

Tree Recruitment Limitation by Introduced Snowshoe Hares, *Lepus americanus*, on Kent Island, New Brunswick

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Species introductions often have negative consequences for native plant and animal communities of islands. Herbivores introduced to islands lacking predators can attain high population densities and alter native plant communities by selective consumption of palatable plants. We examined the legacy of the 1959 introduction of Snowshoe Hares (*Lepus americanus*) to Kent Island, New Brunswick, by reconstructing a history of tree recruitment on Kent Island and on nearby Outer Wood Island, which lacks Snowshoe Hares. Tree-ring records show pronounced recruitment peaks associated with farm abandonment in the 1930s for Kent Island and in the 1950s for Outer Wood Island. Following the introduction of Snowshoe Hares to Kent Island, tree recruitment plummeted and has remained low ever since. In contrast, trees continued to establish throughout the latter 20th century on Outer Wood Island. The high rates of seedling mortality on Kent Island associated with Snowshoe Hare browsing coupled with high rates of canopy tree mortality threaten to degrade severely the forest of this important seabird nesting sanctuary.

Key Words: Snowshoe Hare, *Lepus americanus*, invasive species, tree recruitment limitation, Kent Island seabird sanctuary, New Brunswick.

Introduced herbivores often cause great damage to island ecosystems and potentially result in plant species extinction (Van Vuren and Coblentz 1987; Moran 1996; Coblentz 1990). The absence of significant predators allows introduced herbivores to reach high population densities and exert intense grazing pressure on poorly defended plants (Krebs et al. 2002; Donlan et al. 2002). Because woody plants are most vulnerable to browsing during their early stages of development and growth (Clark et al. 1999; Liang and Seagle 2002), intense browsing may limit tree regeneration and allow less palatable species to proliferate (Rossow et al. 1997; Heinen and Currey 2000). Shifts in plant species dominance resulting from intense herbivory have been demonstrated in tropical, temperate, and boreal island ecosystems and indicate the community-level impacts of herbivore introductions or predator removal from islands (McLaren and Peterson 1994; Chouinard and Filion 2001; Terborgh et al. 2001).

In 1959, Snowshoe Hares (*Lepus americanus*) colonized Kent Island, an 80-hectare island in the Bay of Fundy, New Brunswick, following intentional introduction to Hay Island, a nearby island connected to Kent Island at low tide (C. Huntington, personal communication). Subsequently, estimates of the hare population in various years have ranged between 50 and 500 individuals based on mark-recapture techniques (N. Wheelwright, Bowdoin College; personal communication). Snowshoe Hares are generalist herbivores that feed on a variety of grasses and shrubs during the summer, but on tree bark, foliage, and twigs during the winter (de Vos 1964). Diet selection studies have demon-

strated that hares preferentially browse deciduous species, but may rely on conifers during winter or during periods of high population density if preferred forage is not available (Aldous and Aldous 1944; de Vos 1964; Parker 1984). Snowshoe Hares often avoid White Spruce (*Picea glauca*) when other browse is available, presumably because of high levels of camphor in the foliage (Sinclair et al. 1988; Rangen et al. 1994; Heinen and Currey 2000). The concentration of secondary compounds in vegetation may also influence diet selection (Fox and Bryant 1984; Rousi 1997; Rodgers and Sinclair 1997). Paper Birch (*Betula papyrifera*) saplings, for example, can effectively deter Snowshoe Hare browsing with high concentrations of secondary compounds (Bryant 1981).

Although Snowshoe Hare browsing of trees is generally limited to heights less than 1 m, hares are important herbivores in boreal forests, and considerable damage to seedlings and saplings in forest plantations has been attributed to hares (Aldous and Aldous 1944; Holl and Quiros-Nietzen 1999; Rao et al. 2003). Based on Kent Island's high population of Snowshoe Hares and on observations of intense browsing of tree seedlings, we hypothesized that browsing by hares effectively halted tree recruitment since their introduction in 1959. To document the impacts of hare browsing on Kent Island, we reconstructed a tree recruitment history based on tree-ring records for Kent Island and for nearby Outer Wood Island, which lacks Snowshoe Hares. We also compared current tree recruitment rates on the two islands by estimating seedling and sapling densities in randomly located plots.

Study Area

Kent Island is at the southern end of the Grand Manan archipelago in the Bay of Fundy, New Brunswick (44°35'N, 66°46'W). The island is an important nesting area for Leach's Storm Petrel (*Oceanodroma leucorhoa*) and Savannah Sparrow (*Passerculus sandwichensis*). Since 1935, Bowdoin College of Brunswick, Maine, has operated a biological station on Kent Island. In 1959, Snowshoe Hares were intentionally introduced to nearby Hay Island, and soon thereafter crossed the tidally exposed land bridge to Kent Island. Hare populations have persisted on both islands since that time. Muskrats (*Ondatra zibethicus*) were introduced earlier in 1941 (Huntington 1956). The forest community contains Balsam Fir (*Abies balsamea*), White Spruce, Red Spruce (*Picea rubens*), Yellow Birch (*Betula allegheniensis*), Heart-leaved Birch (*Betula cordifolia*), and Mountain Ash (*Sorbus americanus*). A mixed forest dominated by White Spruce and Balsam Fir covers approximately two-thirds of the northern half of the island, whereas grassland covers the southern half of the island. In the early 20th century, much of the grassland was either cultivated or used for hayfield and pasture (Gleason 1937). Today seedlings and saplings of any tree species are rare on Kent Island. Those that are found show a pronounced browse line up to 60 cm in height. Canopy trees are suffering high rates of mortality for unknown reasons, and the gaps formed by tree death and windthrow are rapidly colonized by Red Raspberry (*Rubus idaeus*) and Wood Fern (*Dryopteris spinulosa*) rather than trees.

Outer Wood Island (44°37'N, 66°49'W) is approximately 6 km northwest of Kent Island. Forest covers its central area, which is surrounded by grasslands similar to Kent Island. White Spruce and Red Spruce are the dominant canopy species with Balsam Fir, Yellow Birch, and Mountain Ash important locally. Outer Wood Island lacks Snowshoe Hares, but, like Kent Island, has a large introduced Muskrat population. Outer Wood Island was used for sheep pasture throughout the early and middle 20th century (Ingersoll 1991).

Methods

In March 2002, an attempt to eradicate the Snowshoe Hare population on Kent Island was initiated, which resulted in a reasonably accurate population estimate. Eradication efforts have continued up to the present. Prior to the attempted hare eradication, we counted hare pellets in 132 plots (1 m × 1 m) randomly located within forests on Kent Island to document hare distribution on the island, as described by Krebs et al. (2001).

To describe the composition of the forests, we examined trees occurring along the length of nine randomly located 2 m × 50 m transects on each island. Canopy trees were identified to species and their diameter-at-breast-height (DBH) was recorded. To develop tree-recruitment histories, we collected increment cores

from White Spruce, Red Spruce, and Balsam Fir trees in nine randomly chosen circular plots on each island. Within each plot, the ten trees nearest the center and greater than 5-cm DBH were cored at a height ranging between 30 and 50 cm from the ground. The species identity and DBH were recorded for all cored trees. We also took advantage of numerous treefalls that occurred during the winter of 2000-2001 by collecting basal discs from 33 trees. The discs and cores were sanded smooth, and the rings were counted using a binocular Leica dissecting microscope and a Velmex tree-ring measuring system. To account for early growth of the trees, we added five years to the tree-age estimates of basal discs and ten years to the estimates of increment cores (DesRochers and Gagnon 1997; Parment et al. 2000).

On both islands, established seedlings and saplings were quantified in three 78.5-m² (i.e., 5-m radius) sample plots, located 25 m apart along each 50-m transect. Seedlings were defined as any stem less than 1 m in height and saplings were defined as stems greater than 1 m in height and having a DBH less than 5 cm. Height measurements and extent-of-browsing estimates were recorded on isolated White Spruce seedlings on Kent Island and Outer Wood Island.

Results

The density of Snowshoe Hare pellets on Kent Island was 47.1 (± 6.2)/m² and ranged between 6 and 110 pellets/m². Pellet densities were not significantly correlated with seedling abundances. No pellets were found on Outer Wood Island. After one month of hunting in early 2002, 275 Snowshoe Hares had been killed on Kent Island, indicating a minimum density of 3.43 hares per hectare. The hare population was not eliminated during this period of hunting, and the population has subsequently rebounded, although not to its maximum level. Eradication efforts are scheduled to continue in winter 2005-2006.

The recruitment histories of canopy trees of the two islands show patterns of reforestation following farm abandonment and cessation of livestock grazing in the mid-20th century (Ingersoll 1991). Consistent with the timing of land-use change, peak tree recruitment occurred during the 1930s on Kent Island and during the 1950s on Outer Wood Island (Figure 1). On Kent Island, tree recruitment remained high through the 1940s but declined precipitously in the 1950s, whereas tree recruitment on Outer Wood Island was relatively high throughout the 1960s and 1970s, two decades after its peak (Figure 1).

The abundances of saplings and established seedlings (i.e., > 2 yrs old) reveal the disparity in recent tree recruitment on the two islands. Sapling abundance of all tree species was much greater on Outer Wood Island than on Kent Island (OWI = 29.4 ± 13.3; KI = 0.1 ± 0.1; df = 43; t = 2.71; P = 0.01) (Figure 2). The abundance of established seedlings was similarly

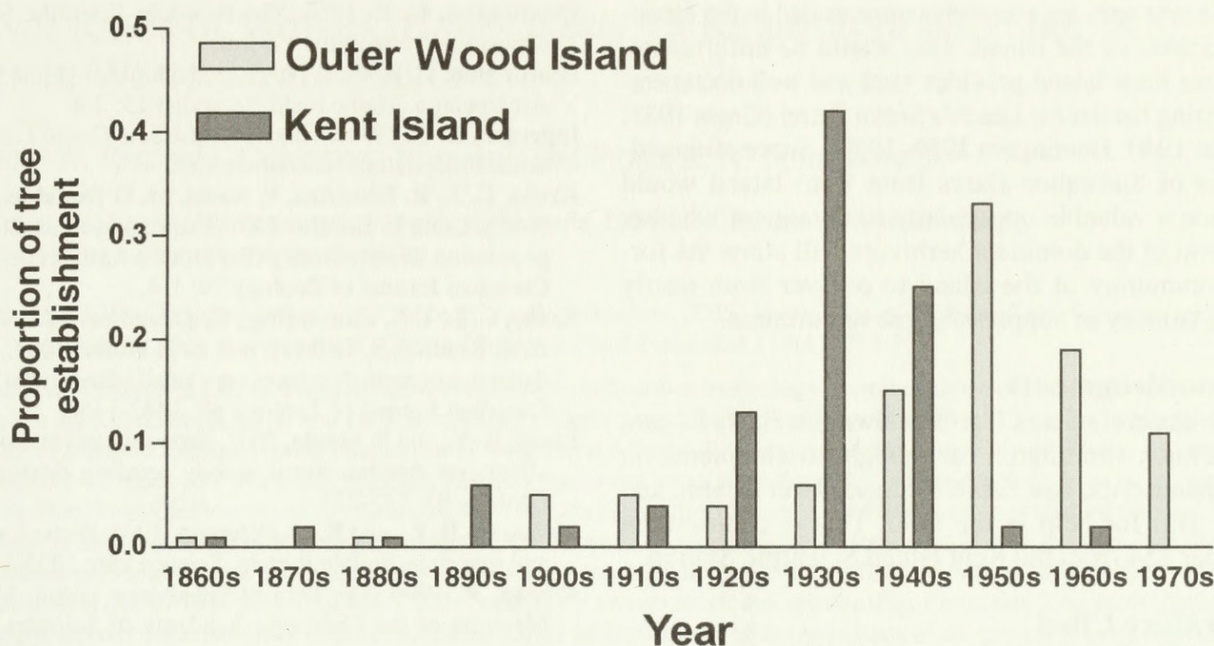


FIGURE 1. Tree recruitment history for Kent Island and Outer Wood Island, New Brunswick derived from tree-ring records. Data given as the proportion of the total number of canopy trees cored for each decade between 1860 and 1980. Snowshoe Hares were introduced to Kent Island in 1959.

much greater on Outer Wood Island than on Kent Island ($OWI = 14.1 \pm 3.5$; $KI = 0.3 \pm 0.2$; $df = 43$; $t = 3.17$; $P = 0.003$). All of the 58 spruce seedlings and saplings examined on Kent Island showed visible signs of browsing. Of these 58 trees, 40 were less than one meter in height, and 18 between 1 and 2 m tall. Of the 40 less than 1 m in height, 24 were missing their apical meristem, whereas of the 18 ranging between 1 and 2 m in height, only one had its apical meristem browsed. On Outer Wood Island, apical stems were present on all 60 of the seedlings sampled, and little or no evidence of browsing was present.

Discussion

The history of tree recruitment on Kent Island and Outer Wood Island demonstrates the long-term, negative effects of intense Snowshoe Hare browsing on tree recruitment in an island ecosystem lacking mammalian predators. The precipitous decline of tree recruitment on Kent Island during the 1950s suggests that the Snowshoe Hare population increased rapidly and that few established tree seedlings survived the onset of hare browsing. While we have no sequential estimates of the hare population density, the lack of saplings and established seedlings suggests that hares were numerous enough to limit tree recruitment severely throughout the past forty-five years. Sustained browsing pressure can cause a shift toward less palatable species (McLaren and Peterson 1994; Heinen and Currey 2000; Terborgh et al. 2001). Because all tree species on Kent Island are palatable to Snowshoe Hares, a shift to less palatable species would result in loss of forest. Currently as canopy trees die, Wood Fern and Red Raspberry replace them. A dense cover of Wood

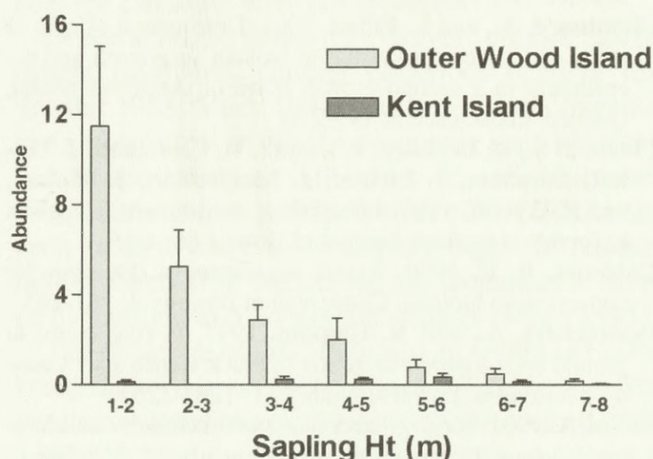


FIGURE 2. Tree sapling abundance for Kent Island and Outer Wood Island, New Brunswick, given for height classes.

Ferns probably also limits tree recruitment as Wood Ferns have been shown to limit the photosynthetic capabilities of coniferous seedlings (Starostina 1988).

This study contributes to a growing body of research documenting pronounced ecosystem-level consequences of herbivore introductions to islands (e.g., Van Vuren and Coblenz 1987; Donlan et al. 2003). Because Snowshoe Hares are the only mammalian herbivores that browse trees on Kent Island, they are responsible for all of the browsing damage since their introduction. If the current hare eradication efforts are not successful, it is likely that this forest will become severely degraded in the future as the canopy trees reach senescence. This outcome may negatively affect the suitability of the island as nesting habitat for Leach's Storm Petrels,

whose nest sites are currently concentrated in the forested portions of the island. This would be unfortunate, because Kent Island provides vital and well-documented nesting habitat for Leach's Storm Petrel (Gross 1935; Griffin 1940; Huntington 1956, 1959). Successful eradication of Snowshoe Hares from Kent Island would provide a valuable opportunity to document whether removal of the dominant herbivore will allow the forest community of the island to recover from nearly half a century of suppressed tree recruitment.

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