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Longevity in Snowshoe Hares

KATRINA L. THEISEN, ALEXANDER V. KUMAR and L. SCOTT MILLS

Abstract

For small mammals subject to predation, individual longevity, or lifespan, is typically unknown. Snowshoe hares (*Lepus americanus*) are used as the focal species of this study to examine the assumption that small prey species do not typically live past one or two years of age. To test this assumption, we analyzed a 20-year capture-mark-recapture database to first index the lifespan of hares. We analyzed this database to determine which factors increased the odds of longevity in hares. Body condition and capture location were significant in increasing the odds of a hare being long lived, whereas sex of the hare was not significant.

Introduction

Many small prey species suffer from high extrinsic mortality caused by predation reducing their potential lifespan (Abrams 1993, Wilkinson & South 2002, Chen & Maklakov 2012). Longevity of many of these species has not been studied in detail. Of the longevity studies that are available, many are on birds (Valcu et. al. 2014, Lindstedt & Calder 1976) or larger mammals such as humans (Clutton-Brock & Isvaran 2007, Maklakov & Lummaa 2013, Millar & Zammuto 1983). These studies indicate that a variety of intrinsic factors are important to determining the longevity of a species, including gender (Chen & Maklakov 2014, Clutton-Brock & Isvaran 2007, Maklakov & Lummaa 2013) and body mass (Lindstedt & Calder 1976). However, extrinsic factors such as habitat and resource availability may also influence longevity (Gigliotti et. al. 2019). Many of these studies indicate that reducing predation as an extrinsic stressor will lengthen lifespan, suggesting that predation may play an important role driving reduced longevity in small prey species.

Gender is an intrinsic factor that often influences longevity, with females living longer than males (Chen & Maklakov 2014, Clutton-Brock & Isvaran 2007, Maklakov & Lummaa 2013). In sexually dimorphic species, usually the male – with a few female exceptions – is larger and/or more vibrantly colored in order to gain female attention during the breeding season. At the same time, sexually selected traits may draw the attention of predators, so that males subsequently experience higher predation-based mortality. In sexually monomorphic species, predation might be expected to be similar between the sexes since males and females are mostly indistinguishable in morphology (although behaviors might be different between sexes).

Body mass itself may be linked to longevity (Lindstedt & Calder 1976). As previously mentioned, larger animals tend to live longer for a variety of reasons (Millar & Zammuto 1983). Within a species, larger individuals may be predated upon less as they might be faster or healthier than individuals with less mass, particularly if the body mass differs in muscle mass versus fat storage (Murray 2002). These heavier individuals may have access to better resources or have been born into a better environment more suited to putting on weight and growing to healthier proportions (Gigliotti et. al. 2019).

Finally, the environment that an animal is in may increase their longevity for a variety of reasons. Animals with access to more beneficial resources can maintain their body mass and health. Some environments provide cover, allowing for the animal to escape predation by hiding or camouflaging themselves. Some environments could even be conducive to prey survival by preventing or inhibiting predator access. All of these factors could contribute to longevity.

In order to examine longevity in a small prey species, we focused on snowshoe hares (*Lepus americanus)*. Snowshoe hares are well-known for undergoing coat color changes, where hares turn white in the winter and brown in the summer to match their background (Zimova et. al. 2018). Hares are not sexually dimorphic, except that female hares tend to be larger than males (Gigliotti et. al. 2019). Hares can also undergo 8-11 year cycles where the populations fluctuate drastically (Krebs et.al. 1995). Predation appears to be the main driver of the cycle (Krebs et.al. 2018). Snowshoe hare predation comes in many forms: famously, Canada lynx cycle with the hares on a slight lag, but coyotes, mountain lions, owls, goshawks, foxes, and martins also prey upon the hares (Hodges 2000). Since predation is so intense, many hares do not live past one or two years of age.

Snowshoe hares typically breed after a year – the summer after they were born (Hodges 2000). This allows them to begin adding to the population quickly and would allow their population to grow even if they only live to one or two years old. Their average annual survival rate has been found to be approximately 0.34 (Kumar 2020), providing further evidence for their short life span. However, one study conducted near Lake Alexander, Minnesota showed that snowshoe hares can live up to five years of age (Green & Evans 1940). The study also suggested there might be common factors that could be measured to determine hare longevity (Green & Evans 1940).

Snowshoe hares prefer certain habitats, especially forests with high horizontal cover (Griffin & Mills 2009, de Bellefeuille et. al. 2001). These habitats provide dense cover during the growing season, providing forage and shelter from predators (Feierabend & Kielland 2014). One study showed that snowshoe hares retreat to dense brush areas during periods of low population, indicating that these patches of habitat are preferred by hares (Keith 1966). It would be interesting to know if snowshoe hares that reside in these dense, high-cover patches of habitat would live to old age compared to younger or more open habitat.

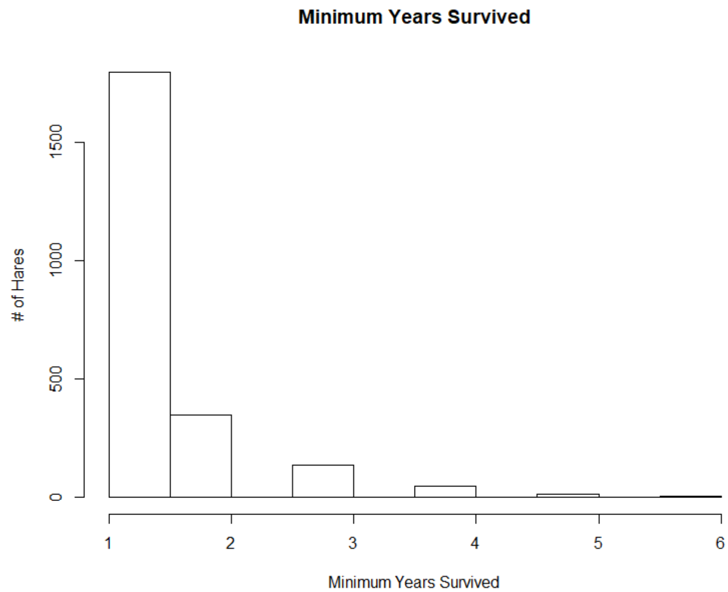
We examined hare longevity using a twenty-year snowshoe hare capture-mark-recapture dataset (Mills et al. unpublished data; Kumar 2020). This data was collected from 1998 to 2018 in the northwest region of the Rocky Mountains in Montana. From this dataset we first determine the longevity of hares and identified long-lived hares. For these long-lived hares, we test the hypothesis that one or more of the following four factors will increase the odds of a hare being long-lived: sex, capture location, and relative body condition (weight/Right Hind Foot [RHF]). Specifically, we predict hares with higher body condition are more likely to be long lived, females are more likely to be long lived than males, and certain capture locations will increase the odds that a hare will be long lived, specifically the dense, mature (CLOLD) sites.

Methods

Our snowshoe hare database included summer live trapping data (May-August) from 1998 through 2018 (see Supplemental Table 1 for dates). For all sites and years, 50-80 live traps were arranged in a grid, with each trap set 50 meters from another, resulting in a 10 x 5 or 10 x 8 grid (Mills et. al. 2005, Kumar 2020). Sites were in two areas of western Montana: near Seeley Lake and near Glacier National Park in the Tally lake Ranger District (Tally). Seeley contained two sites, Inez and Spring Creek, and each site contained four grids, Closed Old (CLOLD), Closed Young (CLYNG), Open Old (OPOLD), and Open Young (OPYNG), to describe different vegetation types. The Tally region contained nine sites, Boo Boo, Bullwinkle, Burn, Crash, Moose Butt, Pigskin, Plume, Rooster, and Vortex. Trapping sessions lasted 3 to 6 days. We marked each new hare capture with an ear tag (a metal tag with a specific number sequence), weighed them, measured their right hind foot (RHF), punched their ear for a DNA sample, and sexed and aged them (juvenile or adult based on weight); weight was taken at all subsequent captures. We caught many hares only once and then never saw them again and caught some a few times during a single trapping session. But there were many hares that came back year after year, within the same grid and were easily identifiable by the tags in their ears.

We estimated hare longevity from the trapping data. For each hare we calculated the minimum number of years survived based on the first and last capture year. We assumed adults were one year of age at first capture and juveniles were 0-3 months old. We also assumed mortality occurred immediately after the most recent capture date. For hares with multiple captures, we recorded their maximum weight. An average weight would not have made sense, as many of the recaptured hares had aged from juvenile to adult between captures. We also estimated body condition, which is weight/Right Hind Foot (RHF), and we did this by dividing the maximum weight by the RHF recorded on the same capture to get an accurate body condition for that hare on that day. Finally, we created a binomial “long lived” covariate. If the hare lived for 1 year or 2 years, we determined it to be “short lived”. Any hare living to 3, 4, 5, or 6 years was “long lived”. We chose anything living more than 2 years as the cutoff for “long lived”, as these hares represented less than 10% of the data.

We calculated the expected portion of the hare population to live to certain years using annual adult survival (0.34) and capture probability (0.69) (Kumar 2020), using the following equation: 0.34 * population from previous year * 0.69. We used the observed number of hares that lived a minimum of 1 year as the initial population and calculated expected numbers from there.



	Expected	Observed
1	1798.00000	1798
2	421.81080	346
3	143.41567	133
4	48.76133	46
5	16.57885	10
6	5.63681	4

Figure 1: Observed Hares

We then used a chi-squared test in the Program R to compare the expected distribution to the observed distribution. We also separated the data by capture locations and again performed a chi-squared test. We did not include hares that lived for only 1 year in our chi-squared analysis, as we already assumed the observed and expected hares for this age class were the same.

To examine which factors influence hare longevity, we used generalized linear models (GLMs) in R using the binomial link. Our response was whether or not a hare was long-lived. We tested the following predictors: sex (male vs female), body condition, and capture location (split into region, site, and grid). We present results as odds ratios.

Results

Our chi-squared test comparing expected distribution to the observed distribution was insignificant ($p>0.05$). The second chi-squared test that we performed, separating the data by capture locations, also gave us insignificant results for all of the capture locations. We were unable to rule out the possibility of the long-lived hares living to old age due to chance. This would mean that based on vital rates, we would simply expect to see the number of hares that we observed living to old age. However, when we looked at the GLMs, we saw a different story. Certain factors significantly ($p<0.05$) increased the odds of a hare being long-lived.

	Odds Ratio	P-Value	Confidence Interval
Body Condition	2.4851	3.56×10^{-16}	1.9993 – 3.0989
Tally vs Seeley	2.4753	3.15×10^{-5}	1.6444 – 3.8742
Spring Creek vs Inez	0.8721	0.745	0.3595 – 1.9143
Vortex vs Bullwinkle	4.0432	0.0260	1.3591 – 17.3714
Plume vs Bullwinkle	5.4	0.0066	1.8478 – 23.0099
Pigskin vs Bullwinkle	5.1739	0.0074	1.8097 – 21.8122
Moose Butt vs Bullwinkle	4.08	0.0296	1.3024 – 17.9626
Crash vs Bullwinkle	2.5823	0.1894	0.6598 – 12.5349
Burn vs Bullwinkle	2.1587	0.2647	0.6070 – 10.0461
Rooster vs Bullwinkle	3.3443	0.0529	1.1366 – 14.2911
Booboo vs Bullwinkle	5.2483	0.0082	1.7675 – 22.5355
CLYNG vs CLOLD	0.6748	0.357	0.2876 – 1.5679
OPOLD vs CLOLD	0.7067	0.556	0.1938 – 2.0860
OPYNG vs CLOLD	0.3955	0.157	0.0889 – 1.2724
Male vs Female	0.9805	0.899	0.7232 – 1.3283

Table 1: Results of GLMs. Bolded results are significant. Odds ratios >1 show variables that are more likely to show longevity, odds ratios <1 are less likely.

We found that certain predictors were associated with longer lived hares (Table 1). Capture location, particularly the region Tally, increased the odds of a hare being long-lived (Table 1). Certain sites within Tally were more significant than others. We used Bullwinkle as the reference site, as Bullwinkle had the least number of long-lived hares. In the Seeley region, we found no significant effect for trapping grids (Table 1). Additionally, body condition was shown to significantly increase the odds of being long-lived. As body condition increases, or improves, hares are more likely to be long-lived (Table 1).

Discussion

Capture location having a significant relationship with longevity is the most interesting result. This implies that certain individuals are possibly picking ideal conditions for living and surviving. Alternatively, these individuals are simply lucky to be born in ideal locations. Certain capture locations being significant means there should be something related to that capture location that increases the odds of an individual being long-lived. Regarding snowshoe hares, it was intriguing to find that the trapping grids within the Seeley region did not have a significant effect on longevity (Table 1). Dense, mature (CLOLD) vegetation is considered more favorable by hares and perhaps more likely to increase chances of longevity (Hodson 2010, Lewis 2011, Griffin & Mills 2009), but our findings did not support that prediction.

We found that increased body condition was associated with long-lived hares. We expected to see this positive relationship between longevity and increasing body condition based on the established knowledge that body mass scales with longevity (Lindstedt & Calder 1976, Millar & Zammuto 1983). Intuitively, this appears to make sense, as healthier animals will live longer. However, snowshoe hares typically die due to predation (Wirsing et. al. 2002), so it isn't necessarily intuitive that healthier hares would live longer. Previous studies have shown that an increase in body condition decreased predation rates, and that decreasing condition can cause an increase of risk-taking behavior, leading to higher predation rates (Murray 2002). Snowshoe hares also put on protein-based mass, rather than fat, which would lead to an increase in muscle mass, and could both decrease risk-taking behavior and increase the hare's potential ability to evade predators (Murray 2002, Hodges et. al. 2006). Larger individuals are also more likely to survive the winter, simply because they have more energy stores that would allow them to live through periods of food shortage, regardless of predation pressure (Lindstedt & Boyce 1985, Hodges et. al. 2006). These larger individuals may have spent the summer in areas with abundant food or a lengthier growing season, implying a deeper linkage between body condition and capture location that would require further investigation (Gigliotti et. al. 2019).

The sex of the hare was not significant in determining longevity. In sexually dichotomous species, females are often shown to be more long-lived than males (Chen & Maklakov 2014, Maklakov & Lummaa 2013). Female snowshoe hares tend to be slightly larger than males but show no other obvious dimorphic traits. It was not surprising to find that the two sexes do not differ significantly regarding longevity, given that hares do not experience strong sexual dimorphism.

Conclusion

This study examines different factors that could influence longevity in snowshoe hares. Body condition (scaled with body mass) and capture location are both significant factors affecting the odds of a snowshoe hare being long-lived. Whether or not hares are consciously choosing these better sites is unknown. Further studies that examine why certain sites produce more long-lived hares are warranted. Altitude, average snow depth and duration, canopy or underbrush cover, plant species and predator density may all influence the potential of a site to produce more long-lived hares. Finally, identifying the cause of mortality of hares could provide more insight on drivers of hare longevity. By doing so, longevity in small prey mammals can be better understood, and the effects of prey species living past their expected lifespan under predation can be investigated as well.

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