MANAGEMENT AND BIOLOGY OF SNOWSHOE HARES IN PENNSYLVANIA

2024-2033

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EXECUTIVE SUMMARY

Over the past century, eastern snowshoe hare (*Lepus americanus*) populations have experienced a northerly contraction following the Appalachian Mountains with populations in Ohio, Maryland, North Carolina, and Tennessee becoming extirpated. Small, isolated populations remain in West Virginia and possibly Virginia. Snowshoe hares, the largest lagomorph in Pennsylvania, currently exist most prominently in the Commonwealth's northern regions and higher elevations. The Pennsylvania Game Commission purchased and released over 33,000 hares between 1918 and 1981 to supplement what were thought to be otherwise declining populations and to promote hunting opportunity. The success of these stocking efforts is unknown, but the stockings are unlikely to have influenced long term, statewide population trends which are more closely related to habitat and variable winter conditions. Little research has been done on snowshoe hares in Pennsylvania and the sole source of long-term population monitoring is provided by the Game Commission's annual Game Take Survey. The snowshoe hare was listed as a species of maintenance concern on Pennsylvania's 2005 State Wildlife Action Plan (SWAP) due to sensitivity to habitat alteration, apparent decline, and potential importance of Pennsylvania's population for gene flow between states to the north and south. The hare was not listed in 2015 SWAP because it was deemed to be apparently secure in local areas, but the species' status is being reevaluated given recent evidence of statewide population decline and contraction. Along with apparent population decline, other associated threats include potential for population isolation, declines of suitable habitats, camouflage mismatch, a white hare on a landscape without snow, and disease.

Though little can be done to control or predict the duration of snow cover annually, better habitat and wildlife management practices will directly benefit hares by reducing impact of deer browse on regenerating forests and increasing the quantity and quality of early successional forest, as well as other suitable habitats. Development of a comprehensive snowshoe hare conservation and management plan is needed and prioritized by growing public concern for the apparent decline of snowshoe hares in Pennsylvania and the potential of this species to benefit from focused habitat management. The foundation of Pennsylvania's snowshoe hare management approach rests on this plan's mission statement:

"To maintain or increase snowshoe hare populations and their habitat within the Commonwealth of Pennsylvania for current and future generations."

The snowshoe hare management plan provides a comprehensive and current summary of snowshoe hare biology, historic and current status in Pennsylvania, and habitat and harvest management strategies. The plan also provides supporting objectives and strategies to achieve snowshoe hare specific goals related to population monitoring, assessment and management related to habitat and harvest.

SECTION I. MISSION STATEMENT, MANAGEMENT GOALS, OBJECTIVES, AND STRATEGIES

MISSION STATEMENT: *"To maintain or increase snowshoe hare populations and their habitat within the Commonwealth of Pennsylvania for current and future generations."*

This mission statement requires continued work and new initiatives addressing population monitoring and the assessment and management of habitat. These needs are directly addressed by the following goals and supporting strategies described below.

GOAL 1: MAINTAIN SNOWSHOE HARE POPULATIONS WITHIN EXISTING DISTRIBUTION.

Objective 1.1: Maintain stable to increasing population trends of snowshoe hares in Pennsylvania through 2033.

Strategies

1.1.1 Annually complete hunter/harvest surveys and field surveys by Wildlife Management Unit or other appropriate geographic scale to estimate snowshoe hare population trends.

1.1.2 Annually review snowshoe hare seasons and bag limits and adjust as needed.

1.1.3 Evaluate existing methods of monitoring population trends and spatial distribution by 2027 and revise and implement new procedures as needed.

1.1.4 By 2026, estimate influence of factors such as habitat, predation, climate, and phenotype on annual survival, and cause-specific mortality rates for snowshoe hares.

1.1.5 By 2027, using data from an eastern cottontail focused landscape genetics project and relevant literature, evaluate the threat of rabbit hemorrhagic disease virus serotype 2 (RHDV2) to Pennsylvania's snowshoe hare population.

1.1.6 By 2028, develop method to estimate breeding season and fecundity rates of Pennsylvania snowshoe hares.

1.1.7 Update conservation status rank, if warranted, using information from *Strategies* 1.1.1, 1.1.3, 1.1.4, 1.1.5 and other, external sources by 2027.

Objective 1.2: Maintain stable to increasing spatial distribution of snowshoe hares in Pennsylvania through 2033.

Strategies

1.2.1 Annually complete hunter/harvest surveys and field surveys by Wildlife Management Unit or other appropriate geographic scale to estimate snowshoe hare distribution.

1.2.2 Annually review snowshoe hare seasons and bag limits and adjust as needed.

1.2.3 By 2025, determine factors influencing snowshoe hare distribution, genetic structure, and identify where gene flow is restricted and isolated populations occur.

1.2.4 By 2033, estimate occurrence, distance, and influence of habitat and landscape features on dispersal behavior.

Objective 1.3: Develop models that can be used to predict snowshoe hare core population areas by 2033.

Strategies

1.3.1 By 2027, evaluate historic and predicted trends of snow cover duration and habitat in Pennsylvania and their implications for snowshoe hare population resiliency.

1.3.2 By 2033, project population trends and population connectivity to evaluate the impact of hunting, habitat management (prescribed fire, clear-cuts, etc.), and climate related variables, such as duration of snow cover on snowshoe hares.

GOAL 2: IMPROVE HABITAT TO SUPPORT SNOWSHOE HARE POPULATIONS.

Objective 2.1: Determine snowshoe hare response to current habitat management practices by 2033.

Strategies

2.1.1 By 2026, consolidate Pennsylvania research findings and review literature to identify potential habitat management practices to influence density and diversity of vegetation to benefit snowshoe hares in Pennsylvania.

2.1.2 By 2026, design field experiments to test hypothesized snowshoe hare population response to habitat management practices from *Strategy* 2.1.1.

2.1.3 By 2033, develop strategies to monitor the effect of prescribed fire and timber management on snowshoe hare occupancy and use.

Objective 2.2: Provide habitat management recommendations and resources to improve and maintain snowshoe hare habitat on both private and public property by 2033.

Strategies

2.2.1 By 2033, develop habitat recommendations and resources derived from scientific studies for land managers, foresters, and private resource managers addressing the creation of ideal habitat characteristics and timing and arrangement of timber harvest, timber salvage operations, and prescribed fire relative to snowshoe hare habitat suitability and estimated parturition dates.

2.2.2 Through 2033, identify and propagate appropriate conifer species to incorporate into habitat management including balsam fir, red spruce, and other native evergreen species at Howard Nursery for planting in areas to benefit snowshoe hare.

2.2.3 Continually monitor statewide early-successional forest trends by reviewing available forest inventory data (U.S. Forest Service, Pennsylvania Department of Conservation and Natural Resources, Pennsylvania Game Commission).

Objective 2.3: Identify priority areas to maintain or support future expansion of snowshoe hare habitat and populations on both private and public property by 2033.

Strategies

2.3.1 By 2029, identify and prioritize critical linkages among habitats supporting established hare populations relative to land ownership and planned habitat improvements.

2.3.2 By 2033, determine factors currently limiting expansion into areas lacking well established populations, but with otherwise suitable habitat.

2.3.3 Provide technical assistance to public and private landowners managing priority sites as needed.

Objective 2.4: Develop protocols and inter- and intra-agency support structure for increased monitoring and management of habitat on both public and private property.

Strategies

2.4.1 Develop partnerships for cooperation in snowshoe hare habitat management.

2.4.1a Develop partnerships (e.g., Pennsylvania Department of Conservation and Natural

Resources Bureaus of State Parks [BSP] and Forestry [BOF], U.S. Fish and Wildlife Service, U.S. Forest Service, Pennsylvania Cooperative Fish and Wildlife Research Unit, Ruffed Grouse Society, Center for Private Forests at Penn State, regional initiatives, etc.) to accomplish research, funding, and habitat strategies through 2033.

2.4.1b Annually evaluate progress of Plan implementation and provide ongoing communication with partners and stakeholders.

2.4.2 Identify funding sources to support non-commercial forest management practices that benefit snowshoe hare.

2.4.2a Annually budget monies from the Game Fund for non-commercial forest habitat management.

2.4.2b Explore external funding sources to support non-commercial management of early-successional and otherwise suitable hare habitats and their multiple species value.

GOAL 3: PROVIDE SNOWSHOE HARE HARVEST OPPORTUNITIES.

Objective 3.1: Annually establish snowshoe hare hunting seasons to monitor snowshoe hare population trends.

Strategies

3.1.1 Conduct the snowshoe hare hunter cooperator program and Game Take Survey annually.

3.1.2 By 2033, develop defined process for making snowshoe hunting season recommendations.

Objective 3.2: Evaluate and quantify impacts of various harvest management strategies on hares by 2033.

Strategies

3.2.1 Through 2033, monitor impact of hunter harvest on Pennsylvania snowshoe hare populations to ensure harvest remains compensatory not additive.

3.2.2 By 2033, evaluate relationships among population density, harvest density, harvest per unit effort, and snowshoe hare harvest rates to determine best methods to measure annual impact of hunter harvest by Wildlife Management Unit or other appropriate geographic scale.

GOAL 4: INCREASE PUBLIC KNOWLEDGE OF SNOWSHOE HARES AND THEIR MANAGEMENT.

Objective 4.1: Assess public knowledge and needs regarding snowshoe hares and their management by 2026.

Strategies

4.1.1 Annually track comments and complaints to identify issues of importance to snowshoe hare management.

4.1.2 By 2026, conduct a survey of both hunter and general public opinions, knowledge, and understanding of snowshoe hares and their management.

4.1.3 By 2028, use results of survey to identify key messages, delivery mechanisms, barriers, and opportunities in fostering public support for snowshoe hares and their management.

Objective 4.2: Increase public communications regarding snowshoe hares through 2033.

Strategies

4.2.1 Continually develop presentations and articles describing snowshoe hare life history, population management, habitat management needs, and conservation significance in Pennsylvania.

4.2.2 Periodically distribute updates of snowshoe hare population status and trends, life history characteristics, research findings, and ecological significance using a variety of media outlets.

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TAXONOMY

The snowshoe hare is a member of the order Lagomorpha, which includes the family Leporidae (hares and rabbits). Leporidae occupy most land masses on earth, and two genera, *Sylvilagus* (rabbits) and *Lepus* (hares), are found in Pennsylvania. Hares are larger, turn white in winter, and have precocial young while rabbits are smaller, don't notably change color throughout the year, and have altricial young (Murray 2003).

Snowshoe hares are the smallest of the 26 hare species (Keith 1990) and have been found to be more closely related to southwestern hares, often referred to as jackrabbits, than they are to arctic hare species (Cheng et al. 2014, Halanych et al. 1999). In fact, Cheng et al. (2014) identified 3 genetic groups of snowshoe hares: Boreal, Rockies, and Pacific Northwest based on microsatellite and mtDNA clusters. Pennsylvania hares ($n = 2$) were found to be most closely related to the Boreal clade of snowshoe hares (Cheng et al. 2014). Subspecies of snowshoe hare have been designated by various sources based on cranial morphology and pelage color, however, the validity of some of these designations have been called into question due to apparent continuity of cranial morphology across North America (Nagorsen 1985) and lack of genetic support (Cheng et al. 2014, Dalquest 1942, Hall 1981).

PHYSICAL CHARACTERISTICS

Snowshoe hares are most easily distinguished from other lagomorphs in Pennsylvania by their large size, their disproportionately large feet, and their ability to molt into a white pelage during winter, a characteristic for which they have been given the nickname varying hare. Snowshoe hares throughout the majority of their range replace brown guard hairs with white during fall. This seasonal camouflage advantage evolved as snowshoe hares inhabit snow covered areas. Not all snowshoe hares turn white, however. Some populations in the Pacific northwest have evolved to remain brown throughout the year (Jones et al. 2020). These brown winter hares are believed to be the result of a mutation of the agouti gene caused by hybridizing with black-tailed jackrabbits (Cheng et al. 2014, Jones et al. 2018). It was believed that during winter in Pennsylvania, snowshoe hares were white except for the black tops of their ears (Merritt 1987), however, Gigliotti et al. (2017) reported that Pennsylvania snowshoe hares exhibited more variability in their coat color and a small percent did not change color at all. The molts that result in pelage change are controlled by photoperiod or day length and in

Pennsylvania have been found to initiate in October and finish by April; but is most often listed as November through March (Boyd unpublished data, Merritt 1987, Zimova et al. 2014, Zimova et al. 2018).

The body size of hares varies regionally with smaller hares occurring in western populations (Dalquest 1942, Nagorsen 1985). Snowshoe hares are slightly larger in Pennsylvania than in other areas of their range, an exception to Bergmann's Rule (1.6-1.9 kg; Gigliotti et al. 2019). Snowshoe hares have large hind feet (12 to 15 cm) relative to their body mass (1.5-1.6 kg) which help hares to easily move through snow (Gigliotti 2016, Keith 1990, Merritt 1987). Females weigh more than males on average, with the greatest difference occurring when females are pregnant (Gigliotti 2016, Murray 2003). Hares tend to experience lowest body weight during winter, however, a study in Pennsylvania found average body condition for males did not differ between summer (11.98 ± 0.58 g/mm) and winter (11.88 ± 0.15 g/mm; $P = 0.528$; Gigliotti 2016).

BREEDING BIOLOGY AND REPRODUCTION

Snowshoe hares begin breeding the spring after they are born and are reproductively active from March through August in most populations. During this time, hares are polygamous, and a female can have anywhere from 2 to 4 litters per year with number of litters and young per litter varying geographically and within litter cohort (see review in Murray 2003). The potential for high reproductive rate in part comes from the anatomy of the female's reproductive tract which has 2 uteri and allows for immediate postpartum breeding (Bittner and Rongstad 1982, O'Donoghue and Boutin 1995). Lagomorphs are placental mammals with gestation ranging from 34 to 40 days (Bittner and Rongstad 1982, Meslow and Keith 1971). The beginning of parturition ranges from mid-March to late April (Murray 2000, Murray 2003), but may be delayed by poor winter nutrition (Vaughan and Keith 1981). In Pennsylvania, the earliest documented leveret capture is 20 April (Boyd unpublished), but actual parturition date and overall reproductive rates have not been assessed in state. A pregnant female with two leverets weighing 55g and 67g was also observed from hunter harvest (late December).

Early litters tend to be smaller than subsequent litters, but the pregnancy rate for the first litter is highest. Snowshoe hares in western states produce fewer, but larger litters than eastern populations, which suggests that productivity may be relatively similar across North America (Murray 2000). Possible causes of low productivity include poor food resources (Boutin 1984a, Murray et al. 1998, Vaughan and Keith 1981) and high stress levels caused by high predation risk (Boonstra and Singleton 1993, Boonstra et al. 1998a).

Leveret growth and development is rapid. Leverets are precocial and are born fully furred with eyes opening very soon after birth. Birth weight ranges from 40-82 g and varied based on study area (reviewed in Murray 2003). Hares have nutrient dense milk which allows the young to nurse once a day and otherwise remain hidden in cover (O'Donoghue and Bergman 1992, Rongstad and Tester 1971). A practice which likely reduces risk of predation. Juvenile growth rates may be linked to maternal condition (Boonstra et al. 1998a, b, Sheriff et al. 2010 and 2015, Sinclair et al. 2003). A leveret's home range size expands quickly and reaches the size of an adult female around 8 weeks after birth (O'Donoghue and Bergman 1992, Rongstad and Tester 1971). Hares typically reach adult body weight at 9 to 11 months (Keith and Windberg 1978).

MORTALITY AND DISEASES

In a literature review of snowshoe hare mark-recapture studies, Murray (2003) found that adult hares generally had higher annual survival rates than juveniles, although some populations had equal adult and juvenile mortality. Mark-recapture studies do not easily account for dispersal and may overestimate mortality (Murray 2003). Some studies have shown evidence that smaller hares, mostly juveniles but also malnourished individuals, are more vulnerable to predation (Sievert and Keith 1985, Wirsing et al. 2002, Wirsing 2003). Leveret survival from birth to 53 days was estimated to be 67%, based on mark-recapture, (Adams 1959) and 56% survival to 35 days based on radiotelemetry (Griffin 2004). Seasonal survival has been inconsistent among studies and evaluating seasonal survival is confounded as snow cover duration and population size varies annually. Some studies have found survival to be highest during the winter while others have found greatest survival in summer (Griffin 2004, Wirsing et al. 2002). Winter is likely a critical time of year for hares as they may be more susceptible to becoming malnourished or experience mismatch. Hodges et al. (2001) suggested that a survival rate greater than 28% was required to increase hare populations in the Yukon. A study in Pennsylvania found adult hare survival rate over 1 year to be 32% (95% CI = 18%-50%) with most mortality occurring in March (Gigliotti 2016).

Disease and Parasites

While predation has been found to be the primary cause of mortality in most studied populations; disease, infection, and nutritional deficiency, as well as human-related causes account for some mortality as well. Infection and parasites do not often kill hares but may increase vulnerability to predators (Murray et al. 1997). External parasites include ticks and fleas, while internal parasites include warbles, lungworms, tapeworms, and roundworms (Bookhout 1971, Merritt 1987). Hares are known to take dust baths (Merritt 1987) likely to reduce external parasite load. Hares can become infected with coccidiosis, salmonella, and tularemia (Hoff et al. 1970, Merritt 1987), but are not thought to succumb to these diseases at levels that would impact overall populations. Hunting is likely the greatest cause of human induced mortality of hares but is not believed to influence overall population size in most areas (Hodges 2000a). Hunting accounted for 10% of mortality in a Pennsylvania study (Gigliotti 2016).

In early 2020, rabbit hemorrhagic disease (RHD) was detected for the first time in wild lagomorph populations in the United States. The virus responsible for the current outbreak in the Western United States is rabbit hemorrhagic disease virus serotype 2 (RHDV2) (Creekmore 2022). Rabbit hemorrhagic disease virus serotype 2 is extremely contagious and, in addition to being spread between wild and domestic hares or rabbits via direct contact, the virus can be transmitted indirectly via equipment, cages, enclosures, insects, and scavenging animals. Because this disease spreads rapidly and causes widespread mortality, it is a serious threat to both domestic and wild lagomorph populations, including snowshoe hares in Pennsylvania.

When RHD emerges in wild populations, it is almost impossible to control or manage. Snowshoe hares in Pennsylvania likely exist in relatively isolated populations, however, RHDV2 can infect all domestic and North American wild lagomorph species. Eastern cottontails are commonly found across the Commonwealth, including areas adjacent to humans and domestic rabbits as well as among snowshoe hare populations. The disease may easily spread to more isolated populations of species of conservation concern through landscape connectivity of other lagomorph species, particularly eastern cottontails. It is likely that RHDV2, once in the wild, will continue to spread, and that mortality rates in affected populations of snowshoe hares will be substantial.

Hares and Predators

Predators account for the majority of snowshoe hare mortalities (Boutin and Krebs 1986, Cox et al. 1997, Ferron et al. 1998, Fies 1993, Hodges et al. 2001, Keith et al. 1984, Keith et al. 1993, Murray et al. 1997, Sievert and Keith 1985, Wirsing et al. 2002), with predation representing 73% of deaths in Pennsylvania (Gigliotti 2016). A suite of mammalian and avian predators, including, but not limited to, coyote (*Canis latrans*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), mink (*Mustela vison*), northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), great-horned owl (*Bubo virginianus*), barred owl (*Strix varia*), and the common raven (*Corax corax*; Review in Murray 2003) will prey on adult snowshoe hares. Gigliotti (2016) found more mammalian predation events (59%) than avian (14%) in Pennsylvania. Predation is the primary cause of mortality for hares of all ages including juveniles, however, abandonment can also lead to neonate mortality (O'Donoghue 1994). In addition to predators of adult hares, red squirrels (*Tamiasciurus hudsonicus*), short-tailed weasels (*Mustela erminea*), and American kestrels (*Falco sparverius*; Hodges et al. 2001, O'Donoghue 1994, Stefan 1998) have been found to predate leverets.

Where abundant, hares can be an important link in the food chain and represent a staple in the diet of many predators. The great diversity of potential predator species in Pennsylvania and the northeastern states may explain why hare populations in Pennsylvania are thought to not cycle. In theory, generalist predators should have a stabilizing influence on prey populations because they do not rely on a single prey species and can prey on other species when one becomes scarce. Conversely, specialist predators, those that feed primarily on single species such as the Canada Lynx (*Lynx canadensis*), are believed to be instrumental to population cycles observed in other snowshoe hare populations (Krebs et al. 1995, Sheriff et al. 2015). Comparing predator and prey diversity across broader geographic scales is confounded by differing monitoring methods and study objectives used for the snowshoe hare research. Many studies have focused on predator populations and report prey data as a by-product. The importance of hares to Pennsylvania predators is unknown. One study found that extirpation of snowshoe hares likely led to an increase in predation pressure on porcupines, but not ruffed grouse (Wilson et al. 2022).

Snow conditions influence the distribution, movement, energy expenditure, and hunting success of snowshoe hare predators. Animals like snowshoe hare and Canada lynx have specially evolved feet that allow them to easily maneuver in deep snow. The Canada lynx is listed as threatened in the lower 48 states, and its dependence on the snowshoe hare for prey increases the importance of understanding hare biology to wildlife managers. It is unknown whether other predators who are typically generalist specialize on hares as some have been found to do in boreal forests (e.g., great-horned owl and coyote; O'Donoghue et al. 2001).

ABUNDANCE AND DISTRIBUTION

Snowshoe hares are only found in North America and have the most widespread distribution of any North American *Lepus* species (Ellsworth and Reynolds 2006). They inhabit forested areas from Alaska to Newfoundland and range south along higher elevation mountains (Figure 1). The southern boundary of the species' distribution is likely determined by duration of snow cover and increasing habitat fragmentation caused by human development and habitat suitability inherent to the restriction to higher elevation (Buehler and Keith 1982, Sievert and Keith 1985). Across this broad distribution, hares occupy diverse forest types. During the last century, snowshoe hare populations in the southeastern part of its range have experienced widespread declines and extirpation (Campbell et al. 2010). The extent of these declines is

Figure 1: Distribution of snowshoe hare in North America (IUCN 2022) and Pennsylvania (Boyd 2019, Diefenbach et al. 2016). Note that southern population distribution follows mountain ranges. Figure by E. Clees, PGC.

unknown and efforts to restore these populations have been largely unsuccessful (Fies 1991 and 1993, Glazer 1959).

Historically, the snowshoe hare was found more commonly and in more areas of Pennsylvania than they are currently thought to occupy. Between 1918 and 1990 the Pennsylvania Game Commission released over 33,000 hares to supplement declining populations. Despite these efforts, the snowshoe hare currently experiences limited distribution throughout the state (Figure 1). Snowshoe hares are thought to be limited to parts of the state with the greatest amount of snowfall (Figure 2), such as the mountainous sections of the northern Pennsylvania (Diefenbach et al. 2016) and small, isolated populations in higher elevations of southern parts of the state (Boyd 2015). The distribution of snowshoe hares in Pennsylvania was shown to have contracted in recent years by Diefenbach et al. (2016) through the use of hunter mail surveys. Habitats for snowshoe hares in Pennsylvania likely include 5-to20-year-old clear-cuts, wetlands, forests with mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron maximum*), hemlock, scrub oak (*Quercus ilicifolia*), and spruce (*Picea sp.*; Brown 1984, Diefenbach et al. 2016, Gigliotti 2016, Scott and Yahner 1989). Diefenbach et al.

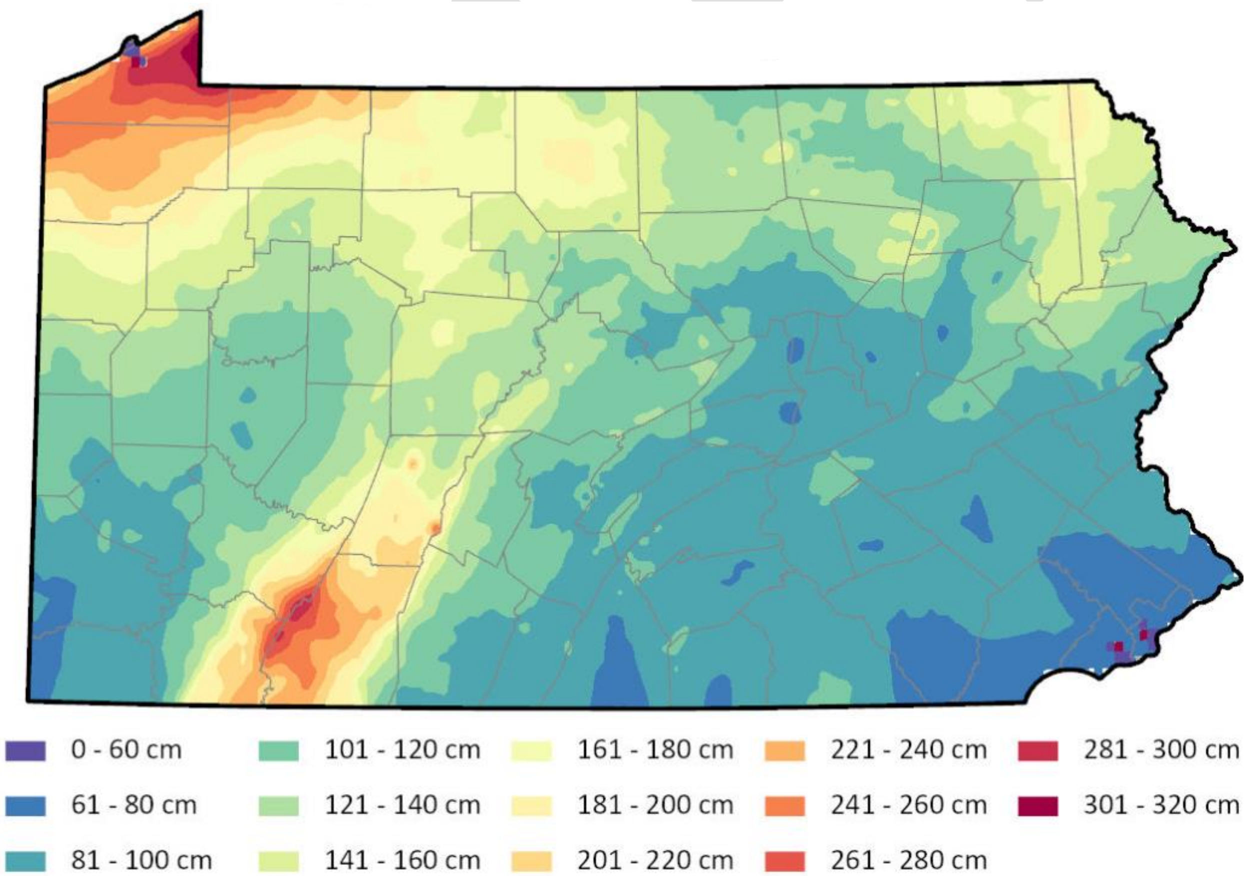

Figure 2: Average annual snowfall (cm) in Pennsylvania from 2009-2020. Figure by E. Clees, PGC.

(2005) described hare distribution north of Interstate 80 to be patchy and related to specific habitat type and temperature with concentrations in Warren, McKean, Forest, Cameron, and Elk counties in the northwest and the Pocono region in the northeast. There has been little work done to analyze the distribution of hares south of I-80. In recent years hares have been reported in each of the 3 Pennsylvania Game Commission's southern regions as well, but very little is known about the habitat use, survival rates, or connectivity of these populations. The absence of snowshoe hares in a particular location may be due to reduced periods of snow cover, fragmented habitat, or unsuitable habitat.

Population Dynamics

Population fluctuations are relatively common across wildlife species and can occur seasonally, annually, or over longer periods. A true population cycle is defined as a predictable oscillating trend in population size that occurs at regular intervals ≥3 years (Berryman 2002). The basis for population cycles vary among species and include external variables that are cyclic (e.g. moon phase or seasons), or time-delayed feedback to the fluctuating population size (e.g. predator populations, availability of nutrition, or suitable habitat, etc.) that influence survival or reproduction and recruitment (Review in Murray 2003, O'Donoghue and Krebs 1995, Sheriff et al. 2015).

There have been many theories proposed for what drives snowshoe hare population cycles including sunspots, weather, ultraviolet rays, and natural cyclic variation in plant composition, but these all have largely been discredited (reviews in Ellsworth and Reynolds 2006 and Murray 2003). Disease, parasites, and herbivory induced plant defense chemicals may contribute to overall population dynamics, but are unlikely to have substantial, widespread influence (Bryant et al. 1985, Dodds 1987, Fox and Bryant 1984). Die-offs because of diseases have occurred (Dodds 1987) and it is yet unknown how RHDV2 will affect hare population cycles or snowshoe hare populations in Pennsylvania.

Currently it is thought that snowshoe hare cycles, where they are occur, are caused by an interaction of winter food resources, population connectivity, and specialist predators (Hodges et al. 2001, Krebs et al. 1986, Krebs et al. 1995, Sinclair et al. 1988, Smith et al. 1988). Whether or not this interaction occurs sequentially (Keith 1974, 1981, 1990, Keith et al. 1984) or simultaneously (Krebs et al. 2001a) has conflicting results. Amplitude of cycle booms and busts is likely also impacted by reduced reproductive output during low phases. Hik (1995) theorized that when the risk of predation in a foraging area is high, hares select areas with increased cover, but with potentially reduced food availability or quality, reducing overall hare body condition and reproductive rates. Prolonged periods of maternal physiological stress caused by increased predation risk and reduced food resources have been shown to decrease reproductive output and recruitment (Boonstra and Singleton 1993, Boonstra et al. 1998a, b).

Snowshoe hare populations in Pennsylvania are thought to not cycle (Diefenbach et al. 2005) nor are populations in most other mid-Atlantic states (Murray 2000). Pennsylvania's less severe winters, wide variety of predators who don't specialize on a particular prey, diverse habitat types, and assumed isolated populations are likely why. Using hunter surveys, harvest records, and indices of abundance, Hodges (1999) claimed that hare populations in Pennsylvania were weakly cyclic, however, data sources for Pennsylvania would be questionable for long term credibility prior to the implementation of stratified sampling for the Pennsylvania Game Commission's annual Game Take Survey in 1984. Even though snowshoe hare populations in Pennsylvania are not thought to cycle, foundational elements of population cycles in other areas of the species' range have implications for hare populations locally.

Snowshoe hare population density has been found to be influenced by warmer than normal temperatures across all seasons (Kumar et al. 2022). Over 21 years of snowshoe hare population monitoring, Kumar et al (2022) found lower hare population densities when higher temperatures occurred in spring, summer, and fall. The warm spring and fall seasons experienced shorter periods of snow cover duration and consequently increased periods of snowshoe hare mismatch (Zimova et al. 2016). When summers are particularly hot, greater than 38°C (Hart et al. 1965), leverets have been found to experience greater mortality rates (Krebs et al. 2002). Warmer winters were found to increase hare survival and population density when the overall number of days below -5°C was reduced (Hart et al. 1965, Kumar et al. 2022). Warmer temperatures will also likely impact total snow fall and duration of snow cover. There appears to be a balancing point for the influence of winter temperatures on snowshoe hares. The impact of temperatures on hare populations has not been assessed in Pennsylvania, but considering the different physical characteristics of hares (Gigliotti 2016) and comparably warm temperatures in Pennsylvania, the impact of temperature on snowshoe hare population dynamics is worth further investigation.

Movement Patterns and Behavior

Snowshoe hares are crepuscular, however, they will remain active to some extent throughout the night as well. Field cameras deployed over 11 months in Pennsylvania only detected snowshoe hares between 6 pm and 6 am (Boyd 2021). During the day, they take cover in a "form," where they remain stationary unless disturbed (Keith 1964, Mech et al. 1966, Merritt 1987). Hares have been found to adjust their movement relative to moonlight and snow cover to reduce predation risk (Gigliotti and Diefenbach 2018, Gilbert and Boutin 1991), however, they do not select resting locations based on thermal advantage (Gigliotti 2016). Differences in seasonal activity show that movement peaks in the spring and summer (the reproductive period) and lowest in winter (Gigliotti and Diefenbach 2018).

Snowshoe hares are well known for their flushing behavior. Hares for the most part rely on thick cover and remain motionless to avoid detection. If flushed and pursued, the snowshoe hare will run in a large circle (approximately one mile in diameter) and return to the area from which it was flushed (Merritt 1987).

Dispersal

Common explanations for why animals disperse include intraspecific competition, reproduction, population density, forage availability, and risk of predation. Distinguishing dispersal from regular movement within a home range can be difficult as some hares have larger home ranges (Hodges 2000a). Dispersers tend to be in worse body condition than non-dispersers (Boutin et al. 1985, Windberg and Keith 1976). Decreased food availability and overcrowding may cause dispersal, however, food supplementation did not prevent dispersal (Gillis and Krebs 1999, Murray 1999). Keith et al. (1993) found greater rates of hare dispersal from small habitat patches.

Hares of all age classes and both sexes disperse throughout the year, though dispersal peaks in spring and fall (Murray 2003). Dispersal rates have been demonstrated to vary by age class, with juveniles tending to disperse more than adults (Boutin et al. 1985, Dolbeer and Clark 1975, Keith et al. 1993, Windberg and Keith 1976). There is considerable variation in dispersal rates among studies, ranging from 50% to less than 10% of study populations (See review in Murray 2003). No dispersal studies have been conducted in Pennsylvania to date.

The extent that hares disperse also tends to vary. Griffin (2004) found greater distances travelled in the fall, while Boutin et al. (1985) found greatest dispersal to occur in winter during the cyclic high-phase. Hares have been shown to disperse up to 20 km, however, dispersal typically occurs over much shorter distances (Gillis and Krebs 1999, O'Farrell 1965). In Montana, 90% of dispersing hares moved less than 1.8 km (Griffin 2004).

Barriers to hare dispersal include unforested areas, steep slopes, large rivers, major roadways, and urban areas. The extent to which hares will travel across unsuitable habitats will likely vary and depend on local factors such as distance to suitable habitat, local habitat types, and predation risks. Some occupied areas may essentially be "habitat islands" surrounded by unsuitable habitat. Dispersal corridors, such as forest edges, riparian strips (Darveau et al. 1998), conifer plantations (Parker 1986), shrublands, or patches of woodlands in close proximity to one another (<.5km; Scott and Yahner 1989), are likely critical to linking otherwise isolated populations. Hares seldom venture more than 200 to 440 m from canopy cover into large clear-cuts (>16 ha) less than 5 or 10 years old (Brocke 1975, Conroy et al. 1979). The size, density, and proximity of clear-cuts or managed timber areas may be an important component in the management of hare populations because of their impact on surviving periods of dispersal (Conroy et al. 1979, Monthey 1986, Scott and Yahner 1989).

HABITAT

Across the vast area occupied by snowshoe hares in North America, hares occupy diverse habitat types with many different plant species, snow conditions, and predator populations. However, hares rely universally on a few basic habitat characteristics including dense understory vegetation that provides food, thermal cover, and protection from predators especially during winter (Barta et al. 1989, Belovsky 1984, Berg et al. 2012, Brown 1984, Gigliotti 2016, Rohner and Krebs 1996, Sievert and Keith 1985, Wirsing et al. 2002), but the dense vegetation should also be at least 2m high, preferentially 3m, which provides vertical cover from aerial predators even with snow pack (Carreker 1985, Gigliotti 2016, Litvaitis et al. 1985, Wolfe et al. 1982). Snowshoe hares are more influenced by the structure of vegetation than plant species composition (Carreker 1985) and thermal advantage (Gigliotti 2016). The importance of both stem density and canopy cover for hares may be exemplified by hares in Pennsylvania avoiding areas with high density of tall *Rubus* (≥ 1.5 m; Scott and Yahner 1989) which generally has high stem density but lacks overhead cover. Snowshoe hares are found in higher densities in mixed forests. Edge habitats, created by regenerating clear cuts in mature forests, are likely used by hares despite having greater predator densities, because cover and food are in close proximity (Gigliotti 2016, Litvaitis et al. 1985, Meslow and Keith 1968). Hare populations need contiguous matrices of suitable habitats in close proximity to persist (Berg et al. 2012, Carreker 1985, Scott and Yahner 1989).

Although there are some exceptions, snowshoe hares primarily occupy forests with longer duration of snow cover in winter which tends to restrict their distribution to higher latitudes and altitudes (Diefenbach et al. 2016). The depth of snow cover can also impact habitat suitability and should be considered by managers. If snow fall in an area covers all but the top of saplings and stem density is low, hares will avoid the area (Wolfe et al. 1982). With the exception of hare populations in the Pacific Northwest which remain brown throughout the year, snowshoe hares are not found in areas with short periods of snow cover.

Non-forested areas are usually avoided, as are forest stands that are too young to offer sufficient height, and more mature forests that have little woody vegetation in the understory. Dense forest stands (>40,000 stems per ha) may not be used by hares if browse and understory cover are scarce (Adams 1959, Brocke 1975, Koehler 1990b, Litvaitis et al. 1985). The necessary combination of winter food and cover is typically lacking in very young and mature stands (Koehler 1990a, b, Sullivan 1984, Wirsing and Murray 2002). Griffin (2004) found hare survival in the Rocky Mountains to be greatest in dense forest stands and young forests that were un-thinned.

Regenerative capacity is a critical consideration of landscape management for snowshoe hare as it impacts the duration of time between disturbance and snowshoe hare reoccupation. Factors that influence regeneration include soil type and composition, canopy cover, precipitation, relative humidity, vegetative composition, browsing by wildlife, and topography (Baumgartner et al. 1984, Koch 1996). Snowshoe hare habitat suitability generally follows a pattern post treatment: 1) immediately hares are absent while cover is low; 2) in several years (at least 5 - 15 years in Pennsylvania) small tree and woody shrub regeneration occurs in the stand and hares begin to reoccupy; 3) hare densities reach their peak when regeneration offers cover and food even when there is deep snow for long periods; and 4) hare populations begin to decline as the understory decreases with forest maturation (Brocke 1975, Conroy et al. 1979, Darveau et al. 1998, de Bellefeuille et al. 2001, Ferron et al. 1998, Griffin 2004, Litvaitis et al. 1985, Monthey 1986, Newbury and Simon 2005, Potvin et al. 1999, Potvin et al. 2005a, Scott and Yahner 1989, Sullivan and Moses 1986, Wolfe et al. 1982). A longer growing season and faster-growing tree species in Pennsylvania likely allow clear-cuts to create suitable hare habitat 5-15 years after a treatment (Brown 1984; Storm et al. 2003) depending on the cover type.

Habitat types for snowshoe hares in Pennsylvania include regenerating hardwood stands with intermittent conifer cover, regenerating conifer stands, rhododendron, scrub oak barrens, and wetlands at higher elevations (>450 m; Boyd 2015, Brown 1984, Diefenbach et al. 2005, Gigliotti 2016, Glazer 1959, Merritt 1987). Clear-cuts that were between 5-15 year old were used more than mountain laurel or eastern hemlock (*Tsuga canadensis*) when in close proximity on the landscape. Lower average stem densities have been found to provide sufficient browse and protective cover in Pennsylvania (>10,000 stems/ha) when compared to other areas of the hare's range (11,590-33,210 stems/ha) (Brown 1984, Litvaitis et al. 1985, Murray 2003, Wolff 1980b). Exactly what constitutes not only suitable habitat, but optimal habitat for hares, is uncertain as hares tend to occupy available habitats with key characteristics of high woody stem density that is > 3m in height. Structurally, conifer branches provide three times as much visual cover for hare compared to same sized deciduous branches, as well as additional thermal insulation which prolongs periods of snow cover, but, when compared to northern snowshoe hare range, there is relatively little of this cover type available. Marginal habitat likely allows for hares to exist and persist but does not encourage population growth as is experienced in northern latitudes where population cycles occur (Ausband and Baty 2005, Carreker 1985, Diefenbach et al. 2005, Monthey 1986, Scott and Yahner 1989).

Snowshoe hare distribution in Pennsylvania is limited to the coldest regions that experience longer duration of snow cover and where suitable habitats exist (Figure 3; Diefenbach et al. 2016). Refuge from predators provided by vegetative structure is the most important factor driving habitat selection, not vegetative composition (Ferron and Ouellette 1992, Litvaitis et al. 1985, Murray 2003, O'Donoghue 1983, Parker 1986, Wolff 1980a), or thermal advantage (Gigliotti 2016). Hares are known to vacate forests which have been thinned, despite abundant food, because hiding cover is reduced suggesting that risk of predation changes a hare's movements, and habitat use (Boonstra et al. 1998b, Hik 1995). However, the notion that habitat selection is driven by predator avoidance is not supported by all studies. Hodges and Sinclair (2003) determined that hares chose to browse in areas based on food availability rather than their ability to avoid predators. In some habitats with dense cover, such as mountain laurel, hares may need to forage in areas outside of the cover because of lack of food resources.

Home Range

Despite overlapping home ranges, snowshoe hares are solitary except during the breeding season and tend to occupy the same area throughout the year (Boutin 1980, Boutin 1984b, Gigliotti 2016). Home range size is likely influenced by multiple factors including overall hare population density, forage availability, habitat quality, season, sex, and predation risk (Murray 2003), as well as method used to generate the estimate.

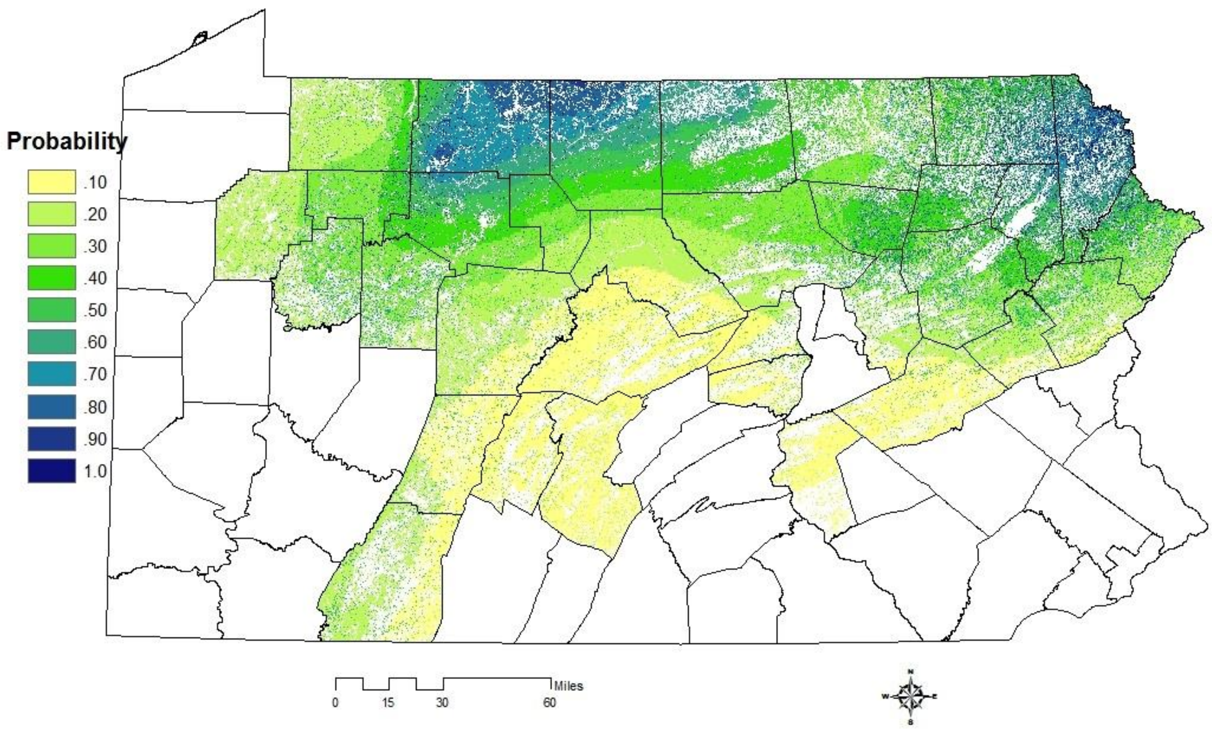

Figure 3: Probability of snowshoe hare occurrence in Pennsylvania counties where snowshoe hares have been reported harvested by hunters (Diefenbach unpublished data).

Two primary methods which have been used to estimate home range size, live-trapping and radiotelemetry, tend to generate different results which makes comparing estimates between studies complicated. The home range size of snowshoe hares has been estimated to range from 5 to 10 ha (Keith 1990, Murray 2003). Studies have found that male hares have larger home ranges (averaging 6.7 and 5.2 ha, respectively; Keith 1990), while others have found no difference in home range size by sex (Dolbeer and Clark 1975, Gigliotti 2016, O'Farrell 1965). A seasonal exception may occur during breeding when males move more to mate with many females (Hodges 1999) and adult females have smaller home ranges when caring for young (O'Donoghue and Bergman 1992). Results from a study in Pennsylvania show that hares in the northwest region of the state use an average of 63.8 ha (±20.6), based on minimum convex polygon estimations while hares in the northeast used an average summer home range of 21.1 ha

(±1.29; Gigliotti 2016, Gigliotti personal communication) indicating that hares in Pennsylvania have larger home ranges than other populations.

FOOD HABITS AND NUTRITIONAL ECOLOGY

Digestion

Hares, like other mainly herbivorous species, are hind-gut fermenters which allows hares to maximize energy gained from the coarse, fibrous materials they consume. Hares further maximize this gain by excreting and consuming soft cecal pellets (cecotropes) (Bjornhag 1994). Cecotropes of hares have been shown to have important nutrients such as nitrogen, potassium, phosphorus, magnesium, and sodium (Pehrson 1983). Coprophagy, the process of consuming cecotropes, is likely vital to prevent snowshoe hares from becoming malnourished. Forage that is too hard to digest is excreted as fecal pellets.

Forage Requirements

Food requirements depend on the amount of energy expended and nutrients that can be consumed and processed. A study using captive hares found a higher basal metabolic rate in summer than winter (Hart et al. 1965). Hares seemed to offset the increased demands of winter thermoregulation with pelage insulation (increased density of hair; Gigliotti et al. 2017, Hart et al. 1965) and they may also use a depressed basal metabolic rate and movement rates as a strategy to save energy in winter (Gigliotti et al. 2017, Thomas 1987). Malnutrition, due to lack of sufficient forage in winter, has been shown to influence survival (Pease et al. 1979).

Browse Selection

Hares exist in diverse habitat types and, as with habitat use, consume many different plant species across their range (Hodges 2000b, Murray 2003, Scott and Yahner 1989); primarily consuming woody browse in winter and herbaceous browse in summer. In summer, they feed on grasses, legumes, wild berries, sedges, ferns, wildflowers, clover, horsetails, and new growth of trees and shrubs while in winter their diet consists of buds, twigs, bark, lichens, moss, and evergreen needles (Carreker 1985, review in Murray 2003). During winter, dense hare populations can lead to widespread sapling mortality by girdling young trees (Merritt 1987). Hares have been observed to eat carrion, but the importance or value of this nutrient source to hares is unknown (Merritt 1987). In Pennsylvania, snowshoe hares browse *Rubus*, striped maple (*Acer pennsylvanicum*), and yellow birch (*Betula alleghaniensis*) more than expected, and browse American beech (*Fagus grandifolia*), pin cherry (*Prunus pennsylvanica*), black cherry

(*Prunus serotina*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*) less than expected (Brown 1984, Scott and Yahner 1989).

Forage selection likely maximizes nutrients gained. Hares preferentially consume high energy and protein-rich plant parts such as new growth, buds, and small diameter twigs (≤ 4mm; Bryant 1981, Fox and Bryant 1984, Hodges 2000b, Hodges and Sinclair 2003, Pease et al. 1979, Rangen et al. 1994, Sinclair et al. 1982, Sinclair and Smith 1984, Sinclair et al. 1988, Wirsing and Murray 2002, Wolff 1980a), and avoid plants or plant parts that are more fibrous with chemical defenses (Bryant and Kuropat 1980, Bryant et al. 1985). The variation of forage selection across studied populations likely corresponds with regional nutrient availability (Murray 2003).

SECTION III. RECREATIONAL SIGNIFICANCE AND PUBLIC INTEREST

Hunting of Snowshoe Hare

The snowshoe hare is a game species in Pennsylvania. Hunting season duration has changed in recent years with some Wildlife Management Units (WMUs) closed to hare hunting or with shorter seasons. Currently, a short hunting season, usually lasting 6 days, occurs statewide between Christmas and New Year's Day. From 2001 to 2013, the bag limit for hares was set at 1 per day with a possession limit of 2. The possession limit was increased to 3 in 2014. Only an estimated 2,512 Pennsylvania snowshoe hare hunters participated during the 2020 season which is a decline from ~16,000 hare hunters in 1991 (Figure 4). The decline of hare hunters may in part account for the decline in harvests and may indicate a reduction in hare distribution (Diefenbach et al. 2005). The Game Take Survey has demonstrated that participation by hunters in the snowshoe hare season is relatively low, averaging 0.28% of licensed hunters from 2011 to 2021. This low participation rate is likely due in part to the limited distribution of

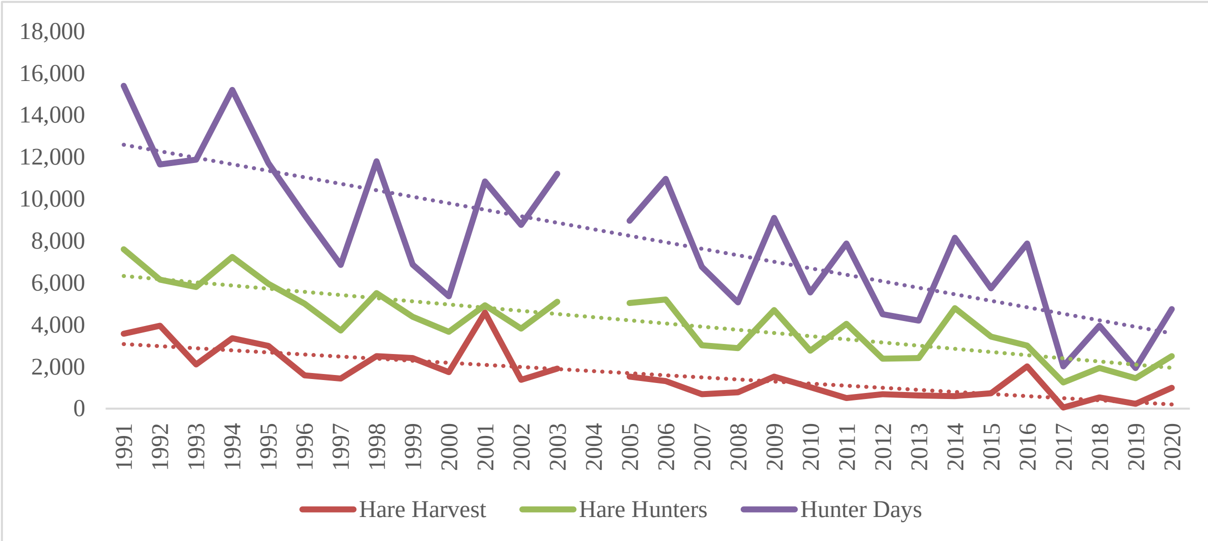

Figure 4: Estimated harvest, number of hunters, and number of hunter-days for snowshoe hare from the Pennsylvania Game Commission's Game Take Survey (1991-2020). The Game Take Survey was not conducted in 2004. In 2012 Wildlife Management Units 3B, 3C, and 3D were closed to hare hunting and from 2013-2015 those same WMUs had only a 3-day season.

Pennsylvania's hare population, the secretive nature of the species, the decline in population, and the short duration of Pennsylvania's snowshoe hare hunting season (Figure 5).

Education and Outreach

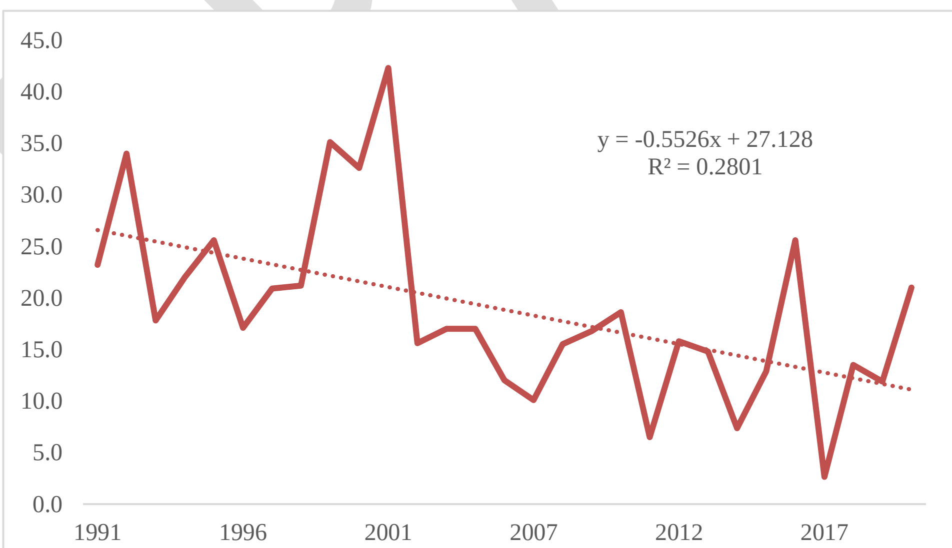

Figure 5: Hare harvest/ 100 hunter days data from the Pennsylvania Game Commission's Game Take Survey (1991-2020). The Game Take Survey was not conducted in 2004. In 2012 WMUs 3B, 3C, and 3D were closed to hare hunting and from 2013-2015 those same Wildlife Management Units had only a 3-day season.

Many Pennsylvanians are not aware that snowshoe hares exist within the Commonwealth. However, certain interest groups, such as hunting dog owners who use their dogs to pursue hares are passionately aware of the species whether they plan on harvesting a hare while hunting or not. Increasing awareness of this unique wildlife resource through various media outlets will help to strengthen the resolve of conservation efforts. Certain conservation and management activities could help ensure the viability of snowshoe hare in Pennsylvania. Pennsylvania consists of more than 28 million acres of land of which almost 85% is in private ownership. About 16 million acres are forested, the majority of which is privately owned, with more than approximately 500,000 landowners controlling 70% of Pennsylvania's forestlands (12.4 million acres; McCaskill 2014). Emphasis of public outreach programs should focus on sustainable forestry, and the influence of forest management decisions on wildlife at both local and broader spatial scales on private and public lands.

SECTION IV. CONSERVATION OF SNOWSHOE HARE

STATUS

Snowshoe hares in Pennsylvania are believed to have experienced a decline in distribution during the twentieth century (Diefenbach et al. 2016). This decline coupled with the importance of Pennsylvania's population's role in maintaining genetic flow between populations to the north and south caused the Pennsylvania Biological Survey to classify hares as vulnerable in its report *Species of Special Concern in Pennsylvania* (Genoways and Brenner 1985). The snowshoe hare was identified as a species of maintenance concern in Pennsylvania's 2005 Wildlife Action Plan. Hares are considered "Vulnerable" to "Apparently Secure" in Pennsylvania and were not included in the 2015 Pennsylvania State Wildlife Action Plan based on anecdotal evidence. However, given the decline and contraction found by Diefenbach et al. (2016), and continued Game Take Survey trend analysis supporting this concern, the species status should be reevaluated in Pennsylvania. Hares are a watchlist-assessment priority for the Northeast region and the species' global rank is Secure (G5, Steele et al 2010).

Pennsylvania Snowshoe Hare Population Trends

There has been relatively little focus on population status of hares on the southern edge of their range, including Pennsylvania, until recently. Likely due to the abundance of hares in northern regions and lack of population status awareness and resources. Monitoring of hares in Pennsylvania has involved the Game Commission's annual Game Take Survey. Diefenbach et al.

(2005) found hare harvest by hunters to be low and highly correlated with hunter numbers (r = 0.83, n = 25) between 1983 - 2003. Based on this survey, there is thought to have been a decline in Pennsylvania snowshoe hare populations and a documented decrease in distribution across the Commonwealth (Diefenbach et al. 2016). Concurrently, with changing temperatures and amounts of snow fall (The Pennsylvania State Climatologist), land use trends have also changed in recent decades (Albright et al. 2017). The better we understand snowshoe hare habitat use and ecology on the distribution's southern edge now, the better managers will be able to manage peripheral hare populations for years to come.

THREATS

Mismatch

Snowshoe hares in mismatch, referring to a white hare with brown background, experience up to a 7% higher weekly mortality rate due to predation than hares whose color provide camouflage (Zimova et al. 2016). Snowshoe hare range in Wisconsin contracted northward almost 30 km over the past 36 years likely due to shorter duration of snow cover, as continued occupancy on the southern edge of the Wisconsin range was predicted by longer snow cover duration (Sultaire et al. 2016). Hare occupancy in Pennsylvania was found to be correlated with the coldest areas of the Commonwealth, which also experience the greatest amount of snowfall and duration of snow cover (Diefenbach et al. 2016). Survival rates when in mismatch may vary among habitat types and some habitat types at large enough scales negated the mortality costs of mismatch (Wilson et al. 2018). Without consistent and long-lasting snow cover on the southern fringes of the snowshoe hare's range, habitat becomes a critical factor for resilient snowshoe hare populations.

Given the presumed advantage of seasonal camouflage, one might predict that coat color changing species in the same area would have similar winter coat color, but, in West Virginia, Davis et al. (2019) documented different winter coat colors between sympatric species that are known to turn white in winter. Snowshoe hares in this study were still white in winter while long-tailed weasels (*Mustela frenata*), and least weasels (*Mustela nivalis*) were brown. The cause of this discrepancy is unknown, but drivers of coat color change must be different between species. Snowshoe hares in West Virginia were found to have the lowest genetic diversity by Cheng et al. (2014)'s range-wide assessment of the species' genetics. This isolation may very well lead to a lower likelihood of successfully adapting to prolonged periods of mismatch.

Limited variation or plasticity in the timing of seasonal coat color transition has been observed with other hare populations and was related to duration of snow cover (Kumar et al. 2020, Zimova et al. 2019). However, the plasticity was not sufficient to greatly decrease the disadvantage that mismatched hares experience (Mills et al. 2013, Wilson et al. 2018, Zimova et al. 2016). Snowshoe hares have additionally been shown to forego the winter white molt entirely, remaining brown year-round in some populations. Winter brown morphs seen in the Pacific Northwest and Pennsylvania, or more brown phenotypes (brown eye rings and brown ears) observed in Pennsylvania (Gigliotti et al. 2017), are expected to be selected for as hares in mismatch are more vulnerable to predation (Mills et al. 2018, Wilson et al. 2018, Zimova et al. 2016). Brown phase winter hares in other studied populations have been found to have a mutation in the agouti gene caused by breeding with jackrabbits (Jones et al. 2018). Jackrabbits are not native to Pennsylvania and there is no known extant jackrabbit population in Pennsylvania. Snowshoe hares released by the Game Commission over the last century were primarily sourced from Maine (Kosack 1995), New York, and Wisconsin (Grove 1991) and are unlikely to have brought in any of the previously documented agouti gene mutation based on genetic relatedness work (Cheng et al. 2014).

Changes in total amount of snow that falls, the type of snow that falls, and how long that snow stays on the ground can influence climate adapted specialists like the snowshoe hare (Zimova et al. 2016). Overall Pennsylvania's statewide annual snow fall remained stable, but variable in a 120 year analysis (Figure 6). The variation in annual snow cover duration shown by available Pennsylvania data poses a threat to hares, which are not able to adjust when the transition of coat color occurs within a year though some limited plasticity has been observed in timing of transitions between geographic areas (Kumar et al. 2020). Diefenbach et al. (2016) predicted that as little as a 2-5 C° increase in temperature will decrease the probability of hare occupancy across northern Pennsylvania by half.

Focused habitat management for hares is important for the conservation and management of this species as amount and duration of snow cover varies greatly between years without a consistent increasing or decreasing trend (Figure 6). Creating habitat that reduces the

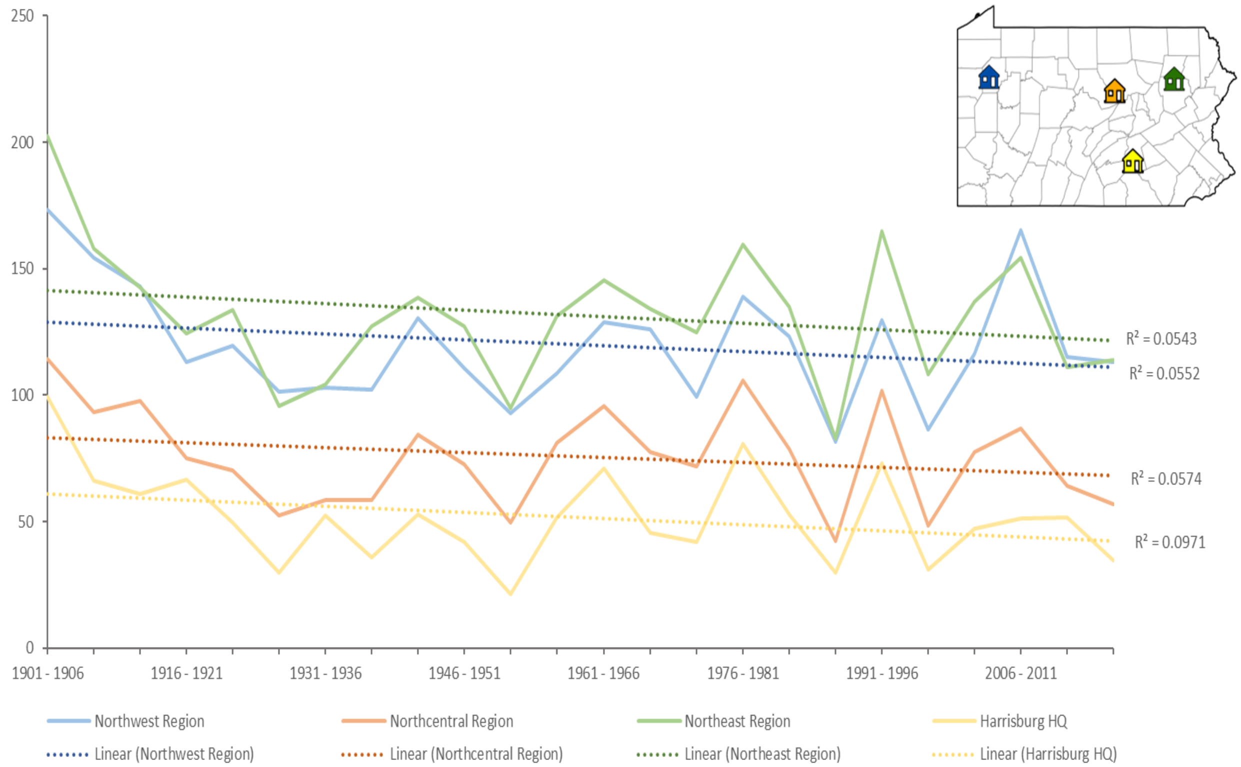

Figure 6: Annual precipitation as snow estimates (mm) averaged by five-year intervals from 1901 - 2021 (ClimateNA). Figure by E. Clees, PGC.

vulnerability of hares in mismatch, a brown hare on a snow-covered landscape or a white hare on a landscape without snow, may allow the species to remain resilient in Pennsylvania regardless of future snow cover duration trends.

Habitat

Habitat is the most critical variable that managers can directly impact to benefit hares in Pennsylvania. Without management intervention, the ephemeral nature of early successional habitat will lead to loss of suitable habitat and corresponding decline in habitat connectivity. Many wetland and barrens habitats known to be used by hares were included on the 2015 Pennsylvania State Wildlife Action Plan as habitat of conservation concern given their own decline and management and protection needs. Early successional habitat has been decreasing for decades in Pennsylvania and the Northeastern United States (Alerich 1993, King and Schlossberg 2013, McWilliams et al. 2007).

Over the past 100 years, land use in Pennsylvania has changed (Albright et al. 2017). Diefenbach et al. (2016) found that overall percent forest cover had not declined in recent decades, but early successional forest has been declining (Albright et al. 2017, Alerich 1993, Trani et al. 2001) due to forest succession and human development which has negative implications for snowshoe hares. The destruction of forest habitat due to human development permanently reduces the overall area of habitat available to hares. Developed areas often offer little snowshoe hare habitat value, increase overall habitat fragmentation, and reduce landscape connectivity. Although property is conserved annually under state and private programs and public-private partnerships for the purpose of wildlife management, Pennsylvania is still recording a net loss of 28,000 acres of wildlife habitat annually (PGC-PFBC 2015). This acreage does not include the additional acres degraded through habitat fragmentation. Continued expansion of human development will likely have negative impacts on snowshoe hares in Pennsylvania.

Silvicultural practices can improve or adversely affect habitat quality for hares. Properly applied silvicultural practices will ensure forest regeneration with high stem densities, but these practices are not as common on private lands which make up the majority of forest in Pennsylvania. Instead, exploitative logging that is more common on private lands, often results in too much shade for abundant tree regeneration or native trees are outcompeted by invasive species such as ferns. Poor forest regeneration caused by some management practices and excessive browsing by white-tailed deer (*Oedocoileus virginanus*; Scott and Yahner 1989) are also likely to have adversely impacted snowshoe hares in Pennsylvania. The growing human population and development of Pennsylvania is causing permanent habitat fragmentation which has negative implications for the connectivity of snowshoe hare populations.

Fragmented landscapes increase edge habitats which hares use (Gigliotti 2016), but where they are more vulnerable to predation. Fragmentation also increases the likelihood that a dispersing hare will be unable to find suitable habitat or be predated while looking for new habitat (de Bellefeuille et al. 2001, Wirsing et al. 2002, Wolff 1980 a, b). Declines in the abundance and connectivity of suitable habitats will change hare survival, dispersal, population connectivity, decrease genetic diversity, and reduce the ability of hares to adapt to pressures such as varying duration of snow cover (Griffin 2004, Keith et al. 1993, Wirsing et al. 2002, Wolff 1980a, 1981).

Timber management and tree removal can benefit hares for periods of time because mature forests are reset (Koehler 1990a, b, Sullivan and Moses 1986), however, it is important to understand that hares will initially vacate newly logged areas (Ferron et al. 1998, Potvin et al.

1999). Managing hare habitat via forest management practices will require continuous work and evaluation of available habitat across the landscape. Landscape level impacts of timber harvesting on snowshoe hare in Pennsylvania are not well understood and worthy of further investigation. Promoting a continuous matrix of suitable hare habitat, will benefit snowshoe hares in Pennsylvania.

Other concerns exist for Pennsylvania's forests and consequently snowshoe hares. Poor forest regeneration caused by some management practices and over-browsing by white-tailed deer (Bookhout 1965a, b, Glazer 1959, Scott and Yahner 1989) has likely contributed to the decline of hare populations in Pennsylvania. Pennsylvania's predominately hardwood forests lack significant conifer cover that snowshoe hares likely benefit from especially in winter. The hemlock wooly adelgid (*Adelges tsugae*) will likely reduce or eliminate the hemlock which could further reduce Pennsylvania's habitat suitability for snowshoe hare. Loss of hemlock cover may be mitigated by planting other conifer species, such as spruce and fir, and managing forest lands to create and maintain areas with high woody stem density.

Human Facilitation of Predator Movement in Snow

Snowshoe hares have specially evolved feet which allow them to move easily in snow and continue to access areas that might otherwise have too deep snow conditions for other wildlife species, especially predators. Trail compaction caused by snowmobiles, logging activities, and natural gas development and maintenance could allow certain predators to access areas with deep snow that they would otherwise be restricted from (Ruediger et al. 2000). Coyotes and other predators have been shown to select and use these compacted pathways more than other available movement options across the landscape (Bunnell et al. 2006, Dickson et al. 2005, Kolbe 2005). Human infrastructure, including logging roads, can also decrease mean patch size and increase edge habitats on the landscape (McGarigal et al. 2001). Natural gas well development is a relatively widespread practice across Pennsylvania's snowshoe hare range, (McKenzie et al. 2012). The influence of these land uses on predator movement in Pennsylvania is not well understood.

Disease

As discussed in the Disease section of this Management Plan, diseases are not typically thought to have population level effects on snowshoe hares. However, the detection of RHDV2 in wild North American lagomorphs certainly poses a threat to the persistence of snowshoe hares in Pennsylvania which are already facing pressure from mismatch and the connectivity and suitability of habitat. Once RHDV2 reaches our wild lagomorph populations, it will be almost impossible to control its continued spread and RHDV2 is expected to cause substantial mortality in populations that it reaches.

SECTION V. MANAGEMENT APPROACHES AND RESEARCH NEEDS FOR SNOWSHOE HARES

The lack of inventory and monitoring data on wildlife species is one of the most critical issues in wildlife conservation today. It is difficult to evaluate the status of wildlife and conserve habitats without data on where species occur, what habitats they use throughout the year, what trends are occurring in their populations, and what factors influence those trends. A comprehensive approach is needed.

The Pennsylvania Biological Survey designated the snowshoe hare as vulnerable due to its sensitivity to habitat alteration and recognized population decline since the 1980s (Genoways and Brenner 1985). This designation occurred before disadvantages brought by mismatch became mainstream concerns for snowshoe hares. Stocking or human based movement of snowshoe hares into or across Pennsylvania should be discouraged to maintain biological integrity of endemic populations and to reduce introduction or spread of diseases and parasites not currently found in the Commonwealth. Rather, snowshoe hare habitat use, the influence of habitat characteristics on survival, the prevalence and degree of advantage brought by Pennsylvania’s phenotypes, and overall distribution of snowshoe hares in Pennsylvania need to be better understood.

It is important for managers to understand that hares in Pennsylvania may be more impacted by annually varying and long-term trends of snow fall, duration of snow cover, and habitat fragmentation than other hare populations because Pennsylvania is at the southeastern most geographical extent of the species’ range. However, temperature, total snow fall, and duration of snow cover are independent of forest and wildlife managers’ sphere of influence. As a result, habitat management which prioritizes promoting overall habitat suitability and landscape connectivity for hares will be vital to the continued presence of hares in Pennsylvania. Forest management and propagation of conifer species will be particularly important to effective hare management in the southernmost extent of the hare’s range. Research projects, as have been laid out in the goals, objectives, and strategies of this management plan, should be designed to support effective population and habitat management.

WILDLIFE MANAGEMENT UNIT BASED POPULATION MANAGEMENT

Snowshoe hares are likely not in imminent danger of extirpation from Pennsylvania, however, there is cause for concern for the future of a well-distributed, resilient hare population that is able to support hunting opportunities. Monitoring hunter participation and harvest is the longest running monitoring method for hares in Pennsylvania. Prior to the development and implementation of Wildlife Management Units, the Game Take Survey monitored populations at the county level. County level analysis of snowshoe hares provided a finer scale estimate of hare distribution and was used by Diefenbach et al. (2016) to conclude that Pennsylvania's snowshoe hare population had likely contracted. Snowshoe hares are thought to recently have occupied the following WMUs: 1B, 2B, 2C, 2D, 2E, 2F, 2G, 3A, 3B, 3C, 3D, WMUs (Figure 7). However,

Figure 7: Map of 2023-2024 Wildlife Management Units (WMUs) in Pennsylvania (pgc.pa.gov).

within the 2021-2022 hare season, hare harvests were only reported in 2 WMUs: 2F and 3A while in 2020-2021, hare harvests were reported in 3 WMUs: 2C, 2F and 3A. The proportion of WMUs reporting snowshoe hare harvest has declined overall in recent years (Figure 8) and most distribution has declined statewide and that more species-specific monitoring is warranted.

Wildlife Management Units will continue to be evaluated annually to assess changes in hare abundance and distribution along with management options and harvest opportunities. From 2013 through 2015, all WMUs were open to snowshoe hare harvest, but WMUs 3B, 3C, and 3D had a shortened 3-day season. The 2016 snowshoe hare hunting season returned to a 6-day

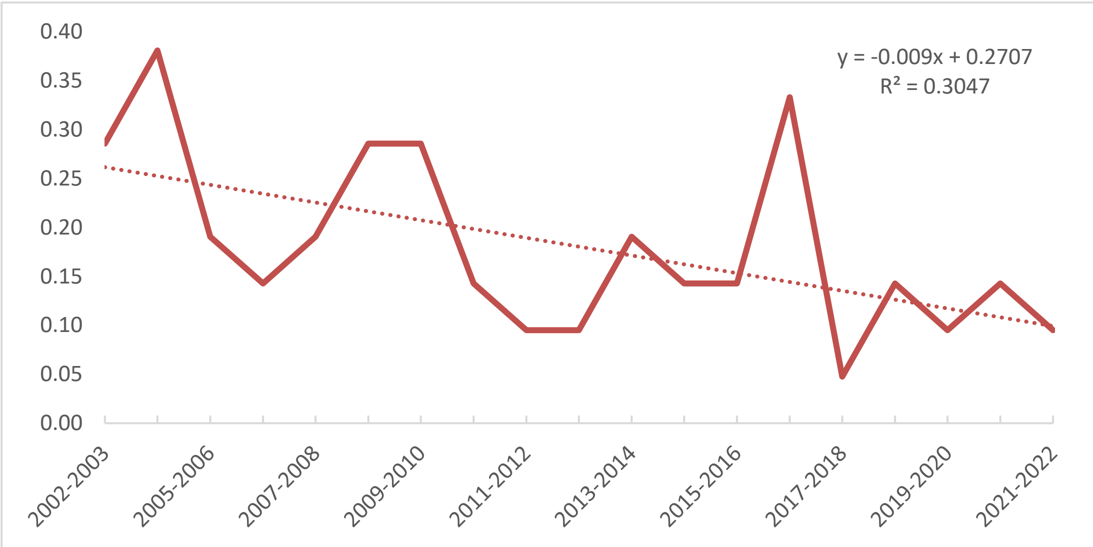

Figure 8: Proportion of Pennsylvania Wildlife Management Units (WMUS) that reported harvesting snowshoe hares from 2002 to 2021. In 2012-2013 the snowshoe hare season was closed in all WMUs except 2F, 2G, and 3A. From 2013-2016 the 6-day hare season was open statewide, except in WMUs 3B, 3C, and 3D.

season statewide. It is recommended that all WMUs have the same hunting season regulations until such time as research indicates population differences between WMUs and the influence of hunting on hare populations in Pennsylvania is better understood. Currently, hares are incorporated in 78 State Game Land (SGL) management plans as either present or a management goal species. Determining habitat connectivity within and around these Game Lands should be one of the first steps in Pennsylvania snowshoe hare management.

Snowshoe Hare Harvest

Snowshoe hare harvest rates are assumed to correspond with population abundance and hunter effort (Diefenbach et al. 2016). Gigliotti (2016) found harvest in Pennsylvania to account for 10% of all mortalities (*n* = 3). Recent declines in hare hunter numbers and hare hunter days are likely contributing factors to most of the decline in hare harvest. Harvest frequency analysis of 2016-2021 seasons shows >75% (*n* = 64) of hare hunters harvested 0 hare, 16.4% (*n* = 15) harvested 1 hare, and only 1.4% (*n* = 2) harvested 3 hares in a season. If we apply the proportional breakdown of hunter harvest frequency to harvest estimates over this same time period, hunters harvesting 2 to 3 hares in a season account for only 20% of total harvest. With our current understanding of Pennsylvania hare hunting and hare hunter harvesting, it is unlikely that reducing the season limit further at this time would have much impact on actual number of hares harvested.

Considering the value of the Game Take Survey and hare hunting for long term population trend analysis; it is recommended that the snowshoe hare hunting season remains open with uniform duration throughout the Commonwealth until such a time that harvest is found to be negatively impacting hare populations or hare reintroduction efforts are instituted. It is also recommended that harvest rates be found for hares using mark recapture methods throughout the Commonwealth and that the influence of hunting on hare populations be better understood.

Reintroduction and Stocking

During the past century, snowshoe hare stocking programs have attempted to reintroduce or supplement low density or declining populations along the southeastern extent of the species' range. Hodges (2000b) compiled stocking program information and found that stocking had been implemented in Connecticut (Behrend 1962), Maine (Severaid 1942), Massachusetts (McDonough 1969), Pennsylvania (Glazer 1959), and Virginia (Fies 1993). Hares overall tend to have high mortality rates, but released populations experienced even greater ones (Fies 1993, Hodges 2000b, Sievert and Keith 1985). Fies (1993) found that released hares in Virginia experienced 93% mortality due to predation with an average survival duration of only 24 days (Fies 1993). Introductions of snowshoe hares from other states could reduce the genetic integrity of endemic populations which could influence timing of molts, prevalence of unique phenotypes, and ultimately increase periods of mismatch, in addition to introducing new parasites and diseases into the state. Ultimately, stocking does not address what caused the local population to decline (Genoways and Brenner 1985) unless connectivity prevents hares from reoccupying a site.

Since 1918, the Pennsylvania Game Commission has purchased and released more than 33,000 snowshoe hares. Most animals have come from Maine, New Brunswick, and Nova Scotia (Kosack 1995, Grove 1991). During 1980 when 1,015 hares were released, the cost was $6.75 per animal. An attempt to reestablish snowshoe hares in Centre County during the 1950s was thought to be unsuccessful for 3 main reasons: 1) habitat was not suitable; 2) hares are less likely to become established where white-tailed deer had reduced available browse consequently affecting forage and cover for hares; and 3) hares that were trapped and transferred experienced detrimental levels of stress during the process (Glazer 1959). Historically, Pennsylvania's deer population has fluctuated dramatically, but there have been definite periods of extensive deer browsing leading to losses of understory components that are crucial to species like the snowshoe hare.

The most recent known release of hares in Pennsylvania was in the Laurel Highlands area of southwest Pennsylvania in the late 1990s-early 2000s. No official monitoring of these hares was conducted until 2014 when a small population of hares was found there. More survey efforts are needed to determine if hares remain in other areas of the Laurel Highlands, a high elevation area in Pennsylvania that historically supported snowshoe hare populations or other, more southern areas. With increased habitat management, this area could be a prime location to consider for focused snowshoe hare population management, especially considering the proximity to extant snowshoe hare populations in West Virginia.

Releases of wildlife in Pennsylvania are regulated by the Pennsylvania Game Commission (58 Pa. Code, § 137.1). The Commission may import and release wildlife taken from the wild for enhancement of endemic fauna. Commission Policy 2.30 (B) states, "The Pennsylvania Game Commission shall introduce species only when research deems it appropriate and feasible." Should reintroduction efforts be found to be appropriate, long term financial, public, agency, and cooperator support will be necessary. It is possible that areas where reintroductions occur may have to close to snowshoe hare hunting until populations become established.

HABITAT MANAGEMENT

Habitat is the most important manageable factor affecting population distribution and status of snowshoe hares at this time and is the area that managers should focus on to promote snowshoe hare populations. Hares in Pennsylvania likely use a wide variety of habitat types. Naturally occurring events such as wind, fire, and insect damage that serve to promote early successional habitat are ideal for snowshoe hare. Managers can use additional methods to increase habitat suitability for snowshoe hares including timber management, prescribed fire, shrub cutting, and invasive species management (Berg et al. 2012). In certain forest types, such as conifer stands with thick understory (i.e., spruce), hares may prefer mature as well as young stands. Managers should also seek to maintain deer populations at levels that allow regeneration of stems in disturbed stands (Brown 1984). Where deer are abundant, deer exclosure fencing should be considered to allow for stem regeneration that provides cover and forage for hares.

Hares are generally associated with high woody stem density which is typical of early successional forests that are created through disturbance. Managers should keep in mind that the method used, the scale of the treatment, and the overall forest composition influence tree regeneration. Fire and timber harvest, for example, vary in their influence on characteristics and timeframe of regeneration which have direct implications for snowshoe hares. Disturbance over large areas can be detrimental because these may locally wipe out hare populations until stand conditions become more suitable for hare, especially where hares are restricted to narrow ridgetops. Alternatively, small-scale or patchy disturbance patterns may benefit hares by increasing habitat connectivity, but if there is little suitable habitat otherwise, these small areas may lead to hares being more vulnerable to predation and serve as population sinks.

Timber Management

It is unlikely that a single management approach will be suitable in all areas or easily extracted from available snowshoe hare literature because Pennsylvania has more diverse habitats with varying regeneration rates. Specific timber management practices (i.e., clear-cut, shelterwood harvest), management location, stand composition, and timber sale size have the potential to have positive or negative impacts on hares. The effect on hares will be dictated by surrounding available habitat, regeneration time, and stand species composition. In Pennsylvania, clear cut stands are thought to reach suitable age for hare habitat between 5 and 15 years after harvest (Brown 1984), however, this timeframe likely depends on stand regeneration capabilities. The larger landscape should be examined and contain stands in optimal condition for hares to maintain hares across the landscape while regeneration occurs. The most beneficial landscape habitat matrix for hares is likely site specific (de Bellefeuille et al. 2001, Ferron et al. 1998). It was recommended by Brown (1984) to maintain 16% of a forest management unit (ca. 900 ha) in a 60-year rotation in the optimal age class for hares to maintain suitable habitat. The Young Forest Project recommends creating new young forest land every 5 years within a habitat matrix to maintain continuous habitat suitability over the landscape.

Despite most snowshoe hare habitat research occurring in other habitat types, we can use findings of other these other studies to make preliminary management recommendations. For example, uneven age stand management may help to reduce some of the immediate negative effects of clear-cutting for snowshoe hare. Residual habitat patches, areas not cut in a timber sale, may provide suitable cover for some hares to survive until forests regenerate depending on size, placement, and condition of the reserve patch at the time of harvest (de Bellefeuille et al. 2001). Larger residual areas may support more hares (Ausband and Baty 2005, Bull et al. 2005, Griffin 2004). Relatively small areas of tree removals, 10 m diameter in precommercial lodgepole pine in northeastern Oregon, were found to be a beneficial thinning technique for snowshoe hares (Bull et al. 2005). Additionally, making soft edges up to 100 m wide around timber blocks may help to improve hare habitat across the landscape until the stand regenerates to a suitable condition (Potvin et al. 2005b).

A matrix of diverse habitats in close proximity is likely ideal for hares. In mixed conifer forests in Montana, Griffin (2004) showed hares used thinned stands with 0.25 ha reserve patches making up about 20% of the entire stand were used more than thinned stands with no reserve areas. Areas with reserve stands, however, still experienced a decline in hare density when compared to untreated, control areas. Importantly, this evaluation was very soon after the timber management was completed. A follow up study to assess long term impact would have been very informative. Griffin (2004) suggested that larger reserves, or reserving a larger percent of the area, may help to better maintain hare abundance. However, another study in Montana showed hare populations increased more after treatment in unthinned stands than in thinned stands and the size of reserve areas (8% and 35%) did not influence the relative abundance of hares (Ausband and Baty 2005).

Another method to improve habitat suitability overall for hares, or to decrease the time of reoccupancy post-harvest, is leaving some thinned trees or branches, also known as coarse woody debris, on the ground (Bull et al. 2005, Sullivan and Moses 1986). The benefits of coarse woody debris varies by how it remains in the stand post-harvest (piles vs scattered), species, and size of the trees or branches. This technique has not always resulted in increased hare survival however (Cox et al. 1997) but may prove to be beneficial in hardwood dominated landscapes as are found in Pennsylvania. A good time for this type of management occurs during a crop tree release. The timing of re-entry for these releases to benefit hares in various Pennsylvania forest types is also a critical knowledge gap.

Two key issues when planning timber harvests are: 1) the proximity, scale, and percent cover of currently and soon to be suitable hare habitats across the landscape; and 2) long term versus immediate impacts of timber harvests (Ellsworth and Reynolds 2006). Studies should be designed to analyze the most beneficial matrix of timber management (including size, layout, and timing), forest composition, the size of reserve patches required to provide source population for repopulating treated areas, and barriers to snowshoe hare population connectivity. These studies will improve landscape level management.

Fire Management

Naturally occurring wildfire has been suppressed nationally for the past century which has changed the dynamics of our forest ecosystems. The significance of wildfire has yet to be determined as a factor affecting habitat suitability for hares, but it is likely to benefit hares in certain situations. Prescribed burns have been used to increase forest regeneration by opening up the forest canopy and removing competing vegetation, leading to regeneration with greater stem density. Continued use of prescribed burns is particularly beneficial to scrub oak habitat in Pennsylvania, which, though restricted in its own distribution, is used by snowshoe hares. Gigliotti et al. (*in prep*) found that hares avoid scrub oak stands that had been mown and burned 0-6 years prior. This study showed that at 7 years post-burning hares begin to select these treated scrub oak stands and survival of hares was positively associated with an increased amount of the older burned habitat.

It is likely that the benefits of fire to snowshoe hares are highly dependent on scale, intensity, and preexisting stand conditions (Buehler and Keith 1982). Before developing management schemes, careful consideration should be given to stand composition and associated serotiny of species, risk of high-intensity fires, as well as environmental variables such as elevation, aspect, and slope. Fire intensity has implications for which species of flora can regenerate the stand, and regeneration characteristics including stem density, which is especially of concern for snowshoe hare.

Habitat Management Recommendations

Some techniques have already been identified and implemented to improve habitat on SGLs including: creating mosaics of diverse forest age structure, combining commercial and noncommercial silvicultural treatments, establishing and maintaining early successional habitats, leaving coarse woody debris, increasing native vegetative species, prescribed fire to promote scrub oak regeneration, even aged management of aspen and northern hardwood, and uneven aged management of hemlock-northern hardwood stands that otherwise lack structural diversity. These techniques will also benefit habitat for other wildlife species including, but not limited to bobcat, cottontails, wild turkeys (*Meleagris gallopavo*), ruffed grouse (*Bonasa umbellus*), and woodcock (*Scolopax minor*). It is the recommendation of this plan to continue the use of these techniques as planned in SGL comprehensive management plans until such a time as specific components are identified that would most benefit snowshoe hares.

Minimum snowshoe hare habitat management should involve permanently maintained 20 ha (50 acre) patches of forest habitat with suitable understory conditions and coarse woody debris, but an even larger area may be better suited for Pennsylvania given the larger home ranges identified by Gigliotti (2016). Similarly, in Wisconsin larger forest stands were more likely to be occupied by hares (Buehler and Keith 1982). Slash piles, snags, and downed logs should be left after clearing to increase cover and foraging areas. Conifer and hardwood cover that is in the pole or saw log stage should be thinned to allow new growth of hardwood and evergreen seedlings which will provide both food and cover. Small clearing (8 m diameter) or lanes (3 m wide) should be cleared to allow new growth. If blocks or "islands" of potential valuable habitat exist outside of the established base habitat, vegetative travel lanes should be created to provide cover so hares can utilize the new habitat. Forest stands that will likely be heavily browsed by deer should be fenced. These recommendations will likely change as more habitat use information becomes available. A handout of snowshoe hare habitat management recommendations is available in Appendix 4 of this plan.

Partnerships

Coordination of sustainable forest management practices statewide, involving both private and public landowners and interest groups, would greatly benefit the snowshoe hare and many other early successional habitat dependent species. Major public agencies such as the Department of Conservation and Natural Resources, Bureau of Forestry; Pennsylvania Game Commission and Allegheny National Forest as well as private landowners (i.e., industrial forest landowners) could work together to better manage their properties for snowshoe hares and many other wildlife species to decrease distances between suitable habitats and promote dispersal and genetic flow between source populations. Understanding the nature of spatiotemporal dynamics and the role that they play in snowshoe hare cover and forage will be imperative to the effective management of the snowshoe hare in Pennsylvania.

MONITORING AND RESEARCH NEEDS

Although, the biology and ecology of snowshoe hares have been examined in northern boreal forests, there have been few studies in the northeastern United States. Information about the specific needs of hares in the region is needed because of differences in plant composition, topography, precipitation, temperature, snowfall and snow duration characteristics as well as our hares themselves when compared to boreal forest populations (Gigliotti 2016).

Monitoring

Common methods used to estimate hare abundance include live capture/mark-recapture, pellet counts, and winter snow track counts. Recently field cameras have also been used (Jensen et al. 2022). These techniques vary in labor intensity and expense and are appropriate in different situations. Pellet counts, winter snow track counts, fecal pellet DNA, and field cameras are all relatively inexpensive and can be done quickly across large spatial scales. These methods will likely be a valuable first step in further developing snowshoe hare research areas. Establishing an idea of relative abundance first, will help to identify areas where density assessments have the greatest probability of success.

To complete a fecal pellet plot, the plot must be cleared of pellets. Estimates from uncleared plots are unreliable because pellets persist on the ground for an unknown amount of time which could result in inflated estimates (Murray et al. 2005, Prugh and Krebs 2004). Plots can either be rectangular or circular. A Yukon regression equation can then be used for a population density estimate if rectangular plots are used (Krebs et al. 1987, 2001b, Mills et al. 2005). Should further investigation of Pennsylvania snowshoe hare population density and abundance find multiple, highly dense populations, this technique may be useful (Berg and Gese 2010). However, if the pellet plot method is found to be appropriate for use, degradation and defecation rates will need to be evaluated in Pennsylvania. Additionally, as all 3 lagomorph species in Pennsylvania are known to occupy the same habitats (Boyd 2015), DNA analysis of pellets in plots will likely be required to some extent.

Winter track count surveys involve an observer walking a preassigned linear transect of set length to determine relative abundance and habitat use of snowshoe hares (Burt et al. 2016). Disadvantages of winter track surveys are that they cannot be used to measure population density, are restricted to periods of suitable snow cover conditions, must occur during certain time frames after a snow event has occurred, snow conditions influence track identification, and winter conditions can prevent researchers from completing the surveys.

When working in smaller, site specific areas, live trapping hares and using mark-recapture techniques to estimate local population density (Mills et al. 2005, Rexstad and Burnham 1991) may be useful. When hare population densities are low, as is likely to be the case in many parts of Pennsylvania, estimates can be determined from a minimum number alive survey (Murray et al. 2002, Wirsing et al. 2002). Survival monitoring through VHF or GPS collars improves estimates from mark-recapture by establishing a known fate for animals that can't be recaptured (Murray et al. 2002).

Mark recapture studies also provide a means for estimating hunter harvest rates. In Pennsylvania, these mark recapture efforts would be most beneficial to compare WMUs with distinct habitat characteristics where hares are known to exist, such as WMUs 3B, 3C, and 3D and WMUs 2G, 2F, and 3A. While snowshoe hares are not frequently thought to be a species that would be sensitive to hunter harvest, hares in Pennsylvania may experience more pressure from disadvantages of mismatch and habitat fragmentation. The impact these factors have on overall resiliency of snowshoe hares in Pennsylvania is unknown. Concerns of hunters overharvesting hare populations locally have led to season changes and closure in Pennsylvania (Appendix 1), but hunter harvest rate is overall thought to be low (Gigliotti 2016).

Genetic analysis is an increasingly accessible and ideal approach for monitoring snowshoe hares as the technology has decreased in expense, and high defecation rates of the cryptic lagomorph species leaves plenty of genetic material behind. More research is needed to determine the feasibility of completing mark recapture assessments through DNA in fecal pellets.

Factors Limiting Hare Populations in Pennsylvania

Hare populations in the southern extent of their range are likely limited by the diverse group of generalist predators, patchy habitat, and duration of snow cover (Buehler and Keith 1982, Dolbeer and Clark 1975, Keith et al. 1993, Wirsing et al. 2002, Wolff 1980a, 1981). Snowshoe hare habitat is likely fragmented to a greater extent in Pennsylvania than more northern reaches of their range because of not only human development, but also available habitat types and inherent restriction to high elevations as they experience longer periods of snow cover. The impacts of this fragmentation on local hare populations should be evaluated through genetics. Predation is the most influential mortality factor for snowshoe hares; however, predation rates have been linked to habitat characteristics and patch size (Cox et al. 1997, Fies 1993, Gigliotti 2016, Hodges 2000b, Keith et al. 1993, Murray 2000, Wolff 1980a). More studies designed to 1) investigate predation rates in Pennsylvania with respect to habitat characteristics and unique winter phenotypes found in the Commonwealth, 2) analyze habitat and population connectivity for snowshoe hares, and 3) determine vegetation preferences and response to habitat management activities in Pennsylvania are needed.

Habitat Associations

There is limited information available about specific hare-habitat relationships in Pennsylvania (Brown 1984, Diefenbach et al. 2016, Scott and Yahner 1989). Further research is needed to guide management strategies. To develop defensible forest management practices, the interactive effects of stand structure, age, composition, and disturbance history on hare populations should be examined. Variables such as elevation, slope, or aspect might prove to be important, especially in a landscape like Pennsylvania's where these can change substantially over relatively short distances, because they influence snow depth and ultimately vegetation composition. Likewise, there is very little known about how hare abundance changes over time in these forests. For this reason, both manipulative and natural studies should be used to compare different regeneration scenarios. The results of this research and other initiatives will directly benefit habitat management for hares in Pennsylvania by allowing for the creation of occupancy models.

Food Resources

Food habits of hares have not been well explored in Pennsylvania, and no research has been conducted in the Commonwealth on the abundance or nutrition of hare diets. Although the relatively low densities of hares in this state suggest that the gross quantity of woody browse is unlikely to be a limiting factor, even during the winter, areas with better quality food resources may have larger hare populations. To test food/hare relationships, regional and age-specific variability in nutrients and forage chemical defenses should be examined, particularly as a function of hare density and browsing rates. Furthermore, the influence of summer nutrition on body condition, survival, and reproductive rates should be examined.

Geospatial Analysis and Models

A common tool for understanding and prioritizing landscape level habitat management in wildlife populations are geospatial models that predict or reflect distribution and abundance patterns. Hare habitat in Pennsylvania is different than other areas where habitat suitability index (HSI) models have been developed. Consequently, the development of an HSI specific to Pennsylvania would likely benefit our management of hares through better prioritized habitat management placement. Gap Analysis Project (GAP) using habitat type and age class has been used to predict the distribution of snowshoe hares in Wyoming and Colorado (Ellsworth and Reynolds 2006, Scott et al. 1993) and may be another valuable tool in Pennsylvania's management of the species. Dataset such as the National Land Cover Dataset, Land Fire, Lidar, and NOAA's data related to snow will all be valuable resources for broadly evaluating and monitoring Pennsylvania snowshoe hare habitats. While these approaches are certainly useful, more site specific, fine scale habitat characteristic information is necessary to produce finer-scaled estimates of hare distribution and density in Pennsylvania and to refine management recommendations.

SECTION VI. CONCLUSION

Snowshoe hares are a unique Pennsylvania wildlife resource and one of only approximately 20 vertebrate species in the world that has evolved a winter white transition as seasonal camouflage. Hares have no control over the timing of this transition and, regardless of future predictions of winter conditions, the variability that exists in Pennsylvania's annual snow cover durations poses threats to the resiliency of Pennsylvania's snowshoe hare population. To accommodate climatic variability, habitat conditions can be created through management to greatly reduce the mortality disadvantage experienced by snowshoe hares in mismatch. In addition, hares in Pennsylvania are exhibiting unique, more brown phenotypes which may further reduce the disadvantage experienced by hares with greater percent white coats in winter. This species will greatly benefit from increased understanding of general ecology, habitat use, and targeted habitat management across the landscape they inhabit.

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APPENDIX 1. HISTORY OF FRAMEWORK DATES, SEASON LENGTHS, AND DAILY BAG LIMIT FOR HUNTING SNOWSHOE HARE IN PENNSYLVANIA.

Year	Opening Date	Closing Date	# Hunting Days	Daily Bag	Possession Limit	Season Limit	Digest Comments/Footnotes
1915-16	1-Nov	30-Nov	26	3	NA	30	Limit of 15/ week
1917-18	1-Nov	15-Dec	39	3	NA	15	
1925-26	1-Nov	30-Nov	25	3	NA	15	
1928-29	1-Nov	30-Nov	14	3	NA	15	Thursday, Friday and Saturday only
	1-Dec	15-Dec	12		NA		
1929-30	1-Nov	30-Nov	26	3	NA	15	
1933-34	Nov 1, 2, 6, 7, 10, 11, 16, 17, 18, 20, 21, 22, 27, 28, 29, 30		16	3	NA	15	
1934-35	1-Nov	30-Nov	26	3	NA	15	
1935-36	CLOSED				NA	NA	
1936-37	CLOSED				NA	NA	
1937-38	1-Nov	13-Nov	12	2	NA	8	
1938-39	31-Oct	12-Nov	12	2	NA	8	
1939-40	CLOSED				NA	NA	
1940-41	CLOSED				NA	NA	
1941-42	CLOSED				NA	NA	
1942-43	31-Oct	14-Nov	13	2	NA	6	
1943-44	22-Nov	27-Nov	6	2	NA	6	
1944-45	15-Nov	22-Nov	6	2	NA	6	
1945-46	17-Dec	1-Jan	14	2	NA	6	
1946-47	16-Dec	1-Jan	15	2	NA	6	
1947-48	22-Dec	1-Jan	10	2	NA	6	
1948-49	20-Dec	1-Jan	12	2	NA	6	
1949-50	19-Dec	2-Jan	13	2	NA	6	
1950-51	25-Dec	1-Jan	7	2	NA	6	
1951-52	24-Dec	1-Jan	8	2	NA	6	
1952-53	1-Jan	10-Jan	9	2	NA	6	
1953-54	1-Jan	9-Jan	8	2	NA	6	
1954-55	1-Jan	8-Jan	7	2	NA	6	

1955-56	2-Jan	7-Jan	6	2	NA	6	
1956-57	29-Dec	5-Jan	7	2	NA	6	
1957-58	28-Dec	4-Jan	7	2	NA	6	
1958-59	27-Dec	3-Jan	7	2	NA	6	
1959-60	26-Dec	2-Jan	7	2	NA	6	
1960-61	26-Dec	2-Jan	7	2	NA	6	
1961-62	26-Dec	1-Jan	6	2	NA	6	Closed in Bedford, Blair, Cambria, Centre, Elk, Huntingdon, Jefferson, Somerset, and Warren
1962-63	26-Dec	1-Jan	6	2	NA	6	Closed in Bedford, Blair, Cambria, Centre, Elk, Forest, Huntingdon, Jefferson, McKean, Somerset, and Warren
1963-64	26-Dec	4-Jan	9	2	NA	6	
1964-65	26-Dec	2-Jan	7	2	NA	6	
1965-66	27-Dec	1-Jan	6	2	NA	6	
1966-67	26-Dec	2-Jan	7	2	NA	6	
1967-68	26-Dec	1-Jan	6	2	NA	6	
1968-69	26-Dec	4-Jan	9	2	NA	6	
1969-70	26-Dec	3-Jan	8	2	NA	6	
1970-71	26-Dec	2-Jan	7	2	NA	6	If poor hunting conditions prevail, the GC may extend the hare season to Jan. 9
1971-72	27-Dec	1-Jan	6	2	NA	4	If poor hunting conditions prevail, the GC may extend the hare season to Jan. 8
1972-73	26-Dec	30-Dec	5	2	NA	4	
1973-74	26-Dec	29-Dec	4	2	NA	4	
1974-75	Dec 26 Jan 3	Dec 28 Jan 4	5	2	NA	4	
1975-76	Dec 26 Jan 1	Dec 27 Jan 3	5	2	NA	4	

1976-77	Dec 31 Jan 7	Jan 1 Jan 8	4	2	NA	4	
1977-78	26-Dec	2-Jan	7	2	NA	4	
1978-79	26-Dec	1-Jan	6	2	NA	4	
1979-80	26-Dec	1-Jan	6	2	NA	4	
1980-81	26-Dec	1-Jan	6	2	NA	4	
1981-82	26-Dec	2-Jan	7	2	NA	4	
1982-83	27-Dec	1-Jan	6	2	NA	4	
1983-84	26-Dec	31-Dec	6	2	NA	4	
1984-85	26-Dec	29-Dec	4	2	NA	4	
1985-86	26-Dec	4-Jan	9	2	4	NA	
1986-87	26-Dec	3-Jan	8	2	4	NA	
1987-88	26-Dec	2-Jan	7	2	NA	4	
1988-89	26-Dec	31-Dec	6	2	4	NA	
1989-90	26-Dec	30-Dec	5	2	4	NA	
1990-91	26-Dec	1-Jan	6	2	4	NA	
1991-92	26-Dec	1-Jan	6	2	4	NA	
1992-93	26-Dec	2-Jan	7	2	4	NA	
1993-94	27-Dec	1-Jan	6	2	4	NA	
1994-95	26-Dec	31-Dec	6	2	4	NA	
1995-96	26-Dec	30-Dec	5	2	4	NA	
1996-97	26-Dec	1-Jan	6	2	4	NA	
1997-98	26-Dec	1-Jan	6	2	4	NA	
1998-99	26-Dec	2-Jan	7	2	4	NA	
1999-00	27-Dec	1-Jan	6	2	4	NA	
2000-01	26-Dec	30-Dec	5	2	4	NA	
2001-02	26-Dec	1-Jan	6	1	2	NA	
2002-03	26-Dec	1-Jan	6	1	2	NA	
2003-04	26-Dec	3-Jan	8	1	2	NA	
2004-05	27-Dec	1-Jan	6	1	2	NA	
2005-06	26-Dec	31-Dec	6	1	2	NA	
2006-07	26-Dec	1-Jan	6	1	2	NA	
2007-08	26-Dec	1-Jan	6	1	2	NA	
2008-09	26-Dec	1-Jan	6	1	2	NA	
2009-10	26-Dec	1-Jan	6	1	2	NA	

2010-11	27-Dec	1-Jan	6	1	2	NA	
2011-12	26-Dec	31-Dec	6	1	2	NA	
2012-13	26-Dec	1-Jan	6	1	2	NA	Season closed in all WMUs except 2F, 2G, & 3A
2013-14	26-Dec	1-Jan	6	1	2	NA	All WMUs except 3B, 3C, & 3D
	26-Dec	28-Dec	3			NA	WMUs 3B, 3C, & 3D
2014-15	26-Dec	1-Jan	6	1	3	NA	All WMUs except 3B, 3C, & 3D
	26-Dec	29-Dec	3			NA	WMUs 3B, 3C, & 3D
2015-16	26-Dec	1-Jan	6	1	3	NA	All WMUs except 3B, 3C, & 3D
	26-Dec	29-Dec	3			NA	WMUs 3B, 3C, & 3D
2016-17	26-Dec	31-Dec	6	1	3	NA	Statewide
2017-18	26-Dec	31-Dec	6	1	3	NA	Statewide
2018-19	26-Dec	31-Dec	6	1	3	NA	Statewide
2019-20	26-Dec	1-Jan	6	1	3	NA	Statewide
2020-21	26-Dec	1-Jan	6	1	3	NA	Statewide
2021-22	27-Dec	1-Jan	6	1	3	NA	Statewide
2022-23	26-Dec	31-Dec	6	1	3	NA	Statewide

Note: Our earliest season record is 1915. In 1915 hunters could harvest 3 hares per day, 15 a week and 30 a season from Nov. 1-30. From 1917-1934 the daily bag was 3 and 15 per season. Seasons varied from 14 to 36 days in November to mid-December.

APPENDIX 2. HISTORY OF HARE RELEASE AND REINTRODUCTION EFFORTS BY YEAR IN PENNSYLVANIA.

Year	Hares Purchased & Released	Year	Hares Purchased & Released
1918	64	1950	0
1919	514	1951	0
1920	7540	1952	0
1921	2681	1953	0
1922	582	1954	0
1923	556	1955	0
1924	2251	1956	0
1925	2132	1957	135
1926	0	1958	474
1927	0	1959	651
1928	0	1960	587
1929	0	1961	500
1930	2037	1962	459
1931	1504	1963	484
1932	2003	1964	0
1933	0	1965	0
1934	0	1966	0
1935	0	1967	0
1936	0	1968	0
1937	0	1969	127
1938	0	1970	600
1939	0	1971	600
1940	0	1972	0
1941	0	1973	0
1942	0	1974	445

1943	0	1975	1000
1944	0	1976	522
1945	0	1977	887
1946	0	1978	1268
1947	0	1979	1168
1948	0	1980	1015
1949	274	1981	0

Total 33060

APPENDIX 3. GAME COMMISSION ADMINISTRATIVE REGIONS

NE-northeast- Bradford, Carbon, Columbia, Lackawanna, Luzerne, Monroe, Montour, Northumberland, Pike, Sullivan, Susquehanna, Wayne, Wyoming

SE-southeast- Berks, Bucks, Chester, Dauphin, Delaware, Lancaster, Lebanon, Lehigh, Montgomery, Northampton, Philadelphia, Schuylkill

NC-northcentral- Cameron, Centre, Clearfield, Clinton, Elk, Lycoming, McKean, Potter, Tioga, Union

SC-southcentral- Adams, Bedford, Blair, Cumberland, Franklin, Fulton, Huntingdon, Juniata, Mifflin, Perry, Snyder, York

NW-northwest- Butler, Clarion, Crawford, Erie, Forest, Jefferson, Lawrence, Mercer, Venango, Warren

SW-southwest- Allegheny, Armstrong, Beaver, Cambria, Fayette, Greene, Indiana, Somerset, Washington, Westmoreland

APPENDIX 4. SNOWSHOE HARE HABITAT RECOMMENDATIONS FOR PENNSYLVANIA

Size and Location of Managed Areas: In Pennsylvania, snowshoe hares are restricted to areas with longer durations of snow cover such as northern regions as well as high elevations (>1,500ft). The most important habitat component for hares is cover. They require "base cover" and "travel cover." Base cover, the dense (ideally coniferous) cover should have low horizontal visibility (5,000-13,000 stems per acre) and be at least 8 to 15 feet tall to provide cover from aerial predators. Travel cover can be thinner (1,000 to 3,000 stems per acre) and more mature forest. In area managed for snowshoe hare the following breakdown of habitat types is recommended: travel cover (45%), base cover (30%), herbaceous (10%), and regeneration (15%). Managers should focus on landscapes of at least 500 acres in otherwise suitable areas (duration of snow cover) for snowshoe hare targeted habitat management. This scale allows hare populations enough area to persist and reoccupy regenerating stands despite pressure from hunters and predators.

Suitable snowshoe hare habitat should have interspersed suitable cover throughout the managed area because snowshoe hares generally do not travel far from cover. Many species of vegetation with dense growth forms are ideal, but also regenerating forests and conifers with branches close to the ground. Creating small mechanical (bull dozer, chain saw) disturbances of 1 to 5 acres through a matrix of habitat will benefit hares. Disturbance initially eliminates or greatly reduces suitability of habitat for hares and it may take years for hares to reoccupy stands where especially large-scale management has occurred, even when it is designed for hares. Consequently, a habitat management matrix across the landscape is recommended where areas are treated at different times and at appropriate spatial scales. Disturbance should be created every 5 to 10 years in the managed matrix so that habitat suitability throughout the landscape is maintained.

Plant Conifers and Evergreens: Conifers or evergreens benefit snowshoe hares especially in winter. Plantings should occur in clusters to create patches of cover across the landscape. Recommended spacing between plantings varies by species. If the trees are close together, they will provide cover sooner, but will also need to be thinned sooner. Species of spruce and fir, white pine, eastern hemlock, rhododendron, and mountain laurel are likely beneficial to hares in Pennsylvania. In areas where white-tailed deer are densely populated, managers may consider fencing conifer plantings to protect them from over-browsing.

Timber Harvest: Considering the relatively low density and abundance of conifer species in Pennsylvania, timber harvests are an effective and economical means of creating suitable hare habitat. Typically, harvested timber areas will return to a suitable condition for hares within 10-20 years post treatment, however, this timeframe will vary due to local conditions and stand composition. Cuts should ensure that adequate light reaches the forest floor to promote dense regeneration. Aspen stands should be released. Stands whose understories have been overrun by fern or other similar regeneration suppressants should be chemically or mechanically managed to promote sapling regeneration. In areas where white-tailed deer are densely populated, managers may consider fencing timber harvested areas to promote regeneration.

Manage Edge Habitats: Cutting a forest edge is one way to improve habitat as it increases both food and cover. Whenever possible remove vegetation that is less beneficial to wildlife and keep woody species that provide the best food and cover. Any cut material can be used to build brush piles or let lie on the landscape providing additional cover for hares.

Two methods can be used. Gradually layering the height of vegetation to decrease from the tallest trees against the more mature forest to the shortest plants at the very edge of the forest will increase plant diversity and should benefit hares. Another way to increase diversity in forest edges is to cut all the edge vegetation for a width of 50-100 feet. Then allow this cut area to regenerate and provide food and cover at a variety of heights. Also consider planting some trees and shrubs within the newly regenerating edge.

Prescribed Fire: Prescribed fire may be used to increase density of regenerating stems and is particularly beneficial to scrub oak or barrens management. Regenerating scrub oak stands likely will not reach suitable conditions for snowshoe hares until at least 7 years post treatment in Pennsylvania, especially those areas that are mowed before the initial burn. Though mowing vegetation for prescribed burn preparation is often essential for safety, mowing full burn units resets the vegetation and prolongs the period before hares will reoccupy the area. Reducing mowed acres while ensuring that burns can still be done safely should be explored.

Brush Piles and Coarse Woody Debris: In areas with otherwise suitable habitats or regenerating habitats, brush piles may be used to provide additional cover. Use rocks or the largest logs to create a base for the brush pile, so that snowshoe hares and other wildlife can get underneath. On this foundation place smaller woody materials, such as tree limbs, to create a pile. Taller piles last longer than shorter piles. Place brush piles near sites where food is available, but cover is otherwise limited. Space them so that cover is dispersed at least 50 yards apart. Overtime, the brush will settle and decays, which decreases their value as protective cover. Maintain brush piles until more permanent natural cover can be established. It is possible that even felling some logs to let them lie as woody debris may benefit hares. Tree felling has the additional benefit of opening the canopy and increasing regenerating stem density.

For more information regarding snowshoe hare habitat management, please refer to the Habitat Management Recommendations section of the Pennsylvania Snowshoe Hare Management Plan and PGC's Habitat Manual.

APPENDIX 5. SUMMARY OF PUBLIC COMMENTS

ACKNOWLEDGEMENTS

The snowshoe hare is a unique species in Pennsylvania whose management and conservation has a long history. This management plan was necessitated by an observed reduction in distribution statewide and a general paucity of information related to this game species. We thank the many biologists, partners, and participants who contributed to the development of this management plan and who continue to provide support for the conservation of the snowshoe hare in Pennsylvania. All data are subject to revisions.

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