Eradication of an ecosystem engineer

In 1959, Wesley Ingalls captured a dozen snowshoe hares (*Lepus americanus*; Figure 1) near his home on Grand Manan Island, New Brunswick, Canada. He asked his nephew, Junior, to help transport them to Hay Island, one of the outermost islands in the Bay of Fundy. There, the two men released the hares and waited for them to multiply. Trapping hares would give them "something to do in winter when we weren't fishing", Junior, now 88 (WebFigure 1), told me in 2015 – and their families could supplement their incomes by selling hares at $3 a head to hunting clubs on the mainland.

Sure enough, the hares quickly proliferated, producing four young per litter and four litters per year. But, as with many biological introductions, this one had unintended consequences. For the next half century, tree recruitment was reduced to virtually zero on Hay Island and neighboring Kent Island, which is connected to Hay at low tide. After numerous failed attempts, snowshoe hares were finally eradicated from the islands in 2007, allowing us to take stock of their capabilities as plant architects and ecosystem engineers.

The original hares "ran over to Kent in the first snowstorm, when the tide was down", Junior said. Compared to the mainland, the islands' forests were depauperate, with only eight tree species: red and white spruce, balsam fir, tamarack, heart-leafed and yellow birch, mountain maple, and mountain ash (for scientific names of species mentioned in this article, see WebTable 1). But seedlings and saplings provided abundant browse for the hares, which moved through the understory like lawn mowers. There were no vertebrate competitors on the archipelago other than muskrats, which prefer herbaceous plants, and no predators other than bald eagles and the occasional wintering snowy owl, neither of which can capture hares in dense cover.

As it turned out, the busy fishermen never found the time to trap a single hare. Soon there were two dozen hares, then two hundred, then triple that. In 1961, Junior went out to Hay to cut young balsam firs for his herring weir. Unlike previous harvests, "this time the forest never grew back". Instead, it was replaced by a thicket of wood fern and raspberry, whose dense root masses and shade prevented establishment of any other plants. By the mid-1980s, winter storms began to knock down Kent Island's aging canopy trees at an accelerating pace (Peterson *et al.* 2005). The islands' forests were becoming transformed into open tangles (WebFigure 2).

Huddled together in their open nests, with soft brown fur and white blazed foreheads, newborn snowshoe hares are – if I may use the word – adorable (Figure 1 inset). The species is native to North America, although the hares had never managed to colonize the remote islands of the Bay of Fundy on their own. But with population densities exceeding four individuals per hectare – roughly 3–50 times the densities found on the adjacent Maine mainland (Homyack *et al.* 2006) – these hares threatened the habitat of several forest-breeding bird species, including Leach's storm-petrels, which have been monitored continuously at the Bowdoin Scientific Station on Kent Island since 1954 (Mauck *et al.* 2004).

Not only did the hares cause a major shift in the species composition of the islands' forests by preventing seedling recruitment, they also modified the morphology of the few saplings that managed to survive. Incessant browsing on the growing tips of young white spruces shaped them into alpine cushion plants. I was initially skeptical of locals' claims that the hares climbed trees in winter when food was scarce, until I noticed clipped twigs, gnawed bark, and white fur on branches 2 m above the ground. Hare droppings occurred at average densities of 50 per square meter throughout most of the islands (Peterson *et al.* 2005). Two years after we fenced in several 4-m^2 exclosures, seedling densities inside the protected plots exceeded 150 per square meter, compared to 0 per square meter outside (Figure 2). Comparisons with nearby hare-free islands also confirmed that it was snowshoe hares, not the Bay of Fundy's salty fog or frigid temperatures, that had arrested recruitment of woody plants for decades.

Figure 1. *Adult snowshoe hare browsing the lower branches of a white spruce. Inset: newborn snowshoe hare.*

Something had to be done to control the snowshoe hares. Authorities on pest control recommended poisons, viruses, antifeedants, falconers, traps, lynx, dogs, and professional hunters. Although viruses and poisons have been effective in numerous island pest removals (Krajik 2005), their application requires extensive permitting and jeopardizes non-target species. Introducing exotic predators such as lynx to control an exotic herbivore seemed ill advised, particularly given the presence of a seabird colony.

So, in 1998, we began hunting and trapping with permission from the New Brunswick government and the help of Junior's son and grandchildren. Two years later, the hare population had rebounded to its former size. We tried again in 2002–3, this time recruiting hunters from Maine and New Brunswick. Although one hunter proudly announced, "I got the last ones!", the hares rebounded again. In desperation, I consulted the Chief of Vertebrate Pest Control of New Zealand, a department whose wildlife managers are famous for eliminating problem species from islands worldwide (Krajik 2005). Her email response was terse. "Eradicating the hares using hunters and dogs from 70 ha ought to be trivial. You're not trying very hard."

Figure 2. *Seedlings of red spruce, balsam fir, heart-leafed birch, and mountain ash inside a fenced 4-m^2 snowshoe hare exclosure erected in 1990.*

Fair enough. Starting in January 2006, with a grant from the Davis Conservation Foundation, we tried harder. Thirty-nine traps baited with apples and positioned at 100-m intervals throughout the archipelago were operated continuously, in all seasons. Twelve hunting expeditions, three of them aided by dogs, scoured the islands. Relentless pressure proved to be key: the last hare was finally trapped on Kent Island in April 2007 (WebFigure 3).

The response of the plant community to the elimination of an introduced keystone herbivore was immediate and dramatic. Millions of tree seedlings now blanket the forest floor. Young heart-leafed birch trees, already 4 m tall, are crowding out wood fern and raspberry. Released from decades of browsing, white spruce "cushions" have emerged from their defensive crouch and bolted skyward (WebFigure 4). Woody plants, including two species new to the island (quaking aspen and shadbush), are invading the open fields, which will now have to be mowed to maintain breeding habitat for savannah sparrows, whose ecology has been studied since the 1960s (WebFigure 5) (Wheelwright *et al.* 2008). The eradication of the hares was especially timely because in 2008, an outbreak of bark beetles decimated many of the island's remaining mature white spruces.

Like islands worldwide, Kent Island has seen its share of introduced species. Nearly one-quarter of its 280 plant species are European in origin, most of them grasses or herbs accidentally brought over with feed for the sheep and cattle that grazed the island throughout the 19th century. But none had the impact that a dozen snowshoe hares had during their 47-year reign. We don't yet know how the islands' ecology will change now that they are gone – proposals from *Frontiers* readers to conduct research on Kent Island are welcome. However, the boreal forests that have long provided nesting habitat for birds and other animals are now able to recover and flourish.

Supporting Information

Acknowledgements and references, as well as additional web-only materials, may be found with the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1221/suppinfo

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NT Wheelwright – Supporting information

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WebReferences

Homyack JA, Harrison DJ, Litvaitis JA, and Krohn WB. 2006. Quantifying densities of snowshoe hares in Maine using pellet plots. *Wildlife Soc B* **34**: 74–80.
Krajik K. 2005. Winning the war against island invaders. *Science* **310**: 1410–13.
Mauck RA, Huntington CE, and Grubb TC. 2004. Age-specific reproductive success: evidence for the selection hypothesis. *Evolution* **58**: 880–85.
Peterson TS, Uesugi A, and Lichter J. 2005. Tree recruitment limitation by introduced snowshoe hares, *Lepus americanus*, on Kent Island, New Brunswick. *Northeast Nat* **119**: 569–72.
Wheelwright NT, Freeman-Gallant CR, and Mauck RA. 2008. Asymmetrical incest avoidance in the choice of social and genetic mates. *Anim Behav* **71**: 631–39.

WebFigure 1. *Grand Manan fisherman Junior Ingalls.*

WebFigure 2. *Petrel Path, formerly a dense spruce-fir forest and the site of a 61-year study of Leach's storm-petrels on Kent Island, is now an open wood fern–raspberry thicket.*

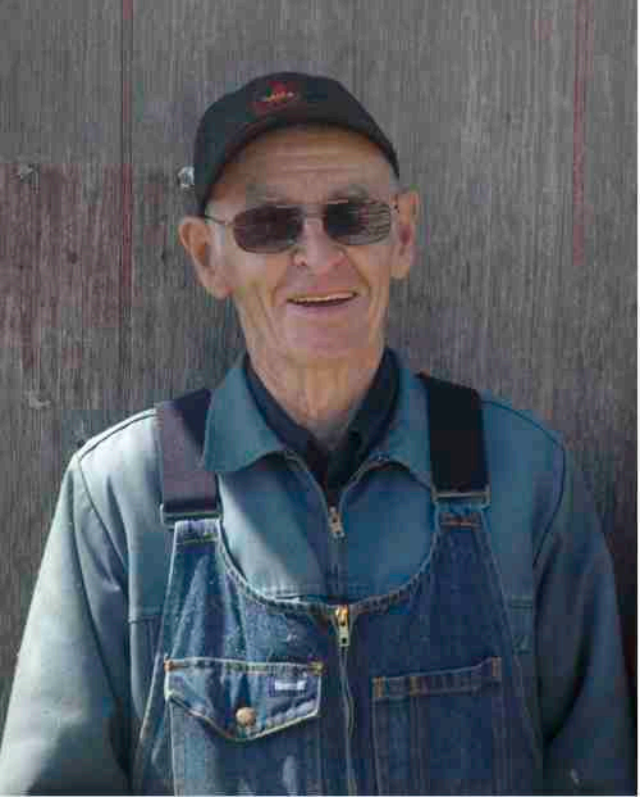
WebFigure 3. *Attempts to eradicate snowshoe hares on Kent Island were made in 1998–9 and 2001–2, but sustained hunting and trapping pressure in 2006–7 were what finally proved to be successful.*

WebFigure 4. *White spruce sapling, decades old, finally released from snowshoe hare browsing in 2007.*

WebFigure 5. *After eradication of hares in 2007, heart-leafed birch and other woody plant species are colonizing the forests and fields of Kent Island.*
Photo credit: P Cunningham

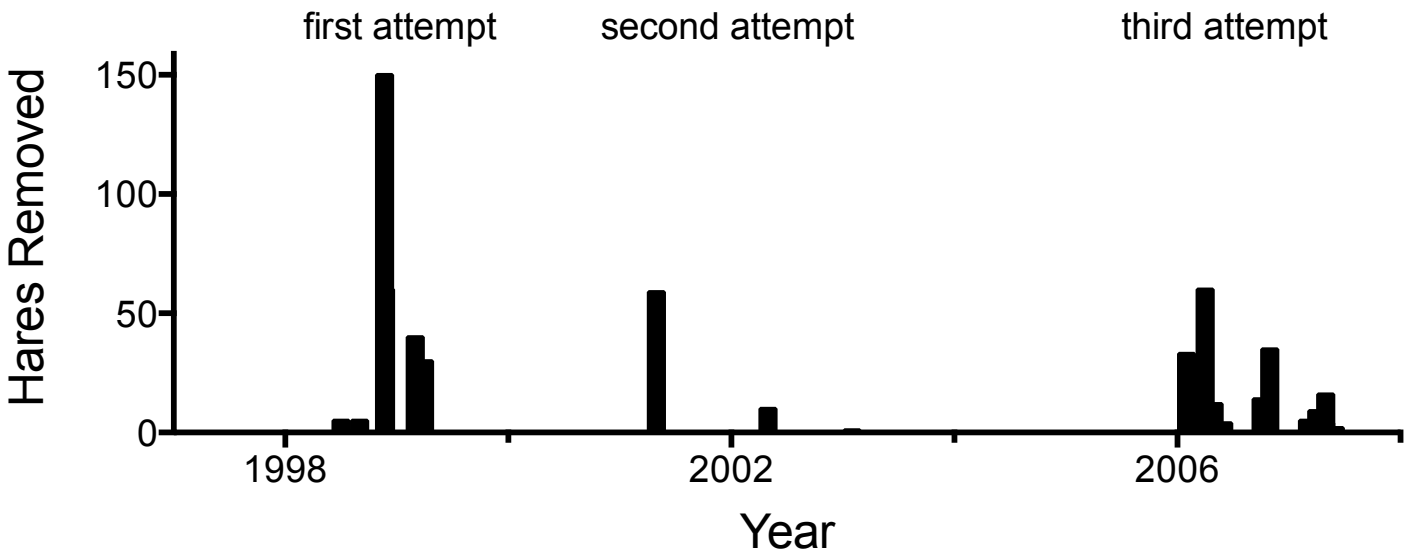
WebTable 1. Scientific names of species mentioned in the text

Common name	*Scientific name*
Plants	
Wood fern	*Dryopteris intermedia*, *D spinulosa*, *D campyloptera*
Red spruce	*Picea rubens*
White spruce	*P glauca*
Balsam fir	*Abies balsamea*
Tamarack	*Larix laricina*
Heart-leafed birch	*Betula cordifolia*
Yellow birch	*B alleghaniensis*
Mountain maple	*Acer spicatum*
Mountain ash	*Sorbus americana*
Red raspberry	*Rubus idaeus*
Shadbush	*Amelanchier* sp
Quaking aspen	*Populus tremuloides*
Animals	
Bark beetle	*Dendroctonus* sp
Leach's storm-petrel	*Oceanodroma leucorhoa*
Bald eagle	*Haliaeetus leucocephalus*
Snowy owl	*Nyctea scandiaca*
Savannah sparrow	*Passerculus sandwichensis*
Muskrat	*Ondatra zibethicus*
Lynx	*Lynx canadensis*



WebFig. 1

WebFig. 2



WebFig. 3

WebFig. 4

WebFig. 5