Received: 10 August 2021 | Revised: 8 December 2021 | Accepted: 4 January 2022

DOI: 10.1111/ele.13975

LETTER

ECOLOGY LETTERS WILEY

Balancing food acquisition and predation risk drives demographic changes in snowshoe hare population cycles

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Funding information
Natural Sciences and Engineering Research Council of Canada; Northern Studies Training Program; University of Alberta Northern Research Award program; Association of Canadian Universities for Northern Studies; The W. Garfield Weston Foundation and the Government of Yukon

Editor: Andrew Sih

Abstract

Snowshoe hare cycles are one of the most prominent phenomena in ecology. Experimental studies point to predation as the dominant driving factor, but previous experiments combining food supplementation and predator removal produced unexplained multiplicative effects on density. We examined the potential interactive effects of food limitation and predation in causing hare cycles using an individual-based food-supplementation experiment over-winter across three cycle phases that naturally varied in predation risk. Supplementation doubled over-winter survival with the largest effects occurring in the late increase phase. Although the proximate cause of mortality was predation, supplemented hares significantly decreased foraging time and selected for conifer habitat, potentially reducing their predation risk. Supplemented hares also lost less body mass which resulted in the production of larger leverets. Our results establish a mechanistic link between how foraging time, mass loss and predation risk affect survival and reproduction, potentially driving demographic changes associated with hare cycles.

KEYWORDS
behaviour, demography, food supplementation, *Lepus americanus*, population ecology, predator-sensitive foraging

INTRODUCTION

Population cycles are one of the most notable phenomena in ecology, fuelling decades of research that has provided substantial insight into our understanding of the dynamics, regulation and persistence of populations (Blasius et al., 2020; Elton & Nicholson, 1942; Krebs et al., 1995; Myers, 2018). Despite the demography of cycles being well characterised, the causes of these demographic changes remain controversial (Andreassen et al., 2021; Korpimäki et al., 2004; Krebs et al., 1995; Oli, 2019). Consumer-resource models involving vegetation-herbivore, predator-prey and parasite-host interactions have been shown to be capable of generating cyclic dynamics (Oli, 2019; Turchin, 2003). Others point towards the potential importance of self-regulation (social interactions; Krebs, 2013). However, empirical studies and experiments have not led to a consensus on which causal factors are involved in creating multiannual density fluctuations.

Population cycles have been documented in many herbivores including grouse, lemmings and voles (Myers, 2018; Oli, 2019; Turchin, 2003). In the boreal forest, the snowshoe hare (*Lepus americanus*) is a keystone species (Humphries et al., 2018; Peers et al., 2020a) that along with its main predator, Canada lynx (*Lynx canadensis*), fluctuates in abundance every 9–11 years (Krebs et al., 2001a). Major demographic changes occur during the four phases of the cycle with survival and reproduction being highest in the increase phase and lowest during the decline phase (Hodges et al., 2001). The proximate cause of mortality in hares is predation; therefore, the main factors hypothesised to drive these dynamics consist of direct predation (Krebs et al., 1995; Trostel et al., 1987), potentially in combination with food limitation during the winter (Keith, 1983; Smith et al., 1988), or non-consumptive effects of predators (Boonstra et al., 1998; Sheriff et al., 2009). Previous experiments on hare populations included manipulations of food supplementation, terrestrial predator exclusion and combined food supplementation and predator-exclusion over an entire cycle (Krebs et al., 1995). Single-factor manipulations increased hare densities 2–3-fold, whereas the combined treatment of food supplementation and predator exclusion increased densities 11-fold, suggesting a potential interaction between food supply and predation (Boutin et al., 1995; Krebs et al., 2018). Densities in all experimental populations declined with a 1–2 year lag, except for food supplemented populations which declined at the same time as control populations. The overall conclusion stemming from this body of research was that change in predation rates was the dominant driver of hare cycles, but the mechanism of interaction between food supply and predation remained unexplained.

Assessments of resource limitation in ecology have often involved the supplementation of high-quality food at the population level. In general, the result of these experiments has been an increase in density through immigration rather than changes in survival or reproduction (Boutin, 1990; Prevedello et al., 2013). In many cases, these results have led researchers to reject resource limitation as an important driver of cycles (Krebs et al., 2018; Oli et al., 2020). However, interpretation of population-scale food supplementation results may be confounded by the artificially high densities created by immigration (Prevedello et al., 2013), which may lead to unequal access to supplemental food (Newey et al., 2010), and attraction of predators to the treated areas (Boutin, 1990). This creates an ecological trap, where the food addition site is perceived as high-quality habitat, but survival and reproduction are reduced due to the artificially created intense predator presence coupled with increased competition (Gilroy & Sutherland, 2007; Prevedello et al., 2013). As a result, these experiments may fail to reveal the potential importance of food limitation, and manipulative approaches that eliminate these confounds are required.

Food availability and changing predation risk may interact through predator-sensitive foraging. Areas with high-quality food resources (i.e. shrub habitat) are considered the most risky (Hik, 1995), and predators may restrict access to high-quality resources forcing hares to forage in a predator-sensitive manner at the cost of their condition (McNamara & Houston, 1987; Oates et al., 2019). Conversely, a poor nutritional state caused by lower food availability can impact risk-taking behaviour (Houston et al., 1993; Kotler et al., 2004); animals in poor body condition maintain foraging at the cost of antipredator behaviour, increasing their risk of predation (Lima & Dill, 1990). Despite previous food supplementation experiments failing to alter reproduction (O'Donoghue & Krebs, 1992) or limit population decline (Krebs et al., 1995, 2001a), food limitation (through quantity, quality or accessibility) could be impacting hares through changes in body condition affecting reproduction, or indirectly through changes in behaviour (movement and habitat use) altering their vulnerability to predators (McNamara & Houston, 1990; Murray, 2002; Sinclair & Arcese, 1995). However, behavioural responses to either food supply or predation risk have not been thoroughly evaluated as an intrinsic driver of demography (but see Hik, 1995), largely due to the difficulty of monitoring hare behaviour in the wild (Brown et al., 2013).

Here, we describe the results of an individual-based food supplementation experiment carried out across the late increase, peak and decline phases of a hare cycle in southwestern Yukon, Canada, which naturally varied in predation risk (Figure 1). Treatment hares were fed from micro-chip enabled feeders and compared to control hares living in the same area but with no access to the feeders. By feeding hares individually, population densities were not inflated due to food-related immigration (Boutin, 1990; Prevedello et al., 2013), and we were able to accurately identify which individuals used the supplemental food. We examined differences in survival and various reproductive parameters across each treatment and cycle phase while tracking late-winter foraging and vigilance behaviour using accelerometers, habitat selection using GPS collars, and body condition using individual mass change. We linked measures of behaviour and condition with reproduction to further investigate the potential pathway through which food limitation could influence the system. If food limitation and predation interactively drive cycle dynamics, we predicted significant

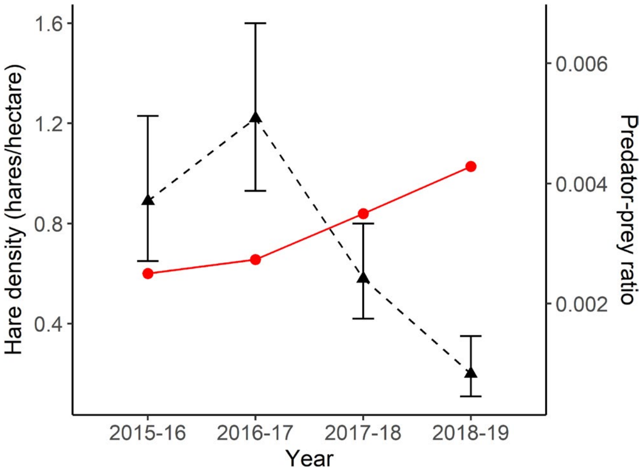

FIGURE 1 Changes in hare density (*Lepus americanus*) and predation risk in the Kluane Lake area from 2015 to 2019. Changes in spring snowshoe hare density (hares/hectare) are shown as mean density ± 95% confidence intervals (black triangles) and correspond to the late increase (2015–2016), peak (2016–2017) and decline (2017–2018 and 2018–2019) phases of the cycle. The ratio of lynx (*Lynx canadensis*) and coyote (*Canis latrans*) to snowshoe hares is presented as the predator-prey ratio (red circles). All data were gathered from the Community Ecological Monitoring Program (Krebs et al., 2020)

differences in survival, reproduction, behaviour and body condition between treatments, and variation in both groups across years that varied in predation risk. Overall, our work provides new insight into how behaviour, food limitation and predation interact to affect hare condition, reproduction and survival over a cycle, and more broadly how these factors regulate population density.

MATERIALS AND METHODS

Monitoring snowshoe hare demography and behaviour

Our study was conducted in the Kluane Lake area of southwestern Yukon, Canada (61°N, 138°W), where studies of snowshoe hares have been ongoing for the last four decades (Krebs et al., 2018; Oli et al., 2020). Our study occurred throughout four winters from 2015 to 2019, during which snowshoe hares were in the late increase (2015–2016), peak (2016–2017) and decline (2017–2018 and 2018–2019) phases of their population cycle (see Supplementary Methods). Snowshoe hares were captured approximately every 3 weeks using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI, USA). Trapping occurred on three separate trapping areas within 8 km of each other and included a long-term control area trapped each spring and autumn to estimate hare density (see Figure S1). All newly captured hares received an ear tag (Monel #3 National Band and Tag Co., Newport, Kentucky, USA) and at each capture, tag number, sex, right hind foot length (RHF), mass and reproductive condition were recorded (Krebs et al., 2001b).

Female hares weighing >1100 g were fitted with VHF collars (Model SOM2380, Wildlife Materials Inc., USA; <40 g, <5% body weight), with a subset containing a GPS unit (Gypsy 5, Technosmart, Guidonia, Rome, Italy) and an accelerometer (model Axy3, 4 g, Technosmart, Rome, Italy) as equipment was available. We monitored hare survival daily between November and May from 2015 to 2018 and January to May in 2019. All transmitters emitting a mortality signal (increased pulse rate) were located and the cause of mortality was determined when possible through the presence of predator tracks in the snow, and parts of the carcass remaining (Peers et al., 2020b). GPS units were set to record a location (10 fixes) at either 5-min, 15-min or 30-min intervals. We averaged the last four fixes for each location to improve precision, and GPS error was ~15 m. Accelerometers, used to measure hare behaviour, rested on the dorsal side of the neck and recorded acceleration on three-dimensional axes at 1 Hz with a resolution of ±8 g-forces (Studd et al., 2019).

Hares can have up to 4 litters per summer, but we focused on the first litter, which is born mid to late-May, as we assumed that this litter was most likely to be affected by winter food availability (Hik, 1994), and may have a strong influence on hare demography relative to late summer litters (Peers et al., 2021). We placed individuals in 0.6 m × 1.2 m maternity pens near where they were live-trapped 24–48 h prior to them giving birth and provided *ad libitum* food (fresh browse and rabbit pellets) and water daily (O'Donoghue & Krebs, 1992). We determined the sex, mass, and length of the RHF of each leveret within 24 h of birth, and mother and leverets were then released (see Supplementary Methods for more details). All handling and collaring procedures were approved by the University of Alberta Animal Care and Use Committee (Protocol: AUP00001973) and permitted by the Government of Yukon.

Food supplementation

We conducted a supplemental feeding experiment throughout November to May in all years except 2018–2019 when supplementation began in January. Females captured in October were assigned to either the food supplemented or control treatment, based on matching adult and juvenile numbers between treatments and achieving a sample size of ≥20 food supplemented females each year. We further selected food supplemented hares based on their spatial proximity (determined by trapping and telemetry) to maximise our sample size given the number of feeders available. Once assigned to a treatment group, hares remained in that treatment and were monitored for the duration of our study or until they dispersed or died. Each autumn, newly trapped individuals were added to existing treatment groups based on the criteria above. Supplemented females had pit tags attached to their telemetry collars which allowed them to access commercial rabbit pellets *ad libitum* (see Table S1), from selective feeders (SureFeed Microchip Pet Feeder, Sure Petcare, Cambridge, UK), while control females could not access the feeders. The feeders could hold approximately 200 g of rabbit pellets and the food was replenished or replaced every 2–3 days.

A total of 14 feeders were deployed each year in spruce habitat in locations that afforded partial cover and allowed all supplemented females to have shared access to 1–3 feeders. In all years, control and food supplemented hares had home ranges that overlapped or were adjacent to each other, which allowed us to compare supplemented and control hares living in similar conditions. At each feeder, we placed a motion-triggered infrared camera (PC900 Hyperfire^{TM} RECONYX, Inc., Holmen, Wisconsin, USA) to ensure supplemented hares (and no control hares) had access and used the food. We identified individual hares using unique barcode patterns made of heat shrink that were attached to their collar antenna. Most hares spent only a small portion of their active time at feeders (<1 h/day), and thus the majority of their time was spent participating in other activities and behaviours outside of feeder use. We scored if food supplemented hares visited a feeder each day and calculated the proportion of days they visited a feeder throughout their time in the study.

Statistical analyses

Effect of food supplementation on survival, reproduction and mass change

Across the four years, we monitored the survival of 224 female hares daily throughout the winter for a total of 275 individual hare winters. We assessed the influence of food supplementation on over-winter survival using a semiparametric Cox proportional hazards model (Cox, 1972). We used a right-censored design with time-at-risk (days) based on time since the start of the food supplementation (1 November in all years except 1 January for winter 2018–2019). Only individuals captured in the 30 days after the start date of the experiment each winter were included as the addition of new individuals throughout the season can bias survival estimates (Murray & Bastille-Rousseau, 2020). We grouped all causes of death (i.e. lynx, coyote, birds of prey and unknown predator) in our models, and censored individuals because of the removal of their collar prior to the completion of the study (n = 2). We suspected collared hares that went missing and were never subsequently re-trapped (n = 23) to represent collar failure caused by extremely cold temperatures (−30°C) at the time of mortality, and therefore, classified collar failures as mortality events in our survival models (see Supplementary Methods). However, models that censored these individuals revealed qualitatively similar results (Table S4).

We used a model selection approach and built Cox proportional hazards (CPH) models that included either treatment, year, treatment and year or their interaction. Each of these models satisfied the proportionality assumption of CPH models based on the cox.zph function in the survival package in R (Therneau & Lumley, 2020), and we selected the best model using Akaike information criterion (AIC) corrected for a small sample size, ΔAICc (Burnham & Anderson, 2002). Based on the top supported CPH model, we predicted 30-day survival rate for each treatment for each year using the predict function in R. We further plotted the over-winter survival differences between treatment groups using Kaplan-Meier curves for each year using the survfit function in the survival package in R (Therneau & Lumley, 2020).

We examined the effect of food supplementation on total litter mass, number of offspring, individual leveret mass and length of right hind foot (RHF). We tested for normality in each response variable using the Shapiro-Wilk test (Shapiro & Wilk, 1965). For analyses where normality was not satisfied, we used generalised linear mixed effect models (GLMM) with a gamma distribution and log link or a Poisson distribution for the analysis of the number of offspring. We used a model selection approach and built candidate mixed models for each response variable that included either treatment, year, treatment and year or their interaction as predictors, and individual ID as a random variable. We selected the best model using ΔAICc (Burnham & Anderson, 2002), and all models were built in the R package glmmTMB (Magnusson et al., 2017).

To determine the effect of treatment and year on over-winter mass change, we used mass data from all individuals that were collared during the four study years that had two mass measurements >60 days apart between December and April (n = control: 33, supplemented: 57). We converted mass loss into a daily measure to account for variation in duration between capture events. We then used a model selection approach, as described above, and included the initial mass of individuals as a variable in our model selection. For 42 control individuals that had mass measurements and reproductive data, we examined the influence of late winter (March, April) body mass on total litter mass using linear regression. This subset includes individuals monitored in the spring of 2015 prior to the food supplementation experiment. We further examined the effect of female body mass on individual leveret mass and right hind foot length using models that included litter size as a predictor variable, as we assumed the number of offspring would influence leveret mass and skeletal size.

Effect of food supplementation on foraging time, vigilance and habitat selection

We monitored the winter foraging behaviour of 92 female hares equipped with accelerometers for a total of

10,496 hare days. The behavioural classification was done using a previously validated algorithm that classifies hare accelerometer recordings in our project into three broad behavioural categories which represent 91.8% of observed hare behaviour (see Supplementary Methods). These categories included not moving (which includes both resting and vigilance), foraging (consumption interspersed with single-hop travel) and travelling (sprinting or multi-hop travel) (Studd et al., 2019). We calculated the daily time spent foraging for each individual in late winter from February to April, and only included individuals that were monitored for greater than 6 days. To examine the effect of food supplementation on daily time spent foraging, we used the same model selection framework as above. We further extended the behaviour classification to separate short bouts of not moving while animals were active as an index of vigilance from long bouts of not moving that likely indicate rest. We defined short bouts as a consecutive not moving period with a duration of <5 min in between bouts of foraging and/or travelling. Therefore, in this study, we assumed animals with more frequent short bouts of not moving while foraging were more vigilant. We calculated the proportion of foraging time spent vigilant using the following formula:

$$\text{Proportion of foraging time spent vigilant} = \frac{\text{vigilance time}}{(\text{vigilance time} + \text{foraging time})}$$

We examined the effect of treatment and year on the proportion of foraging time vigilant using the same model selection framework as above, for individuals that had >6 days of accelerometer data for the corresponding season. Additionally, for 37 control individuals that had subsequent accelerometer data and multiple mass measurements over winter, we examined the influence of daily foraging rate in the winter (January through March) on over-winter mass loss (as described above) using linear regression.

We compared third-order selection (Johnson, 1980) by supplemented and control hares for each year using a land cover map developed by Boudreau (2019), which classifies habitat into six different classes (roads, cliff faces, barren ground, aspen, shrubs and conifers; see Supplementary Methods). We focused our analyses on conifer, the dominant habitat class. We used a selection ratio approach to examine habitat selection in snowshoe hares because all covariates used were categorical (Manly et al., 2002). We compared land cover type at hare locations to random locations (5 random to 1 hare location) within their yearly winter 95% UD (i.e. February–April), and calculated selection of conifer for each individual that had ≥50 locations that year. Individual selection ratios were summarised across each treatment and year, and bootstrapped (500 times) to estimate 95% confidence intervals. Each bootstrapped dataset included resampled individual selection ratios, with replacement, until the number of selection ratios in the resample (i.e. for each treatment and year) equalled the original dataset. Confidence intervals not overlapping 1 indicated significant selection for (>1) or against (<1) conifer habitat (see Table S18).

RESULTS

During our study, predation risk increased each year and nearly doubled as indicated by the predator (coyote [*Canis latrans*] and lynx) to prey ratio (0.0025 to 0.0043 predators/hare from 2015–2016 to 2018–2019). The proximate cause of mortality in both treatment groups was predation (99.4% of known mortalities). Based on a Kaplan-Meier analysis that combined all years, six-month over-winter survival for food supplemented hares (0.57, 95% confidence interval: 0.48–0.69) was double that of control hares (0.26, CI: 0.20–0.33; see Figure S2). The effect of food supplementation on survival varied across years, with the strongest effect occurring during the late increase phase (2015–2016; Figure 2). Based on modelled 30-day survival rates from a Cox proportional hazards model, survival of supplemented individuals in 2015–2016 was 0.96 ± 0.02 standard error (SE) vs. 0.81 ± 0.04 for controls. However, the effect of food on survival was diminished in 2018–2019, suggesting food limitation had minimal effect on survival when the predator-prey ratio was highest (second year of decline; control = 0.82 ± 0.05; supplemented = 0.87 ± 0.05).

Food supplementation significantly improved the reproductive output of snowshoe hares (Figure 3), with supplemented females producing first litters that were 21% larger in mass (36.52 g ± 11.23 SE, $p = 0.001$). This effect

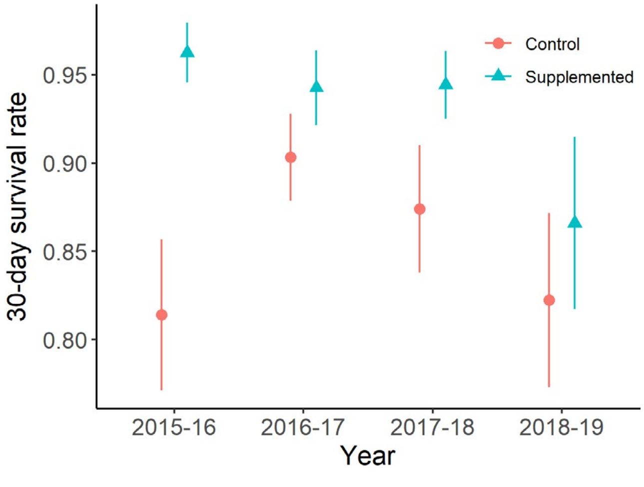

FIGURE 2 Modelled 30-day winter survival probability and standard error for control (red; circle) and food supplemented (blue; triangle) snowshoe hares (*Lepus americanus*) during the increase (2015–2016), peak (2016–2017) and decline (2017–2018 and 2018–2019) phases of the cycle, based on coefficients from the top supported Cox proportional hazards model. Survival monitoring began on 1 November in all years except 2018–2019, where it began on 1 January

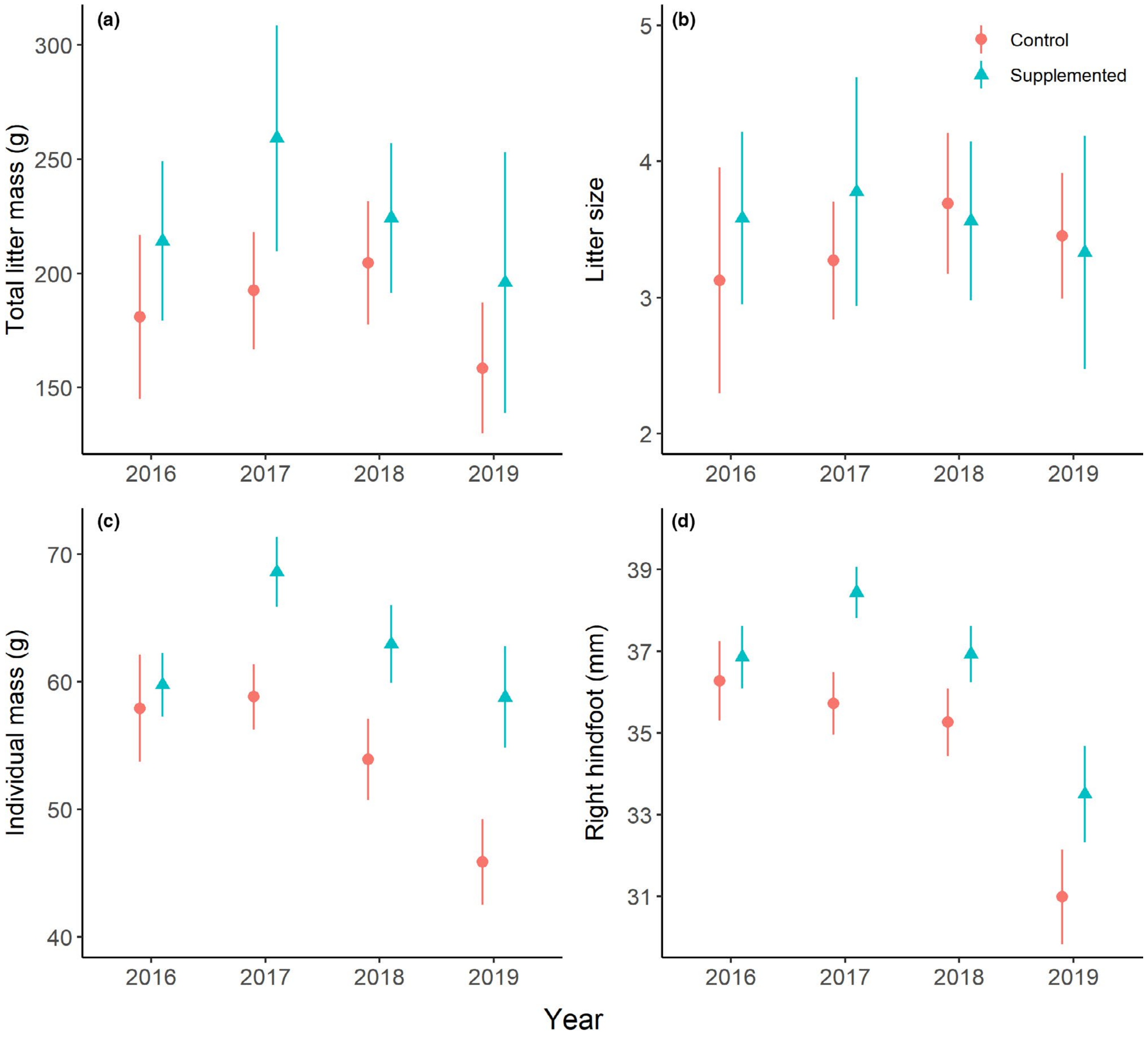

FIGURE 3 The effect of food supplementation on (a) total litter mass, (b) litter size (number of offspring), (c) individual leveret mass and (d) right hind foot length, between control (red; circle) and food supplemented (blue; triangle) snowshoe hares (*Lepus americanus*) across the increase (2015–2016), peak (2016–2017) and decline (2017–2018 and 2018–2019) phases of the cycle. Values represent means ± 95% confidence intervals

was not driven through an increase in the number of leverets produced in a litter (Figure 3b), but rather through an increase in individual leveret mass, as supplemented females gave birth to leverets that were 16% heavier and had 5% larger right hind foot length. Overall, the difference between control and food supplemented litter mass varied across years, but food supplemented individuals had larger total litter mass in all years. Litter mass decreased for both control and supplemented hares in the decline, with the lowest total litter mass being recorded in 2019 (second year of decline; Figure 3c).

The foraging behaviour of female hares was influenced by both food and predation. The amount of time hares spent foraging per day (feeding mixed with single-hop movements) was significantly lower (~1 h per day) in food supplemented hares (−1.05 h ± 0.23 SE, $p < 0.0001$), and this effect remained consistent across all years (Figure 4a). The proportion of foraging time spent vigilant was also significantly higher in food supplemented individuals (0.03 ± 0.01 SE, $p = 0.003$). Individuals in both groups decreased their foraging time with increasing predation risk, as females foraged 2.78 h less per day on average in 2019 (second year of decline) relative to 2016 (late increase phase: −2.78 h ± 0.30 SE, $p < 0.0001$). Vigilance in both treatment groups increased in 2017 (peak: 0.082 ± 0.014 SE, $p < 0.0001$), 2018 (decline 1: 0.080 ± 0.014 SE, $p < 0.0001$) and 2019 (decline 2: 0.065 ± 0.015 SE, $p < 0.0001$) relative to 2016 (late increase phase; Figure 4b).

Winter mass loss was impacted by both food limitation and predation risk. Change in mass was

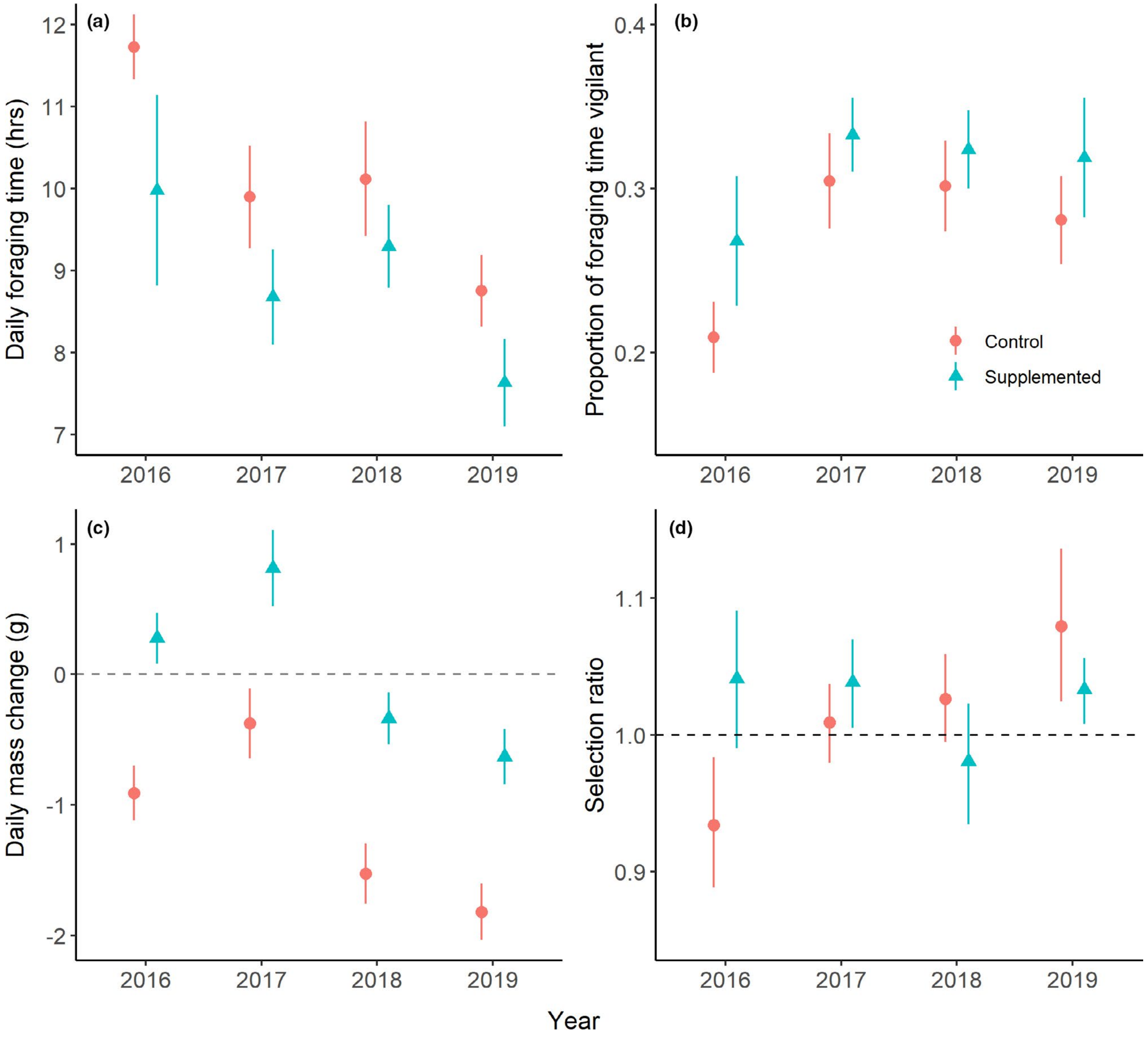

FIGURE 4 The effect of food supplementation on late winter behaviour and condition for control (red; circle) and supplemented (blue; triangle) snowshoe hares (*Lepus americanus*) during the increase (2016), peak, (2017) and decline (2018–2019) phases of the cycle. Shown are the (a) mean (±95% CI) daily time spent foraging, (b) the proportion of foraging time spent vigilant (±95% CI), (c) the modelled daily mass change of a 1500g individual (±standard error) and (d) selection ratios for conifer habitat with 95% bootstrapped confidence intervals

reduced significantly with food supplementation (1.19 g/day ± 0.18 SE, $p < 0.0001$), and the effect was consistent across phases (Figure 4c). Mass change also varied with changes in predation risk, as the greatest loss for both control and food supplemented individuals occurred in the second year of the decline when the predator-prey ratio was the highest (2019; −0.91 g/day ± 0.24 SE, $p < 0.0001$).

Reproductive differences between treatments and years were likely related to the changes in foraging time and body mass loss. For 37 control individuals for which we had body mass measurements and accelerometer data, time spent foraging per day was significantly correlated with over-winter mass change ($R^2 = 0.37$, $p < 0.001$). Individuals who foraged >11.2 h per day maintained body mass throughout the late winter, whereas individuals who foraged 2 h less lost ~1.4 g per day (Figure 5a). Furthermore, for 42 females with mass and reproductive measurements, late winter mass was positively correlated with the total mass of their first litter ($R^2 = 0.28$, $p < 0.001$; Figure 5b). For example, a female weighing 200 g more relative to other individuals in late winter would produce a first litter mass that was 14.9% larger. Based on linear models that included litter size and female body mass, larger females gave birth to offspring that had greater mass (0.028 ± 0.005 SE, $p < 0.0001$) and right hind foot length (0.006 ± 0.002 SE, $p = 0.001$; see Figure S3).

Individual habitat selection for conifer habitat, which consisted of closed or dense spruce, in late winter was influenced by both food supplementation and predation

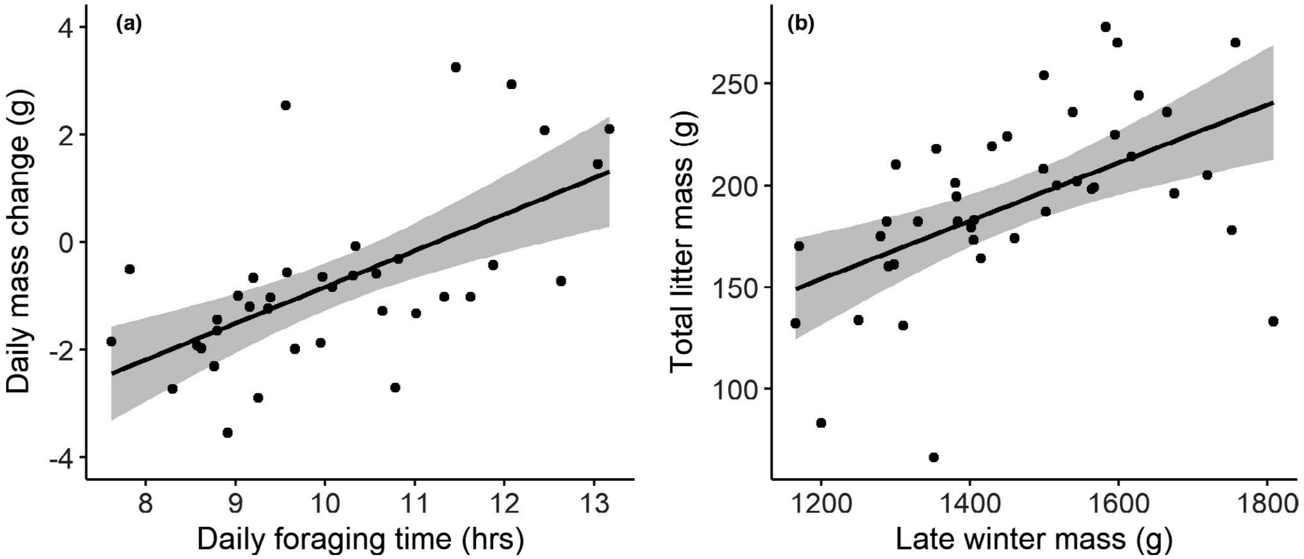

FIGURE 5 The relationship between (a) daily foraging time in hours and late-winter daily mass change (g) and (b) late winter mass of females (g) and their total litter mass (g) for control female snowshoe hares (*Lepus americanus*) monitored from 2015 to 2019

risk. Selection for conifer only occurred in control females during the winter of 2019 (selection ratio = 1.08, CI: 1.02–1.14) when predation risk was highest (Figure 4d). Control individuals selected against conifer in 2016 (0.93, CI: 0.89–0.98), and had no selection in 2017 (1.01, CI: 0.98–1.04) or 2018 (1.03, CI: 0.99–1.06). In contrast, supplemented individuals selected for conifer habitat in 2016 (1.04, CI: 0.99–1.09), 2017 (1.04, CI: 1.01–1.07) and 2019 (1.03, CI: 1.01–1.06), and showed no selection in 2018 (0.98, CI: 0.93–1.02; Figure 4d).

DISCUSSION

Our results suggest both food limitation and predation interactively influence snowshoe hare demography through changes in behaviour and condition. These changes in behaviour and condition may explain the multiplicative effect on hare abundance observed in previous studies involving food supplementation combined with predator removal treatments (Krebs et al., 1995). Consistent with the prediction that hares are food limited, supplementation doubled overwinter survival relative to control animals during the late increase, peak, and first year of decline. These increased survival rates were similar to those observed in years of population increase from previous cycles (Hodges, 2000; Krebs et al., 2018). However, improved survival of food supplemented hares was not sustained into the second year of decline suggesting that hares were unable to avoid predators when predation risk became severe (as measured by predator-prey ratios) despite having access to high-quality food. Across study years, supplemented hares significantly decreased foraging time, increased vigilance rate and more consistently selected for conifer habitat. These behavioural changes likely contributed to the improved survival for supplemented hares, given increased activity has been linked to an increased likelihood of encountering a predator (Réale et al., 2007; Wohlfahrt et al., 2007). Supplemented hares also lost less mass over-winter, which contributed to them having increased first litter reproductive output (biomass), through larger leveret mass (Figure 3). Broadly, these results indicate seasonal food limitation and predation contribute to the demographic changes observed during the late increase, peak, and decline phases of the hare cycle.

Our results further indicate that predator-sensitive foraging may have substantial impacts on hare condition and could explain the reproductive cutbacks observed during the decline phase. According to the predator-sensitive foraging hypothesis, animals will prioritise survival and minimise exposure by reducing foraging time and choosing safer habitats at the cost of their condition (Creel et al., 2007; McNamara & Houston, 1987). During the peak when per capita resources are presumably lowest, control individuals lost the least mass over-winter, while supplemented hares gained mass. However, during the decline phase, mass loss increased when densities were lowest, but predation risk was highest, and food supplemented individuals lost mass despite continued access to high-quality resources. In the second year of decline, (which coincided with the highest predator-prey ratio; Figure 1), individuals in both treatments also spent the least amount of time foraging and selected for conifer habitat (Figure 4). This may indicate hares are prioritising protection from predators (Gilliam & Fraser, 1987) since conifer habitat represents increased cover for hares (Hik, 1995). Finally, in this same year, supplemented hares used feeders at nearly half the rate of previous years (see Figure S4). In combination, our results suggest that intense predation risk during the decline may limit access to high-quality resources (Zanette et al., 2013), lowering condition and subsequently reducing reproductive output, even when food is abundant. Therefore, predator-induced changes in foraging behaviour, regardless of resource availability, likely influence the reproductive cutbacks observed during population declines.

Foraging-driven changes in reproduction are further supported by the relationships between the time spent foraging, over-winter mass loss and reproductive output observed in control individuals over our study (Figure 5). Predator-sensitive foraging may occur separately or in conjunction with increased cortisol concentrations due to predator-induced stress, which has been previously linked to reduced reproductive output in hares (Boonstra et al., 1998; Sheriff et al., 2009). That being said, the predicted changes in chronic stress metrics in the peak and decline phases were not observed during this cycle, despite the expected changes in hare–predator numbers occurring (Lavergne et al., 2021). Taken together, this indicates predator-induced reductions in foraging behaviour have the potential to drive reproductive cutbacks during population declines, regardless of cortisol concentrations. Although reproduction was lowest in the decline phase, we still observed differences between treatments in terms of leveret body mass and skeletal size (Figure 3), indicating food limitation could still alter reproduction during this phase. These differences could occur through changes in forage quality, such as increased plant toxicity following heavy browsing rates at peak hare densities (DeAngelis et al., 2015). However, the factors influencing reproduction during the decline phase should be investigated further.

The strong difference in habitat selection between control and food supplemented hares in 2015–2016 may explain the substantial survival differences observed in that year (Figure 4). Surprisingly, survival of control hares was lowest in the increase phase when predation risk was lowest during our study (Figure 1). We suspect that shallow snow depths in that particular year increased hare vulnerability to predation (Peers et al., 2020b), potentially explaining the lack of correspondence between predation and predator-prey ratios. Our results also contradict previous work that found no effect of food supplementation on hare reproduction (O'Donoghue & Krebs, 1992), and only a minor effect on survival during the increase and peak phases (Boutin et al., 1995). This likely stems from differences in the scale that the supplemental food was administered, i.e. individual vs. population (Boutin, 1990; Prevedello et al., 2013). Therefore, population-level food manipulation experiments should not be the primary source for inferring resource limitation affecting survival and reproduction in species, and past studies that failed to document these changes should be re-examined.

Although our study focused on food limitation as a factor involved in hare cycle dynamics, predation has been shown to play a dominant role in this system (Krebs et al., 1995) and in other cyclic species such as voles and lemmings (Krebs, 2013; Oli, 2019). However, all models involving predation as the key driver in hare (King & Schaffer, 2001) and vole cycles (Hanski et al., 2001; Turchin, 2003) require some form of density-dependence in the prey population (Krebs, 2013). Similar to experiments on hares, results of predator reduction experiments conducted on voles in western Finland showed that delayed density-dependent predation drove vole cycles (Korpimäki & Norrdahl, 1998; Korpimäki et al., 2002), while experiments that combined predator exclusion and food supplementation suggested that winter food limitation allowed predator populations to overtake vole populations and initiate declines (Huitu et al., 2003; Krebs, 2013; Oli, 2019). Our work further suggests that predator-sensitive foraging may be a mechanism explaining the density-dependent effects of resource limitation on cycle dynamics. We recommend that others attempt individually based food supplementation experiments to explore the generality of our findings in other species.

Determining the factors governing cycle dynamics has been a primary focus of ecology (Korpimäki et al., 2004; Krebs et al., 2018; Myers, 2018; Redpath et al., 2006). By experimentally supplementing food for individuals across cycle phases while avoiding potential density-dependent effects of area-wide food additions, we found strong evidence that both food limitation and predation interactively cause important demographic changes observed during the hare cycle, through changes in behaviour and condition. Specifically, predator-sensitive foraging under intense predation risk during the decline phase may result in the reproductive changes observed in this phase. These results provide evidence for a potential behavioural mechanism influencing cycle dynamics in this species and more broadly demonstrate how food limitation and predation may interactively affect behaviour to regulate population density.

CODE AVAILABILITY

The R code used to analyse the data and produce figures is available in the Dryad Digital Repository https://doi.org/10.5061/dryad.pvmcvdnnj.

ACKNOWLEDGEMENTS

We thank the numerous field technicians that contributed significantly to this project and members of the Boutin Lab and three anonymous reviewers for comments on earlier versions of this manuscript. We also thank Agnes MacDonald and her family for long-term access to her trapline, and the Champagne and Aishihik First Nations and Kluane First Nation for allowing our work within their traditional territory. This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), Northern Studies Training Program, the University of Alberta Northern Research Award program, the Association of Canadian Universities for

Northern Studies, The W. Garfield Weston Foundation and the Government of Yukon.

CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

YNM and SB conceived and designed the study. YNM, MJLP, EKS, AKM, SS and LKM lead data collection. Primary logistic support was provided by SB, with additional support from RB, MH, TSJ, AJK, CJK and DLM. YNM performed the analyses with assistance from PDW, MJLP and EKS. YNM drafted the manuscript with input from all authors.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13975.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pvmcvdnnj.

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How to cite this article: Majchrzak, Y.N., Peers, M.J.L., Studd, E.K., Menzies, A.K., Walker, P.D., Shiratsuru, S., et al. (2022) Balancing food acquisition and predation risk drives demographic changes in snowshoe hare population cycles. *Ecology Letters*, 00, 1–11. Available from: https://doi.org/10.1111/ele.13975