INVADER SPECIES IN ARGENTINA: A REVIEW ABOUT THE BEAVER (*Castor canadensis*) POPULATION SITUATION ON TIERRA DEL FUEGO ECOSYSTEM

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Wild furbearers have aesthetic, economical, and cultural value. On the southernmost tip of Patagonia, native furbearing species are not abundant (Lizarralde and Escobar, 2000; Lizarralde and Elisetch, 2001). For that reason, in 1946, 25 pairs of beaver (*Castor canadensis*) were introduced on the Río Claro of Isla Grande (Tierra del Fuego Archipelago, Argentina) by the federal government (Figure 1). The absence of most natural predators and human hunting, and the availability of suitable feeding and lodging conditions favored rapid population growth and range expansion (Lizarralde, 1993).

Beavers are considered as one of the most important natural agents of landscape alteration as well as a keystone species (Paine, 1966). Beavers modify stream morphology and hydrology by felling trees and building dams. These activities retain sediments and organic matter in the channel, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence biotic community composition and diversity (Naiman *et al*., 1988). Areas abandoned by beavers may produce fertile grasslands. However, the influence of beavers on undisturbed areas such as the southern ecosystems had not been intensively studied.

Tierra del Fuego ecosystems are pristine, fragile, and located in an extreme climatic zone that provides only marginal possibilities for the development of many species. Therefore, introduction of new fauna, particularly beavers, may result in changes in the regional ecology, causing effects on the biotic composition and the physical structure of forests and bogs (Lizarralde and Venegas, 2002).

The beaver introduced in Tierra del Fuego is considered as an invader because it modifies the local ecological interactions. Therefore, intensive studies have been carried out to understand the role of beavers on southern ecosystems and to compare this with boreal ecosystems (Lizarralde, 1993; Lizarralde and Escobar, 1999; Lizarralde *et al*., 1989, 1996a, b, 2002; Coronato *et al*., 2003).

Our research group has studied during 15 years the problems induced by beavers in Tierra del Fuego. This paper is a review of the main data produced about 1) beaver abundance, distribution, and spatial occupancy patterns, 2) habitat preference, 3) landscape alteration effects, 4) management and control, and 5) genetic structure and variability to detect possible genetic bottlenecks and founder effects in this invader species.

Study Area

The Tierra del Fuego Archipelago consists of a large number of islands located between the Pacific and Atlantic Oceans, the largest being Isla Grande (Figure 1). Insular conditions and the Antarctica influence have resulted in a humid climate that is classified as temperate-cold (Pisano, 1981). Isla Grande has three ecological areas with distinctive geographical relief (Lizarralde, 1993): 1) The Andean region is a mountainous area with vast basins and broad stream courses of glacial origin. 2) The ecotone or transitional area, with a flat aspect and gradual undulations influenced by glaciation. 3) The steppe or extra-Andean area.

In the Andean area, the vegetation cover is dominated by an evergreen forest of *Nothofagus betuloides* al-

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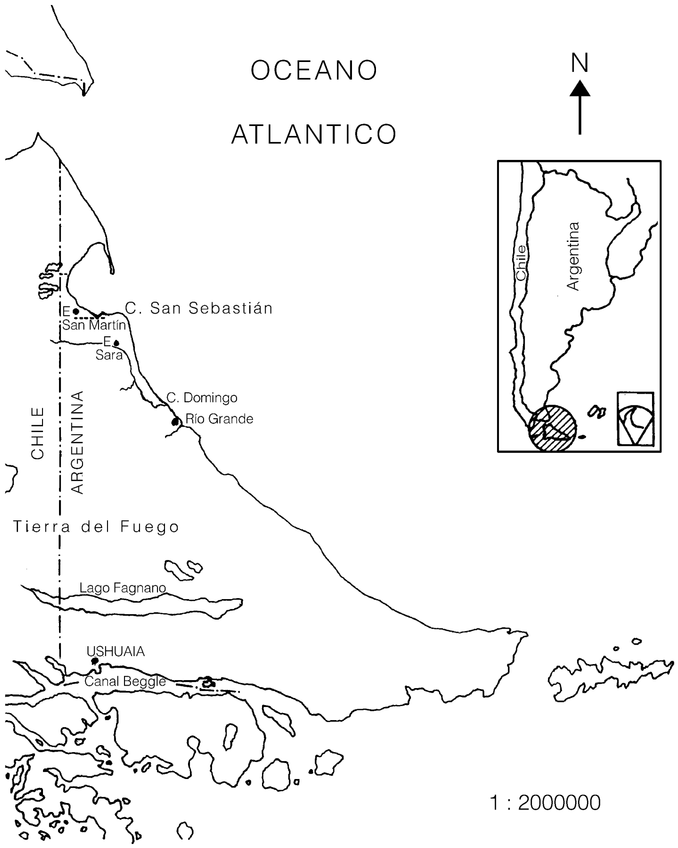

Figure 1. The Tierra del Fuego archipelago at the southernmost tip of South America. The largest island is Isla Grande.

ternating with *Sphagnum* bogs along the Beagle Channel coasts, on the south side of Isla Grande. The area surrounding Lake Fagnano is an ecotone with a vegetation cover of deciduous forest (*Nothofagus pumilio*, *N. antarctica*) that alternates with *Sphagnum* bogs and flat lowlands containing *Carex*. The extra-Andean area has a vegetation pattern typical of the Patagonia steppe.

Materials and Methods

Population surveys

Colonization patterns were determined by analyzing aerial photographs, aerial and field surveys, and beaver census carried out on the Isla Grande according to published procedures (Lizarralde, 1993).

All watersheds of Isla Grande (n=53) were systematically flown over at altitudes of 250-900m to determine beaver abundance and spatial occupancy patterns. Surveys were performed between fall and freeze-up, when food caches were most visible. Census were obtained during seasonal periods from 1988 to 1992, 1994 to 1998 and 2000 to 2002. The population size was estimated from counts of beaver colony sites on stream sections. A colony site was defined as a pond or series of ponds used by a colony of beavers throughout the year or years.

Field surveys were conducted to analyze the areas where beaver colonization, as detected from aerial survey, was high. All indirect evidence of habitat utilization was assessed, including tracks, food caches, scent mounds, wood debris and den banks. The number of active colonies was determined at study sites of Tierra del Fuego National Park to estimate beaver abundance and to compare these data with those from boreal forest areas. The average number of animals per colony was 5 and was determined from the data provided by hunters who trapped all the animals in each colony (Lizarralde, 1993). Height, width and length of beaver dams were measured to estimate pond surfaces and potential volume of sediment accumulation. By mapping pond locations in the streams, it was possible to determine spatial occupancy patterns. Data on foraging and diameters of trees felled by the beavers were recorded from linear transects from the pond to the last felled tree.

The different habitats were classified according to vegetation coverage and geomorphology. The physical characteristics of the streams colonized by beavers were also determined through geomorphological analysis and mapping techniques (Coronato *et al*., 2003).

Animals (n=50) were caught with live (Tomahawks™) and kill (Conibear™) traps. Blood, reproductive tracts, skulls and fresh tissue samples were obtained for cytogenetic, biological and molecular studies. Additional skulls (n=240) and tissue samples (n=20) were collected in the field from animals that died naturally or were killed by commercial hunters. Reproductive performance, age, and sex were determined for each individual. Skull voucher specimens of all of the animals studied were deposited in the Collection at the Ecogenetics Laboratory (CADIC-CONICET, Tierra del Fuego, Argentina).

Mitotic chromosomes were prepared by standard methods, directly from bone marrow and blood cells after *in vitro* tissue cultures. Routine karyotypic analysis was performed on preparations stained with 5% Giemsa solution (Lizarralde *et al*., 1996b).

Nutrient dynamics

The contents of the principal organic elements and inorganic compounds of sediments (n=50), and pond-riffle water samples from beaver altered (n=39) and unaltered control (n=21) sites were examined over a three-year period, from 1991 to 1994 (Lizarralde *et al*., 1996a). Altered sites were chosen according to habitat type, stored organic material, seasonal hydrologic regime, dominant vegetation and lack of evidence of human disturbance. Unaltered control sites were riffles and watercourses without a history of beaver presence. Sediment and pond water were collected from each of the sites during the ice free period (October to May). Sediment cores of 1000-2000g were taken in the ponds behind dams or, in unaltered sites, riparian zones 10 to 20cm in depth. Samples were stored in plastic bags at -20ºC. Concentration of total organic C, organic N, organic P, nitrite (NO_2^-), nitrate (NO_3^-), ammonium, and phosphate were determined by standard methods (Lizarralde *et al*., 1996a).

In water samples, concentrations of carbonate and bicarbonate, Cl, sulfate, Ca, Mg, Na, and K were also measured. Sediment and water pH were also determined (Lizzarralde *et al*., 1996a).

Results

Population analysis

Beavers were found in all streams from the North of Isla Grande to the Beagle Channel coast, covering about 40000km^2. Beavers also occupy Isla Navarino, Isla Hoste, and Península Dumas, with a geographical range of about 70000km^2 (Lizarralde, 1993; Figure 1).

Colony-site densities were estimated to be between 0.2 and 5.8 per km of stream. Extensively colonized habitats (e.g. National Park) showed 0.7 active beaver colonies per km^2. Populations have been increasing at a rate of 20-23% per year (K= 0.20-0.23; Lizarralde *et al*., 1996b). The reproductive season was determined to be from June to November, with an average of four kits per litter and a sex ratio of 1:1 (Lizarralde and Escobar, 1999; Lizarralde, unpublished data).

Chromosome analysis of Giemsa-stained preparations showed a karyotype 2n=40 (n=10 individuals) with 16 pairs of metacentric biarmed chromosomes and four pairs of submetacentrics. The X sexual chromosome is a large metacentric one, and Y is one of the smallest from the complement (Figure 2).

The rate of occupancy of the beaver colony sites was found to be constant over a wide area and a long period of time. Four land capability classes were established (A, B, C and D) to use in planning and resource management (Table I). The classes were determined according to the density of colony sites and geomorphological characteristics. Classes D and C had the highest densities (4.7 and 5.6 beaver colony sites per km^2) indicating they are most suited for beaver production. Field observations were also conducted on study sites in Tierra del Fuego National Park (Class C) and in the Río Moat valley (Class D); 30% of Class C areas and 58% of Class D areas were colonized and altered by beavers over a 20 year period (Lizarralde, 1993).

Figure 2. Conventional karyotype of fuegian beaver, 2n=40.

TABLE I
BEAVER OCCUPANCY PATTERNS AND FREQUENCY OF COLONY SITES.

Class	Ecological area	Basin geomorphology	Total km^2 of watersheds	Number col. sites	Colony per km^2
A	Ecotono	Extra-Andean	655	131	0.2
B	Forest	Andean	135	277	2.05
C	Forest	Andean	506	2390	4.72**
D	Wetlands	Andean	465	2721	5.85

Land capability classes A, B, C and D were identified to use in planning and beaver management. Classes are related to ecological and geomorphological areas of Isla Grande.
** Density of beaver active colonies on 75km^2 Tierra del Fuego National Park study site was 0.7 active colonies per km^2.

Landscape alteration effects

Beavers primarily altered uplands stream valleys in mountainous areas and wetlands. The formation of ponds in streams with flat valley floor increases the area of wetland as wide, flooded zones are formed (Figure 3). In these flat valleys, ponds 120000 to 160000m^2 and adjacent wet areas of about 10,000m^2 influenced by beavers, were observed. Mean surface area of ponds in mountainous areas was 2660m^2 (300-16000m^2, std=3587.89, n=22) depending on the geomorphology of the basins. For steep slopes, riparian areas influenced by beavers were estimated to be about 400m^2.

Beavers colonized all streams and occurred in nearly all aquatic habitats. Low gradient (0-6º), first and second order streams were selected by beavers. Higher-order streams were seasonally occupied (Coronato *et al*., 2003). The rivers of the lateral hanging valleys were more densely occupied than those of the slope units. Clear-cutting by beavers in riparian forests dominated by deciduous (*Notophagus pumilio*) or evergreen *(N. betuloides*) species promoted the formation of grasslands with high productivity, probably due to increased light, organic material, and humidity (Lizarralde, 1993).

Submerged vegetation and algae (Diatoma, Cyanophita and Clorophyta), which indicate high N content, were also identified in beaver sites. It was also noted that these environments are suitable for introduced fish species (*Salmo trusttafario, Salvelinus fontinalis* and *Onchorrychus mybis*), and that they sustain invertebrate communities typical of slow-water habitats. In addition, they became the nesting places of a number of migratory bird species (Lizarralde *et al*., 1996a).

Foraging

Austral beavers forage on trees of the genus *Nothofagus* (*N. betuloides, N. pumilio* and *N. antarctica*)

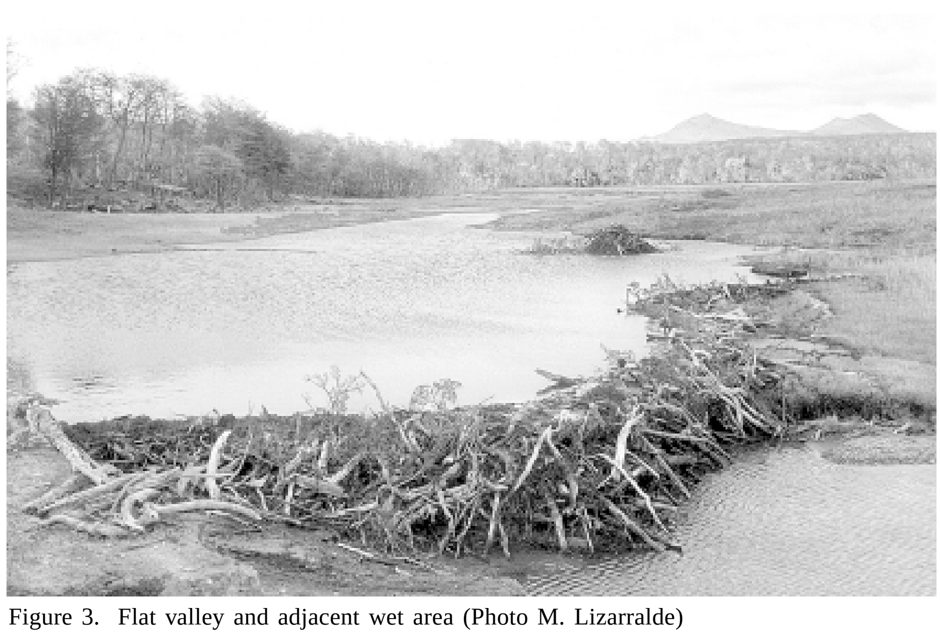
Figure 3. Flat valley and adjacent wet area (Photo M. Lizarralde)

and *Drymis winteri* ("canelo"), shrubs such as *Pernettia mucronata* ("chaura"), *Berberis ilicifolia* ("michay"), and *Chillotricum diffusum* ("mata negra"), and grass of the genera *Marsipospernum* and *Iuncus*.

Branch and trunk diameters (n=1084) were measured close to ponds and at distances up to 30m. One group of felled trees (n=881) with diameters between 0.5 and 56cm (median=5.3, std=1.8) was selected. Large branches and trunks (diameter of 3–56cm; median=11.3, std=8.8, n=139) were cut at distances of 0-14m from the pond, while smaller branches and trunks (diameter of 0.5-28cm; median=3.6, std=5, n=614) were cut between 15 and 30m from the pond (Lizarralde, 1993). Recent data have been analyzed to detect preferences in trunk diameters and behavioral changes related to distance to the central place.

The immediate effect of beaver-induced deforestation was increased erosion because slopes were directly exposed to the winds. Riparian grasslands with high productivity due to increased organic material and humidity were observed in Class A basins.

Nutrient dynamics

Wood debris from fallen trees causes an accumulation of organic material that modifies the biochemical composition of waters, sediments, soils and adjacent riparian areas. Data indicated that beaver dams were able to retain sediment levels from 684 to 120000m^3. Nutrients are probably released to riparian vegetation during seasonal periods of high floods when the ponds are flushed. Standing stocks of principal elements differed greatly between unaltered and beaver-altered sites. Mean organic C, organic N, organic P, and inorganic N (NO_2 and NO_3) were significantly greater in beaver-altered sites. Beaver pond water had significantly greater concentrations of nitrate, nitrite, and K than control water. Beaver ponds stored 7 times more C, 3.5 times more N and 1.85 times more P in sediments than did control ponds. Nitrites (24.75x) and nitrates (11.15x) were also more prevalent in sediments and waters (7–10x) of beaver-altered ponds. (Lizarralde *et al*., 1996a).

Discussion

Plant and animal introductions have genetic and ecological effects on the invader species, as well as on the native ecosystems where they are introduced. North American beavers were introduced in the Isla Grande of Tierra del Fuego about 57 years ago. Several factors favored rapid population growth and range expansion. In 1981 the Government of Tierra del Fuego authorized hunting this species in order to control its increasing population.

Beavers are obligate residents of riparian areas and their construction of dams, channels and lodges produces noticeable effects on the ecosystems. As in boreal forests, we have reported increases in the accumulation of organic compounds and changes in decomposition processes and nutrient cycles as a result of beaver activities. Beavers have also created conflict in areas where timber exploitation is important.

From 1946 up to several years ago, there was no information on the beaver population in Tierra del Fuego. For many years it was not known whether beavers had adapted successfully to the Fueguian ecosystem. Beavers modify stream morphology and hydrology by felling trees and building dams; the latter retain sediment and organic matter in the channel, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, alter the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence biotic community composition and diversity (Naiman *et al*., 1986; Naiman, 1988). Areas abandoned by beavers produced fertile grasslands in Tierra del Fuego. Our results indicate that beaver-altered sites had higher levels of organic and inorganic N (nitrites and nitrates), suggesting that seasonal hydrological changes could be affecting nitrification and denitrification, and also resulting in accumulated organic C and P in the stream channel. Consequently, by changing the hydrological regime, beavers alter the character of stream channels. Our data also suggest that beaver ponds may be considered sources of essential nutrients (P and N) and C. Several characteristics of rivers used by beavers in Tierra del Fuego were found to be similar to those in the Northern Hemisphere (Naiman *et al*., 1988; Smith *et al*., 1991; Coronato *et al*., 2003).

Beavers can be considered major factors influencing nutrient transformation processes in southern beech (*Nothofagus* spp.) forests. They greatly influence microbiological processes such as N mineralization, organic C decomposition, and P availability. Beaver impoundments caused less alteration of ecosystem level processes in wetlands than in uplands, because the soil and vegetation was already in under-saturated conditions before impoundment (Naiman *et al*., 1988; Lizarralde *et al*., 1996a).

Modifications of the aquatic and terrestrial biotic composition were also observed in the southern beech forest. Our studies also found that beavers forage more selectively at increasing distances from the central place (pond). Data obtained from study transects could be related to several predictions of the theory of central place foraging (Orians and Pearson, 1979; Jenkins 1980; Lizarralde *et al*., unpublished data). Basey *et al*. (1988) reported that beavers often select trees with large trunks which probably contain low concentrations of a specific phenolic compound. This phenolic compound, which may act as a deterrent, was found in aspen bark with a significant negative regression of relative concentrations and tree diameter. Future studies should attempt to determine whether similar phenomena occur in *Nothofagus* spp.

Colony site densities in Class C and D are high compared with Class A and B, and also with those reported for the Northern Hemisphere. Several authors have reported that 1.25 colony sites per km^2 represents saturation density, while 0.9 active col/km^2 seems to be the carrying capacity in the Northern Hemisphere (Nordstrom, 1972; Collins, 1976). Since we found densities of about 4-5 colony sites/km^2 in streams of Class C and D, and 0.7 active col/km^2 in Class C, our data suggest that both classes are near carrying capacity.

Chromosome analysis of Giemsa-stained preparations showed a similar karyotype to that of *Castor canadensis* in the Northern Hemisphere (Genest *et al*., 1979; Hsu and Benirschke, 1968; Ward *et al*., 1991; Lizarralde *et al*., 1996b). However, the austral karyotype differs only in the X sexual chromosome because it was more variable and totally metacentric in all the animals analyzed. *C. fiber* and *C. canadensis* karyotypes share a fundamental number (FN=80), but differ by 8 acrocentric pairs present in the *C. fiber* karyotype. Several authors assumed that the *C. canadensis* karyotype has originated by Robertsonian fusions of *C. fiber* karyotype (Lavrov and Orlov, 1973; Sysa and Zurowsky, 1980).

Data revised herein were obtained during an intensive 15-year study. This led to a management plan to control the population through trapping (Lizarralde and Escobar, 1999). Beaver trapping in Tierra del Fuego began to be regulated 3 years ago by the Natural Resources Administration. Kill traps (Conibear model 330™) are used.

The austral beaver is an excellent example of an introduced invader species that rapidly exploited the environment in the new habitat. Twenty-five mated pairs from Canada have grown to a population of 35000-50000 animals. What is the magnitude of the genetic drift that has occurred in this isolated population? This, and many other questions, remain to be answered and require extensive molecular studies. Beavers in Tierra del Fuego also represent a model to study the process of invasion.

At present, molecular genetic markers are being analyzed to detect levels of genetic variation, and to identify DNA polymorphisms and mitochondrial linkages to understand the effects of severe reduction of genetic variability on the survival ability and reproductive success of Argentine beavers. Low levels of variability also have been reported in *C. fiber* and *Ondatra zibheticus* (Ellegren *et al*., 1993; Marinelli *et al*., 1992).

The results of this study will have important implications for biodiversity conservation and wildlife management.

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