krebs et al. 2018); however, the extent to which such stress limits population growth is poorly understood (Lavergne et al. 2021). During the increase phase of the cycle when predator abundance is low, female

hares invest heavily in offspring production, producing up to four litters per summer; during cyclic declines when predator abundance is high, females have as few as two litters, and possibly fewer offspring per litter (Hodges et al. 2000). This reduction in fecundity has been linked to high predator exposure and stress responses in a dog-based manipulation in captive hares (Sheriff et al. 2009). Moreover, during periods of high predation risk, juvenile hares experience increased mortality from predators such as red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) and Arctic ground squirrels (*Urocitellus parryii* Richardson, 1825) (O'Donoghue 1994). Ultimately, low juvenile recruitment is a prominent feature of the decline phase in snowshoe hare population cycles, but the respective contributions of reduced fecundity and post-natal maternal investment to demography remain to be fully understood (Boonstra et al. 1998*b*; Sheriff et al. 2015; Peers et al. 2018).

We assessed the effect of perceived predation risk on maternal reproductive investment and offspring viability in free-ranging snowshoe hares by manipulating perceived predation risk via exposure to a domestic dog (*Canis familiaris* Linnaeus, 1758). Macleod et al. (2018) carried out a similar experimental study on captive hares using a pen design. Based on this and other previous works (Sheriff et al. 2009; Dudeck et al. 2018), we predicted that risk-augmented females would exhibit dynamic parental investment, with females investing less into pre-partum (litter size and offspring quality; see Sheriff et al. 2009) and/or post-partum offspring care (see Dudeck et al. 2018). As a result of lower maternal investment under risk augmentation, we predicted that leverets would display higher mortality rates (as in Macleod et al. 2018) owing to changes in either activity levels or departure from the natal site. This study contributes to a growing body of foundational work uncovering the drivers of variation in demography as it relates to environmental stressors, perceived predation risk in particular (Zanette and Clinchy 2020), and highlights demographic level consequences in wild populations.

Materials and methods

Study area

We worked in the Alsek Valley in southwest Yukon (N60.95443°, W138.02916°) from April to August 2015–2016. The region typically receives ~30 cm precipitation annually (Krebs et al. 2018) and has average temperatures of 13 °C in summer (June–August) and −17 °C in winter (November–February; see Lavergne et al. 2021). The valley is dominated by white spruce (*Picea glauca* (Moench) Voss) and a mixed understory of grey willow (*Salix glauca* L.), bog birch (*Betula glandulosa* Michx.), soapberry (*Sherperdia canadensis* Linnaeus), and other herbaceous plants (Krebs and Boonstra 2001). We conducted our work at four 36 ha sites, which spanned ~17 km along the valley. Our study occurred during the increase phase of the snowshoe hare cycle, with a 45% increase in spring snowshoe hare density and a 47% increase in Canada lynx (*Lynx Canadensis* Kerr, 1792) and coyote (*Canis latrans* Say,

1823) winter track transect indices from 2015 to 2016 (CEMP 2018).

Live-trapping and adult female radio-collaring

Hares were live-trapped in the last 2 weeks in April, May, and June (Tomahawk Live Trap Co. Tomahawk, WI, USA; mean: 13.9 ± 2.7 (standard error, SE) trapping nights per month). Traps were baited with apple and a mixture of rabbit chow, oats, strawberry jam, and molasses (Boudreau et al. 2019*a*) and set and checked overnight. Hares were ear-tagged (National Band and Tag Co., Newport, KY, USA) and sexed at first capture, and females were weighed and assessed for reproductive status via palpation of embryos (Meslow and Keith 1968). During April and May trapping, female hares (>1000 g) caught ≥2 times were equipped with very high frequency (VHF) radio-collars having mortality and activity sensors (Wildlife Materials, Murphysboro, IL, USA, and Telemetry Solutions, Concord, CA, USA).

Predation risk augmentation treatment

We split collared hares into two groups based on their spatial segregation and availability, with two sites consisting of individuals in the treatment group (CEMP Gravel Pit Grid and a non-CEMP area), one site containing individuals in the control group (CEMP Hungry Lake Grid), and one site containing individuals in the treatment and control groups that were segregated by 500 m and which never overlapped throughout the study period (CEMP Beaver Pond Grid). Beginning in mid-May, we used a trained domestic dog to experimentally increase perceived predation risk in free-ranging collared hares in the treatment group. In a team of two, one person used radiotelemetry to approach target hares, while the second person accompanied them with a leashed dog. When the team was within ~20 m of the target individual, the dog handler unleashed and instructed the dog to find and chase the hare. We used change in VHF signal strength or direction as evidence that the hare moved in response to the dog, and once this occurred (typically 20–60 s after the dog left the handler), the chase ended by recalling the dog. Our risk-augmentation treatment was applied 3× per week, on random days, during daylight hours (05:00–23:00 h). Live-trapping in the last 2 weeks of June was used to assess when parturition of the second litter was imminent for each female, and only when parturition seemed to be within ~1 week, which was inferred by palpation and time since first litter parturition (which was assessed by May trapping), did we move females to maternity pens (see below). Our experiment resulted in hares being exposed to increased perceived predation risk from approximately halfway through pregnancy of their first litter to near the end of pregnancy of their second litter, which corresponded to an average of 12.5 ± 0.99 (SE) direct chases (range: 1–19) per female. At no point did the dog ever capture a hare.

Parturition and juvenile tracking

Hares who seemed within ~1 week of parturition were placed in maternity pens under canopy cover within 300 m of their point of capture (see O'Donoghue and Bergman 1992;

O'Donoghue 1994), where they remained until they gave birth (average 6.7 ± 0.4 (SE) days later). Females were given ad lib rabbit chow, natural browse, and water each morning when pens were checked for leverets. The morning of birth, we recorded litter size, and each leveret was weighed, sexed, and ear-tagged (H. Hauptner Mouse Ear Tags, Solingen, Germany), and we measured right hind foot length. A patch of fur was clipped between the shoulder blades and surgical cement was used to attach a 4 g radio-transmitter that included both activity and mortality sensors (SOM-2070, Wildlife Materials Inc., Murphysboro, IL, USA). We built a nest site near the female's capture location made of dry grass within woody debris, placed leverets in the nest within sight of the female, and then released her. This method was previously used successfully to study leveret survival in our system (O'Donoghue and Bergman 1992) and in other leporids (Avril et al. 2012; Rödel et al. 2015). At day 10, leverets were recaptured by hand, and we re-glued the transmitter (2015) or affixed it to an expandable collar (2016). As part of a companion study, in 2015, two individuals from each litter were collected at parturition to assess offspring physiology and neurobiology (Lavergne et al. 2021). Exploratory survival analysis revealed no effect of year on leveret mortality (Fig. S2), implying that these removals did not influence the survival of the remaining littermates, causing us to omit year as a variable in survival analyses. All procedures followed established guidelines for animal care (Sikes et al. 2011) and were approved by the Trent University Animal Care Committee (Protocols 23860 and 23373), as well as Yukon Government Wildlife Research Permit # 0141 and Scientists and Explorers Act License #15-01 S&E.

Female hares nurse leverets at the nest once each night for 2–7 days following parturition (O'Donoghue and Bergman 1992) after which leverets progressively move away from the nest site until fully weaned, at age 25–28 days. Thus, after day $\sim$7, females likely nurse individual leverets in different locations, nightly (O'Donoghue and Bergman 1992). In 2016, we mounted motion cameras (Reconyx, Holmen, WI, USA; Spypoint, Victoriaville, QC, CA; Moultrie, Calera, AL, USA) at nest sites during days 1–10 to monitor maternal visitation, predation, and juvenile departure from the nest. Each day (days 1–10) or second day (days 11–40), we tracked leveret survival and nest departure/distance via telemetry and visual relocation to record GPS coordinate of the animal. Leverets were recorded as undeparted from the nest if they were <0.5 m from the release nest. Using VHF mortality sensors, we checked leveret survival daily and determined cause of death at the site via nest camera footage, site characteristics (such as finding radios in bird nests or in coyote faeces), and through necropsy (such as stomachs full of milk and/or presence of squirrel bites). Leverets were monitored until they died, radio contact was lost, or reached day 47.

Activity monitoring

In 2016, we monitored activity of leverets and adult females using an automated VHF data-logging receiver (Lotek Engineering Inc., Newmarket, ON, Canada). For juveniles,

transmitter pulse rate for active and inactive animals were $\sim$30 beats/min and $\sim$60 beats/min, respectively, with intermediate records (i.e., 40–54 beats/min; <26% of total) being censored. Adult female transmitters also provided activity data, with $\sim$40 beats/min and $\sim$60 beats/min being able to distinguish between activity and inactivity, respectively. We censored female activity records with intermediate values (i.e., 48–52 beats/min; 4% of total).

Statistical analysis

Litter size was analyzed using a candidate set of linear mixed models (R package lme4: Bates et al. 2015), which included experimental treatment and year as main effects, maternal identity as a random effect, and a null model (Table S1). We used Barnard's one-tailed unconditional test (Lydersen et al. 2009) to assess effects of treatment on stillbirth rates by classifying litters as whether they included any number of stillborn individuals and again by classifying individual leverets as stillborn or not. Maternal early-nest abandonment was assessed using Barnard's unconditional test classifying females as having returned to the nest after parturition or not, based on video and images from nest cameras.

We used the residuals of a Model I regression between birth mass and right hind foot length (Murray 2002) as an index of leveret body condition at birth (Fig. S3). Timing of nest departure, distances travelled from the nest, and activity levels of leverets were analyzed using a common set of candidate predictors that included experimental treatment, year, age, sex, and birth condition and a null model (Tables S2, S3, and S5). Because of the different stages and manifestations of leveret movements as they age (Martin et al. 2005), we conducted separate analyses for (1) timing of nest departure and (2) distance from nest site, over time. For timing of nest departure, we used binomial generalized linear mixed models using R package glmmADMB (Skaug et al. 2010). For distance from nest, we used log-transformed distance in linear mixed-effects regressions using the lme4 R package (Bates et al. 2015). Because individual leverets could leave the nest asynchronously, we included leveret identity nested within maternal identity as a random factor in each model.

Leveret survival was analyzed using Cox proportional hazards (CPH) models (R package survival; Therneau 2023) and survival rates were visualized using Kaplan-Meier survival curves (survminer R package; Kassambara and Kosinski 2021). Candidate CPH models included experimental treatment and birth condition, and models were stratified by sex to conform with proportional hazards (Fig. S4). Maternal ID was included as a cluster term. In a second analysis, we used a competing risks framework to identify factors promoting cause-specific mortality, with causes of death grouped as maternally preventable (i.e., starvation and red squirrel predation), not maternally preventable (i.e., predation by coyotes, lynx, and birds of prey), or unknown. Our competing risk model (R package coxme; Therneau 2022) used an interaction term between treatment and cause of death to determine what causes of death were most related to the treatment effect that was identified in the previous CPH model se-

lection analysis and included maternal identity as a random effect.

Given rapid leveret development and the potential impact of age on survival (O'Donoghue 1994), both survival analyses were binned into 5-day age classes using function survSplit in package survival (Therneau 2022); this modification was preferred over a continuous age variable by day to conform to hazard proportionality. Using program MICROMORT, Heisey–Fuller estimates (Heisey and Fuller 1985; Heisey and Patterson 2006) were used to calculate leveret survival and cause-specific mortality rates through pre-weaning (1–28 days) and post-weaning (29–47 days) periods. All model-based analyses of leveret data were right censored at 40 days due to diminishing sample size after this point (nine control and three risk-augmented leverets were monitored longer than 40 days of age and were included in Heisey–Fuller survival rates).

Hares are sensitive to diel patterns (Studd et al. 2019), and we examined leveret activity in relation to experimental treatment, sex, age, and period of day binned in 6 h intervals (night 00:00–06:00; morning 06:00–12:00; afternoon 12:00–18:00; evening 18:00–24:00). Leveret activity was analyzed using binomial (i.e., active vs. inactive) generalized linear mixed models with leveret ID nested within maternal ID and Julian day as random factors (Table S5). Maternal investment in leveret provisioning and protection may correspond to variation in activity levels during the nursing and post-nursing periods. Therefore, we analyzed adult female activity levels with a binomial generalized linear mixed model with experimental treatment, period of day (6 h bins; see above), as well as leveret weaning status (pre-weaning: days 0–28; post-weaning: days 29–40) as main effects. Female identity was included as a random effect, and females whose entire litter had died were classified as post-weaning at the time of leveret deaths.

Candidate models for juvenile litter size, dispersal, survival, and activity were subject to model selection using Akaike information criterion corrected for small sample size (AICc, Burnham and Anderson 2004) using the MuMIn R package (Bartoń 2018), with models ΔAICc < 2.0 being indistinguishable (Burnham and Anderson 2004). Generalized linear model outputs were evaluated as odds ratios (OR; using the oddsratio v1.0.3 R package; Schratz 2017). Adult and juvenile activity results are presented using Wald χ^2 tests for significance of fixed effects because these are more appropriate than F tests for dealing with the degrees of freedom from many observations (Agresti et al. 1990). To avoid sample retention bias (i.e., non-random censorship; see Zens and Peart 2003), model selection was conducted on full dispersal, survival, and activity datasets and then repeated with the same predictors but excluding leverets who survived >10 days; these modifications did not affect our results qualitatively. To ensure that we could compare our results across taxa reported in the literature, we also calculated effect sizes as ln(mean risk-augmented/mean control) per Salo et al. (2010). All model-based analyses excluded three risk-augmented litters from 2015 that were composed entirely of stillbirths or had a single live leveret. All statistical analyses were done in R v. 3.4.1 (R Core Team 2017).

Results

Litter production

In total, we measured 37 litters (risk augmented: 11 (2015), 10 (2016); control: 6 (2015), 10 (2016)), for a total of 191 leverets. Of all litters, 18.9% contained at least one stillbirth, and stillbirth rates were comparable between risk-augmented and control females (Barnard's one-sided test, $P = 0.30$). In contrast, number of stillborn individuals differed by treatment (Barnard's one-sided test, $P = 0.02$), with 14.5% ($n = 110$) of births from risk-augmented females vs. 4.9% ($n = 81$) of births from controls being stillborn; this yielded a treatment effect size of -0.11. Litter size for litters not containing any stillbirths averaged 5.2 ± 0.2 (SE) overall (control: 5.07 ± 0.3, risk-augmented: 5.3 ± 0.3, effect size: $+0.04$), with the top model for litter size including only the year variable, with 1.2 ± 0.4 fewer live leverets per litter in 2016 (Table S1). The effects of litter size (fecundity) and stillbirths (survival at birth) combined resulted in per capita production of un-weaned live offspring of 4.48 and 4.41 offspring at birth for the risk-augmented and control groups, respectively (effect size = -0.07). Newborn body condition index was $185.7\% \pm 20.7\%$ lower in the risk-augmented group ($F_{[1,29]} = 5.62$, $P = 0.03$; Fig. S3).

Leveret nest departure

We released and monitored 145 leverets (risk-augmented: 79; control: 66). While top models for leveret nest departure included varying combinations of maternal treatment, year, and age, the only consistent predictor of nest departure was age (Table S2). The top model also contained an experimental treatment X year term, suggesting that leverets from risk-augmented females left the nest slightly sooner than controls, in the second year of study. We found that by day 7, no leverets from risk-augmented females remained at the nest, while $15\% \pm 0.1\%$ of controls had not yet left the nest at the same age (Fig. S5A). Post-departure, leverets were found at comparable distances from the nest regardless of treatment, with leveret age as the only predictor of distance from the nest (Table S3, Fig. S5B).

Leveret survival

Of 145 leverets monitored, we recorded 78 mortalities and right-censored 55 individuals ($n = 29$ control, 26 risk-augmented) at <40 days due to premature transmitter failure. Censored leverets were monitored on average 30.0 ± 1.4 days prior to censorship, and there was no censoring bias between treatment groups ($\chi^2_{[1]} = 0.44$, $P = 0.51$ per Murray et al. 2010; Murray and Bastille Rousseau 2020). Maternal risk augmentation reduced leveret survival (Fig. 1), with individuals born to risk-augmented females showing 88% greater likelihood of death during the 40-day sampling period, as indicated by consistent experimental treatment term hazard ratios in all supported models (Table S4). Pre-weaning (days 10–28) Heisey–Fuller survival rates were nearly twice as high in controls (0.51; 95% confidence interval (CI) 0.40–0.67) than those born to risk-augmented mothers (0.28; 95% CI 0.20–0.40). Kaplan–Meier curves (Fig. 1) indicate that the primary difference in

Fig. 1. Kaplan–Meier survival curves for second litter snowshoe hare (*Lepus americanus*) leverets from risk-augmented or control mothers in southwest Yukon (summer 2015 and 2016). Dashed lines indicate 95% confidence intervals.
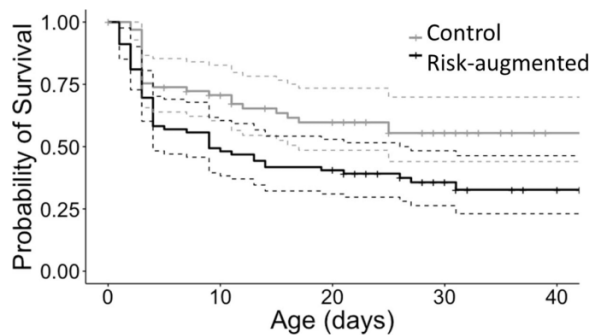
survival between treatment groups was between days 2 and 9, with survival rates thereafter being more comparable.

We found that 61% of leveret deaths were due to maternally preventable causes in the risk-augmented group (starvation: 37%; red squirrel predation: 24%), while 48% of deaths were maternally preventable in controls (starvation: 44%; red squirrel predation: 4%). For risk-augmented females, leveret mortality was 17% from non-preventable causes (terrestrial carnivores: 11%; birds of prey: 6%) compared to 23% of deaths being non-preventable in controls (terrestrial predators: 8%, birds of prey: 15%). Competing risk analysis revealed that leverets born to risk-augmented mothers had a >3-fold higher probability of succumbing to maternally preventable causes of death compared to controls (hazard ratio 3.21 ± 0.4, $z = 2.8$, $P = 0.006$). Unknown deaths comprised 19.2% of mortalities; to test for non-random inclusion of deaths in this category, we conducted sequential versions of the competing risks' analysis with these deaths included in the preventable and non-preventable categories and found that binning unknown deaths into either the maternally preventable or non-preventable category did not affect results appreciably (Table S6) and excluded them from the final competing risk model.

Overall, mortality rates for maternally preventable deaths were 0.59 (0.47–0.72 95% CI) and 0.30 (0.17–0.44 95% CI) for risk-augmented and control leverets, respectively, while non-preventable deaths mortality rates were 0.16 (0.07–0.26 95% CI) and 0.26 (0.13–0.39 95% CI) for risk-augmented and controls, respectively. Cumulative incidence functions revealed that for the risk-augmented group, maternally preventable deaths occurred during the day 2–15 period compared to the day 3–7 period for controls (Fig. 2). Ultimately, risk augmentation resulted in a nearly twofold reduction in the per capita offspring surviving to weaning (risk-augmented: 1.25, control: 2.45), with 28% of live-born young surviving to weaning in the risk-augmented group, compared to 51% of controls (effect size −0.67).

Leveret activity

Leveret activity increased in response to experimental treatment and age (Table S5), with offspring from risk-augmented mothers being $45.6\% \pm 4.6\%$ more active than controls during days 1–10 and $36.7\% \pm 2.3\%$ more active during days 11–40, compared to controls. Overall, treatment group leverets were $39.1\% \pm 2.0\%$ more active than controls and control activity did not vary by age (Fig. 3A).

Maternal behaviour

Cameras at the nest site (2016) revealed that 100% ($n = 8$) of control females returned to the nest at least once after parturition, compared to only 70% ($n = 10$) of risk-augmented females (Barnard's one-sided test, $P = 0.06$). Activity monitoring for females showed that, overall, risk-augmented females were $44.0\% \pm 3.7\%$ more active than controls (OR = 15.72 (9.58–25.35; 95% CI); $\chi^2_{[1]} = 130.62$, $P < 0.001$). In addition, females were $9.5\% \pm 2.1\%$ more active after juveniles had died or were weaned (OR = 1.31 (1.08–1.58 95% CI); $\chi^2_{[1]} = 28.88$, $P < 0.001$; Fig. 3B). Activity in risk-augmented females also differed pre- vs. post-weaning during afternoon and evening (treatment X litter status X period interaction: $\chi^2_{[3]} = 30.78$, $P < 0.001$), with slightly lower activity during the second half of the day (Fig. 3B).

Discussion

In variable environments, life-history variation should be centred around traits that are plastic and have limited cost or low potential for environmental mismatch (Creel 2018). In snowshoe hares, variable investment in juvenile provisioning and protection may be the most plastic response to variable predation risk. Similar to the study by Macleod et al. (2018), females did not reduce litter size or have a higher proportion of litters that contained any stillbirths when subjected to increased predation risk. Captive hares subjected to experimental exposure to a dog also produced offspring of lower quality and produced equal litter sizes as controls (Sheriff et al. 2009), and our effect sizes are consistent with other predator manipulations (Zanette et al. 2011; Zanette and Clinchy 2020). The rate of stillbirths we observed was nearly threefold higher under risk augmentation and offspring were seemingly of lower quality, indicating a reduction in reproductive investment by females pre-partum with demographic consequences. Across taxa, the effects of risk on fecundity are generally small, with effect sizes ranging from −0.19 to +0.03 (Zanette and Clinchy 2020); therefore, it appears that fecundity often contributes but does not drive the main effects of risk on populations. Rather, our results suggest that parental investment and offspring quality may be a more plastic response to risk, a result that is supported by the number of leverets stillborn, which yielded a treatment effect size similar to those reported across taxa (−0.11 to −0.38; Zanette and Clinchy 2020). Our work complements a growing body of evidence of the small yet consistent effect of risk on the production of offspring.

Recent evidence (Zanette et al. 2011; Dewitt et al. 2019) supports the longstanding theory that females can adjust their reproductive effort relative to survival to maximize lifetime reproductive success (Clutton-Brock 1984; Clutton-Brock et al. 1989). We observed multiple lines of evidence to this effect. Stratifying CPH models by age categories allowed us to

Fig. 2. Cumulative incidence functions for juvenile snowshoe hare (*Lepus americanus*) mortality in southwest Yukon in summers of 2015 and 2016. Mortality agents are categorized according to whether the mother could have prevented the death or could not have prevented death.
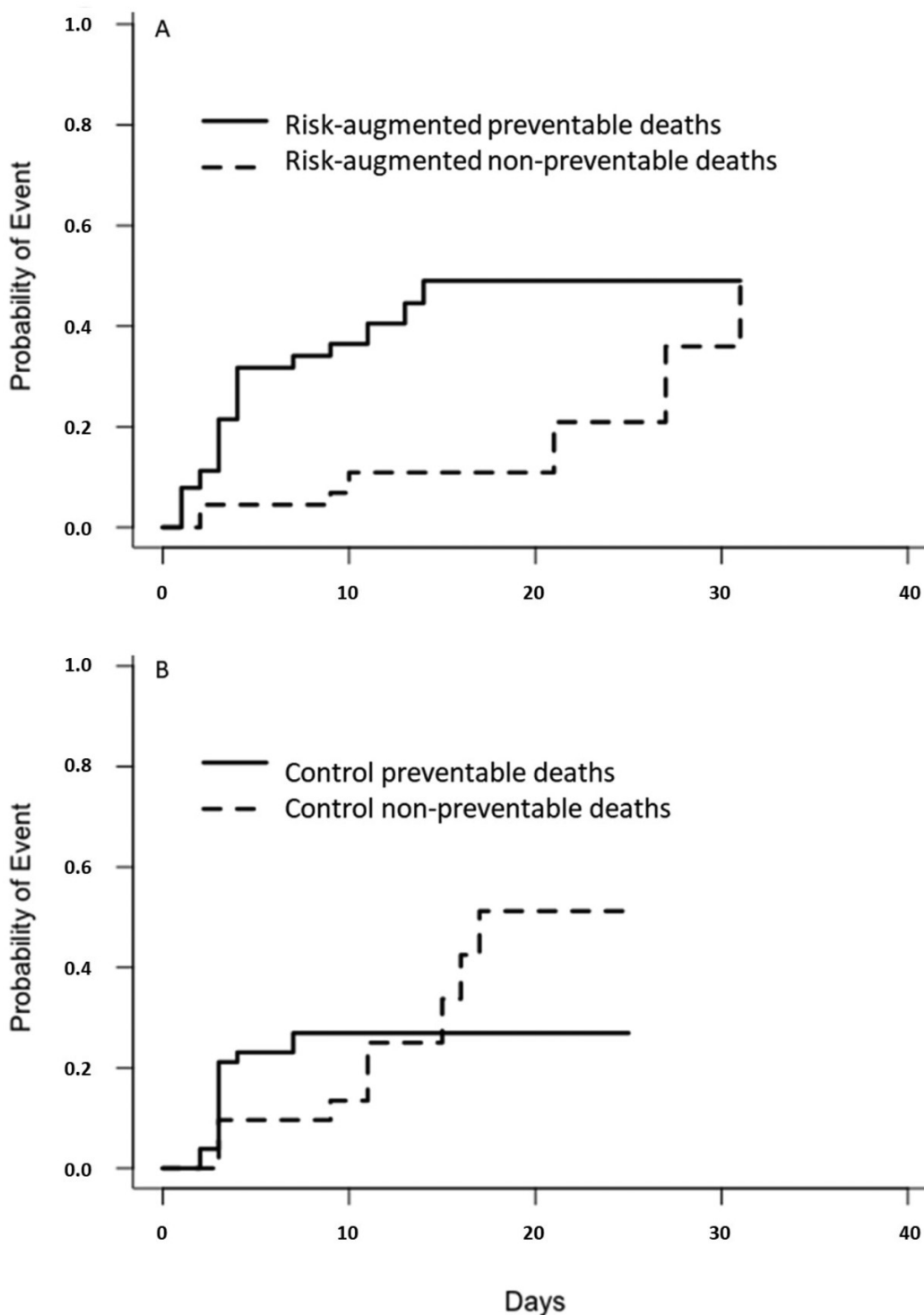

see that maternal risk augmentation was a significant predictor of leveret survival, but that this effect was not proportional between treatment groups over time—because maternal care influences younger leveret survival more than the survival of older leverets; the effect of age varies over time disproportionately between treatment groups. Indeed, Kaplain–Meier curves indicated the maternal treatment effect was important only during the first 10–15 days of leveret life, when curves were non-parallel, meaning the effect of maternal risk augmentation was concentrated on the early pre-weaning period. This was supported by Heisey–Fuller survival rates that showed greater rates of survival after the weaning age. Cu-

Fig. 3. Mean (±SE) activity of snowshoe hares (*Lepus americanus*) in southwest Yukon (% of observations indicative of motion), according to (A) period of day, age, and experimental treatment group (juveniles) and (B) period of day, maternal care status, and experimental treatment group (adult females).
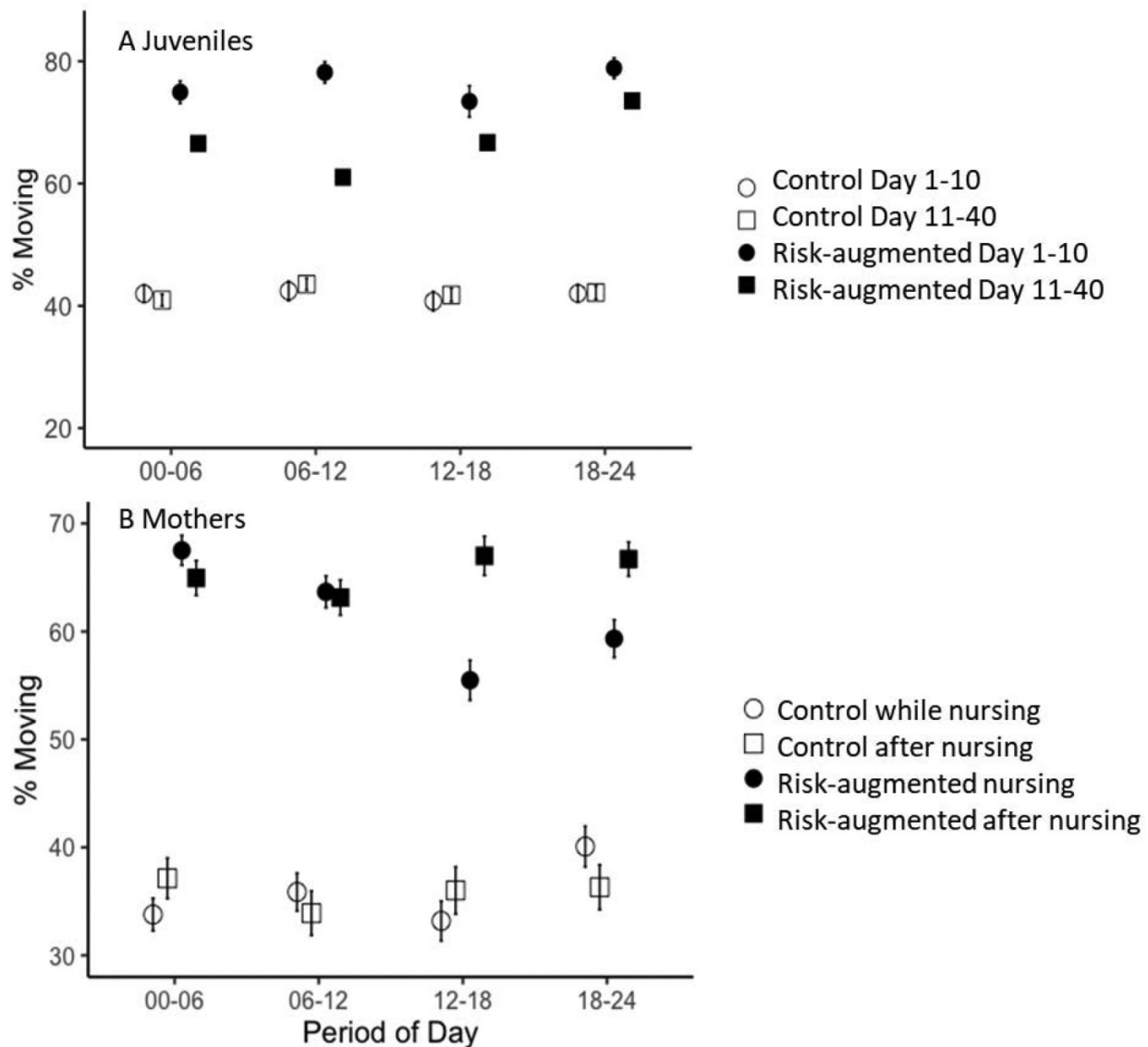
mulative incidence functions showed the same trend, indicating that maternally preventable causes of death were driving the mortality in the risk-augmented group that the CPH models had first identified. Further, females exposed to increased risk showed a marked decrease in their likelihood of returning to the nest site after parturition, and we interpret this as a reduction in parental care, akin to examples in birds (Zanette et al. 2011; Dudeck et al. 2018). Combined, it is clear that maternal risk augmentation was the driver of reduced leveret survival and that maternal inattention is the proximate mechanism for this effect. This is entirely consistent with other risk-exposure experiments, such as that in song sparrows (*Melospiza melodia*, A. Wilson, 1810) whereby fledglings whose parents were risk-augmented displayed lower survival rates during a 7-day period after leaving their nests, but after this initial period, survival between control and risk-augmented fledglings became more compa-

rable (Allen et al. 2022). The demographic trajectory of offspring appears to be determined by the early juvenile period when young are most dependent on parental care. The parents' choice to provide care after producing offspring appears to be the most plastic response to risk. This is supported by the smaller effect size of litter size relative to the effect of offspring survival to weaning, and this is similarly reported across taxa (Allen et al. 2022).

Because our risk augmentation treatment ended prior to parturition, we can link changes in leveret performance specifically to the pre-partum environment experienced by the mothers as leverets from both maternal treatments experienced the same environment once they were born. Although previous manipulations relate predation risk and juvenile mortality to reduced parental care (Dudeck et al. 2018), it has not been possible to disentangle the effect of ongoing predation treatments from maternal life-history trade-

offs because predation simulations continue after offspring are born. This allows the observation of parental provisioning trade-offs under ongoing risk, but simultaneously exposes offspring to the same experimental cues and thus confounds the effect of provisioning from direct offspring responses to the perceived risk, such as altered behaviour. However, when a parent adjusts their behaviour in favour of future reproduction and does not provision offspring sufficiently, the offspring cannot survive no matter their own responses to the environment, something that we show for the first time in an iteroparous mammal.

We found very limited evidence that leverets in the risk-augmented group left the nest site sooner than controls by ~2 days (Fig. S5A), a behaviour in young that is exhibited in risky environments likely as a means of mitigating the loss of an entire reproductive bout to a single event (e.g., such as a predator finding a nest and killing an entire clutch of eggs; Meylan et al. 2002). This response in juvenile hares follows what is seen under increased maternal risk exposure in a variety of species ranging from aphids (Zhang et al. 2009) to birds (Fisher and Wiebe 2006). It is also possible that leverets left the nest in response to maternal inattention, but we were unable to test this explanation. Although we did not find differences in the distance leverets travelled from the nest, we suggest that such differences could manifest after leverets are weaned and no longer bound by proximity to their mother's sphere of influence, something we could not robustly test given high mortality rates before the 28-day pre-weaning period.

We observed greater activity in juveniles from risk-augmented dams that could be a response to reduced maternal attention during the pre-weaning phase. For example, this could be akin to chick begging, where offspring may give signals of need through greater active calling, making themselves more conspicuous (e.g., O'Connor et al. 2014), following parent–offspring conflict theory (Trivers 1974). Greater activity during times of parental absence has been shown to reduce offspring survival, such as in Arctic fox (*Alopex lagopus* (Linnaeus, 1758)) where parental absence from the den prompts higher predation due to increased juvenile activity (Erlandsson et al. 2017). Similarly, juvenile European rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)) die more frequently from predation while exhibiting exploratory behaviour when parents are not present (Rödel et al. 2015). In both these examples, juvenile activity increases in the absence of parental attention, and offspring are predated; this differs from costs associated with juvenile dispersal because it occurs before offspring are independent of parental care (Avril et al. 2012). In support of this interpretation, our leverets showed the greatest increase in activity before they departed from the nest (i.e., prior to age 10 days). While we do not know what behaviours cause this increased activity, understanding this phase of development would be of particular interest in future work, and could be observed at the nest site using better-quality cameras or more cameras than we had available. This may also reveal whether such activities result in predation, as seen in other species (Rödel et al. 2015; Erlandsson et al. 2017).

Avoiding predation can be accomplished through a variety of behaviours, including use of refugia (e.g., Mcintosh and Townsend 1996), reduced movement (e.g., Hertel et al. 2016), or increased vigilance (Storm and Lima 2010). Prey may respond to increased risk with declines in activity (e.g., Schmitz et al. 1997; Van Dievel et al. 2016). It follows that these responses may incur direct costs to prey via reduced feeding and lower energy intake (e.g., Schmitz et al. 1997; Van Dievel et al. 2016), but surprisingly, our risk-augmented mothers were almost twice as active as controls and this change persisted through the reproductive period, even post-weaning, which occurred earlier for females who lost their litters entirely. Our companion study on the behaviours associated with increased activity in adult hares under risk augmentation indicates this may be from a need for greater forage (Boudreau et al. 2019b). Indeed, risk-exposed animals may increase their feeding especially if stress associated with the treatment elicits catabolic consequences of chronic stress (Boonstra et al. 1998a). Notably, hares store little body fat regardless of season (see Whittaker and Thomas 1983; Wirsing et al. 2002), meaning that even slight increases in activity or physiological functions could aggravate nutritional deficits and prompt compensatory feeding (Clutton-Brock et al. 1989; Naya et al. 2008). By inference, such changes could elicit reduced maternal investment into maternally preventable causes of offspring mortality (such as protection), presumably to the benefit of female survival. This tendency has been documented in other species. For example, female porcupines (*Erethizon dorsatum* (Linnaeus, 1758)) faced with increased predation risk increase foraging and reduce reproduction, which in turn can cause population declines (Dewitt et al. 2019). The proximate mechanisms underlying differential maternal investment into reproduction are not fully understood. When resource allocation trade-offs begin, how allocations are prioritized to different components of reproduction and whether reproduction-related activities are entirely replaced by compensatory activities such as foraging are key questions. Here, we showed that the effects of pre- and post-parturition maternal investment can result in large changes in potential recruitment and that this has the potential to impact demography. However, it remains to be discovered at what point offspring responses become independent of the effect of maternal attention, and therefore to what magnitude offspring can influence their own fate. There is also a need to understand whether genome-based epigenetic responses resulting from the in utero maternal environment can influence juvenile viability (Weinstock 2001; Dufty et al. 2002). Additionally, it would also be useful to follow the same adults and see whether trade-offs pay off in future reproductive bouts through greater adult survival and greater productivity when the environment changes and risk reduces. This ought to be an important next step in discovering the mechanisms by which environmental cues cause demographic effects. What we do know from this work is that environmental variation in predation risk does prompt reproductive trade-offs in an iteroparous mammal, with both pre- and post-natal responses in short-term reproductive investment.

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Data generated or analyzed during this study are available partially within the published article and its supplementary materials and fully from the corresponding author upon reasonable request.

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