Extirpation of a Large Black Bear Population by Introduced White-Tailed Deer

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The negative impacts of introduced and invasive species on native fauna and flora have been reported in many systems (Diamond & Case 1986; Williamson 1996; Mack & D'Antonio 1998). One of the greatest challenges of native species is to survive the increased competition for resources generated by the colonization of introduced species. Density-dependent reduction in reproduction and increased mortality through starvation may arise from exploitative competition. As the number of competitors increases, food supply is depleted and less-competitive individuals, or the least competitive species, may starve to death (Sinclair 1989).

Introduced exotic or native species often eliminate or greatly reduce the abundance of native species, especially on islands (Williamson 1996; Drake et al. 2002). For example, the introduced gray squirrel (*Sciurus carolinensis*) is outcompeting the native red squirrel (*S. vulgaris*) in most of the United Kingdom and northern Italy (Gurnell & Pepper 1993), the species richness of ants has dropped by 70% in areas invaded by the fire ant (*Solenopsis invicta*) in the United States (Porter & Savignano 1990), and the introduced bluegill (*Lepomis macrochirus*) is thought to have extirpated the Sacramento perch (*Archoplites interruptus*) from most of its native range in California (Marchetti 1999). Examples of a large mammal extirpating another large mammal, however, are rare. Understanding situations of competitive exclusion by species introduced in natural ecosystems is essential for the conservation of wildlife.

Here, I report on a system in which a population of black bears (*Ursus americanus*) inhabiting a large island was most likely extirpated by introduced white-tailed deer (*Odocoileus virgininianus*) within approximately 50–70 years. Although based on correlations, my report is, to my knowledge, the only documentation of a large herbivore possibly extirpating a successful and abundant carnivore from a large ecosystem.

Black bears occur throughout the boreal forests of North America (Pelton 2003) and formerly on Anticosti Island (49.5°N, 63°W), a large island (7,943 km^2) about 35 km from the north shore of the Gulf of St. Lawrence in Québec. Black bears and deer mice (*Peromyscus maniculatus*) were the only native mammals that fed on vegetation on the island (Newsom 1937). The climate on Anticosti is sub-boreal and the vegetation is typically boreal and dominated by balsam fir (*Abies balsamea* L. Mill.), white spruce (*Picea glauca* [Moench] Voss), and black spruce (*P. mariana* [Mill.] Britton, Sterns, Poggenburg). Although no precise estimates are available, information from as early as 1542 describes black bears as abundant and widely distributed on the island (Crespel 1797; Roche 1865). Anticosti was an important hunting site for black bears by the First Nations and early Europeans until the late 1800s (Cameron 1958; MacKay 1979). Crespel (1797) quotes Thomas Wright who spent a winter on the island and reported that bears were "extremely numerous: 53 were killed within six weeks and many more were seen." During the first half of the twentieth century, however, numbers of black bear plunged, and they became rare on the island by 1950 (Cameron 1958).

Bears cannot accumulate body reserves by feeding only on foliage because they have a single stomach and cannot digest fiber efficiently (Welch et al. 1997). Consequently, they must consume large amounts of food to compensate for the low efficiency of their digestive system. In boreal ecosystems, black bears rely mainly on berries in late summer and autumn to accumulate sufficient body reserves for hibernation and lactation (Hatler 1972; Rogers 1987; Welch et al. 1997).

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About 220 white-tailed deer were introduced on Anticosti Island in 1896. In the absence of predators, their numbers rapidly increased to ≥50,000 deer by 1934 (Pichette et al. 1972; MacKay 1979). Aerial surveys conducted since the late 1960s have provided regular population estimates of 60,000 to 120,000 deer on the island (Rochette et al. 2003). Accounts from the second half of the nineteenth century report the presence of many varieties and large abundances of berries on Anticosti (Cary 1842; Calnek as cited in Stevenson 1874; Documents Joseph Bureau, 1905). In 1853, Roche (1865:27) stated, "The bears upon the island are quite harmless, and, living upon the rich berries and wild fruits, such as currants and gooseberries, which abound everywhere in the summer and autumn . . . ." Once the deer population had reached a high density, however, browsing started to affect the vegetation and gradually extirpated or severely reduced the abundance of all deciduous shrubs on the island (Côté et al. 2005).

During the summers of 2001 and 2002, my students and I surveyed 420 10-m^2 forest plots in 14 different stands on the western part of Anticosti Island and did not find a single twig of *Sorbus americana* Marsh, *Amelanchier* sp., *Diervilla lonicera* P. Mill., *Prunus* sp., or *Viburnum* spp., all species normally common in boreal forests. In 1975–1978, 35 stems of the same deciduous shrubs were found in a survey of 380 2.25-m^2 sampling plots in the same stands (J. Huot, unpublished data), indicating that shrub abundance was already very low in the 1970s and continued to decrease over the past 25 years. Deer usually prefer deciduous species to coniferous ones in winter (Dumont et al. 1998) and therefore first affected the deciduous shrubs on Anticosti. Then, negative effects on coniferous browse were also detected, mainly on balsam fir, which now compose most of the winter diet of deer on Anticosti and is decreasing rapidly (Potvin et al. 2003). In exclosures, where plants are protected from deer browsing, deciduous shrubs, however, are regenerating well (Côté et al. 2005).

Bears consuming berries to build up energy reserves are constrained by intake rate (Welch et al. 1997). Captive bears fed berries ad libitum during autumn showed impressive daily intake rate of about 35% of their own body mass (Welch et al. 1997). Black bears in Alberta gained weight when blueberry (*Vaccinium myrtilloides* Michx.) density averaged 423 berries/m^2 but lost body mass when the annual berry density averaged 66 berries/m^2 (Pelchat & Ruff 1986).

Wild berries are extremely rare on Anticosti, despite early observations reporting them as very abundant before deer introduction (Cary 1842; Roche 1865). In late August 2004, my students and I conducted a survey to estimate the density of the most common shrubs producing berries in the boreal forests of Anticosti (i.e., *Rubus idaeus* L., *Rubus pubescens* Raf., *Ribes* spp., *Vaccinium* spp., and *Cornus canadensis* L.). The number of berries in 27 to 30 forested plots (2 × 2 m) randomly located on permanent transects in five 20 km^2 forested zones were counted ($n = 141$ plots). The average density of berries for all species taken together was only 0.28 berry/m^2. *Cornus canadensis* was the most common species and produced 86% of the berries available. Most shrubs, particularly *Rubus* spp., are browsed the year they become established and, therefore, can never grow tall enough to produce berries (Potvin et al. 2003; Côté et al. 2005). The density of berries currently available on Anticosti is therefore 235 times lower than the minimum 66 berries/m^2 threshold necessary for black bears to maintain body mass (Pelchat & Ruff 1986). Thus, the forest on Anticosti is no longer capable of sustaining black bears foraging on berries and even reintroducing bear into this habitat is not an option.

Numerous alternative explanations for the disappearance of black bears on Anticosti can be proposed, but they all appear less correlated to the decline of bears than the hypothesis of the reduced abundance of berries. Bears were hunted on Anticosti Island in the early 1900s (MacKay 1979). Harvest rates or even the approximate number of bears killed, however, are not available. Access to Anticosti and its bear population was limited because the island was remote and only about 15 km of forest roads were present in the early 1900s (MacKay 1979). In addition, only a few hundred people inhabited Anticosti; thus the impact of hunting on the bear population is likely to have been low and limited to the area near Port Menier, the only village on the island. Similarly, there is no indication that the decline of black bears was associated with disease or climatic variability. No fatal disease of black bears has ever been identified in Québec (H. Jolicoeur, personal communication). Although annual variations in temperature and precipitation may affect the abundance of berries and, therefore, body mass, reproduction, and survival of black bears (Jonkel & Cowan 1971; Rogers 1976; Pelchat & Ruff 1986), there are no examples or indication that climatic variations could drive a black bear population to extinction. Logging at a small scale was initiated on Anticosti in about 1908 but affected < 5% of the surface of the island before the decline of bears (Mackay 1979). In addition, logging at a small scale normally has positive effects on bears because it generally increases the abundance of berries (Rogers 1976).

There was most likely a great abundance of white-tailed deer fawns in the spring to early summer. Black bear predation on cervid neonates, however, is normally limited to the first 1–2 months of a fawn's life (Franzmann et al. 1980; Kunkel & Mech 1994; Vreeland et al. 2004). Although the abundance of fawns probably contributed to the diet of bears in the spring, and perhaps slowed the decline of bears, most fawns would have been difficult to catch during the fall (Kunkel & Mech 1994). Fawns, therefore, were not readily available during the autumn when bears are in hyperphagy and need to accumulate body reserves. Because the forest is boreal on Anticosti, there is no fall mast available to bears (Côté

et al. 2005). In addition, Atlantic salmon (*Salmo salar*) were present on the island but not in sufficient numbers (Carter 1968), and their abundance was already decreasing in the 1930s (Belding & Préfontaine 1938). Therefore, I suggest that the near eradication of shrubs producing berries by deer browsing removed the most important food source for black bears in early autumn. Although alternative hypotheses cannot be ruled fully out, the near elimination of the shrub layer appears to be the main explanation for the bear decline because no other food source was available in sufficient abundance in autumn for bears to accumulate body reserves for the winter.

To my knowledge, this is the first evidence of what appears to be the indirect extirpation of an abundant large carnivore by an introduced herbivore. Many other examples of the strong negative impacts of introduced and invasive species in different communities also exist (Mack & D'Antonio 1998; Vásquez & Simberloff 2003). In terrestrial systems, the ecological impacts of overabundant cervid populations, both introduced and native, can be particularly severe (Côté et al. 2004). Deer populations have been increasing dramatically in many areas in North America and Europe in recent years and reports of strong negative impacts of deer browsing on vegetation and ecosystem functions and properties are also increasing rapidly (Hobbs 1996; Côté et al. 2004).

By foraging selectively, deer affect the growth and survival of many herb, shrub, and tree species, thereby modifying patterns of relative abundance and vegetation dynamics. Deer also exert cascading effects on other animals by competing directly for resources with other herbivores and omnivores and by indirectly modifying the composition and physical structure of habitats of both invertebrates and vertebrates (Van Wieren 1998; Fuller & Gill 2001; Côté et al. 2004). By modifying species abundance and diversity, deer populations at high density can also modify trophic interactions among species (Ostfeld et al. 1996; McShea & Rappole 2000). Effects on interactions within the food web may be particularly important in ecosystems where several species of large herbivores and omnivores cohabit such as in western and eastern North America.

Given the influence that abundant or introduced species can have on other organisms and natural processes, scientists and conservationists should actively participate in efforts to understand, monitor, and reduce their impacts on ecosystems. For example, in areas where the densities of introduced or native deer populations are high and predators are absent or rare, management actions should be undertaken to reduce deer impacts (Côté et al. 2004).

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