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ORIGIN AND HISTORY OF THE BEAVER INTRODUCTION IN SOUTH AMERICA

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ABSTRACT. The introduction of the North American beaver (*Castor canadensis*) to Tierra del Fuego is a widely known example of a successful biological invasion. However, the origin and history of this introduction bears closer scrutiny. Using historical documentation we provide evidence that beaver introduction occurred as a single release event of 20 beavers from northern Manitoba, Canada. This not only clarifies the origin of the invasion, but also suggests that the beaver population of Patagonia descends from a smaller number of individuals than previously assumed.

RESUMEN. Origen e historia de la introducción del castor en América del Sur. La introducción del castor norteamericano (Castor canadensis) en Tierra del Fuego es un ejemplo ampliamente conocido de una invasión biológica exitosa. Sin embargo, el origen y la historia de su introducción merecen mayor análisis. Usando documentación histórica, presentamos evidencia de que la introducción del castor se originó en un único evento de liberación de 20 castores que arribaron desde el norte de Manitoba en Canadá. Esto no solo aclara el origen de la invasión, sino que sugiere que la población de castores en Patagonia deriva de un número de individuos menor que el que se asumía hasta el momento.

Key words: Castor canadensis. Historical records. Propagule pressure. Tierra del Fuego.

Palabras clave: Castor canadensis. Presión de propágulos. Registros históricos. Tierra del Fuego.

Historical information is important to unveil key features of a biological invasion, such as the number of individuals introduced or the number of introduction attempts. So-called "propagule pressure" has been proposed as one of the main factors predicting invasion success across a variety of taxa (Lockwood et al., 2005). Under the propagule pressure hypothesis a single introduction event of a few individuals will be less likely to lead to a

biological invasion than multiple introduction events of numerous individuals. This mainly happens because small populations are strongly affected by demographic stochasticity, and multiple introductions buffer the effects of environmental stochasticity (Simberloff, 2009). Information about the origin of the founding population is also important and can help to elucidate the history and spread of the invasion (Fitzpatrick et al., 2012). As the founding

population is a smaller subset of the source population, propagule size can determine how much genetic variation is present in the founding population, and the origin can indicate which genetic information may be contained in this population. The issues laid out above ultimately relate the introduced individuals fitness and adaptability and influence their establishment in a new habitat.

The North American beaver, Castor canadensis Kuhl, 1820 (Rodentia, Castoridae) was introduced to the main island of the Tierra del Fuego Archipelago (TDF, from now on) in 1946, and by the 2000s, beavers were estimated to impact 20-40% of the stream length of the island (Anderson et al., 2014). Beavers are purportedly responsible for the most drastic landscape alteration in TDF in the Holocene (Anderson et al., 2009), affecting the hydrology and composition of the southern beech forests (Nothofagus spp.) and allowing other species of riparian plants to invade the ecosystem (Anderson et al., 2006). Predator release has been suggested as one of the major drivers of the beaver's invasion success in TDF (Wallem et al., 2007). In 1997 the species' presence was confirmed in mainland Chile (Brunswick Peninsula), threatening to spread throughout continental Patagonia (Wallem et al., 2007). Recently a beaver was captured close to Puerto Natales, Chile, 200 km north of the previous record, confirming further spread of beavers to the north in Patagonia mainland (La Prensa Austral, 2013).

Beavers were brought to TDF by the Secretary of the Navy of Argentina in November 1946 to "enrich" native fauna and foster a fur trade (Daciuk, 1978). But primary source information about the origin and number of beavers that were introduced has proven elusive. Godoy (1963) mentioned that 25 pairs were released in the northeast of Lake Cami (= Fagnano) around the Claro river in November 1946. Several authors later cited this as a primary or secondary literature source or simply stated that 25 pairs of beavers were released without references (Table 1). Furthermore, there is ambiguity as to the source of the introduction, which is mostly cited as "Canada". For example, Wallem et al. (2007) assigned "Nova Scotia" or "Ontario" as the possible sources of the founding population, based on personal communication, and Fasanella et al. (2010) mentioned Alberta as the putative origin of the invaders, without references. Therefore, we reviewed historical documentation in order to clarify the details of the introduction of beavers in South America.

We conducted an extensive search of historical books and gray literature in 2 of the largest historical archives of Ushuaia (Museo del Fin del Mundo and Museo Marítimo), the closest city to the area where beavers were introduced. As the Secretary of the Navy and the Secretary of Agriculture were directly involved in the transportation of beavers to Tierra del Fuego we also looked for documentation related to beaver introduction in their national archives. Canada has been recurrently cited as the country origin of the source population. Thus, we conducted additional literature searches in the Hudson's Bay Company Archives and the Archives of Manitoba which harbor most of the historical records of beaver fur trade in Canada. After narrowing down our search, we researched online sources using Google as a search engine.

We found documentation that links the founding population of beavers to the province of Manitoba in Canada. First, in an article published on October 25, 1946 in the Schenectady Gazette, the anonymous author describes the trip of Thomas Lamb, a Manitoban bush pilot, from Canada to Argentina as follows: "Lamb and the beavers traveled by rail from Moose Lake (Manitoba) to New York, by air to Miami, and will leave tomorrow aboard a clipper to Argentina," providing the first concrete geographic reference to the origin of TDF beavers. Moose Lake is further confirmed as the location from which beavers departed by "Sucesos Argentinos," a newsreel released by the government of Argentina in 1946. In a letter written to a friend on November 21, 1969 (available online http://www.lambair.com/resources/Argen-Beaverswells.pdf) Thomas Lamb gives a personal account of the capture and transportation of the beavers to Argentina. Lamb mentioned 3 sites where beaver capture took place: Caroline Lake (53°38'18"N, 100°23'52"W), Devils Portage (53°40'25"N, 100°29'48"W), both located

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Number of beavers and origin of the individuals released in Tierra del Fuego, Argentina, according to different authors.

Number of beavers released	Origin	Number of citations and references	
50	Canada	8 (Godoy, 1963; Daciuk, 1978; Fabro, 1989; Lizarralde, 1993; Jaksic et al., 2002 ^c ; Lizarralde et al., 2004; Anderson et al., 2006 ^c ; Skewes et al., 2006 ^c)	
50	Nova Scotia or Ontario	1 (Wallem et al., 2007°)	
50	Alberta	1 (Fasanella et al., 2010)	
20 ^{a,b} or 50	Canada	1 (Massoia and Chebez, 1993°)	
50	Not mentioned	8 (Sielfeld and Venegas, 1980; Navas, 1987; Lizarralde et al., 2008; Anderson et al., 2009 ^c ; Moorman et al., 2009 ^c ; Anderson et al., 2011; Anderson et al., 2014; Valenzuela et al., 2014)	
Not mentioned	Canada	1 (Goodall, 1979)	

^a Massoia and Chebez (1993) cite 3 sources of information, 2 are included in this table -Godoy (1963) and Daciuk (1978)- while the third is an unpublished report from a Captain of the Argentine Navy and also confirms that only 20 beavers were released in TDF.

a few kilometers south and southwest of Moose Lake, respectively, and a third place called "Big Creek," likely close to the former sites (William Watkins from Manitoba Conservation Office, pers. com.).

A relevant fact is that the beaver population in northern Manitoba (i.e. the founders of the TDF population) probably had a mixed origin. An article published on April 9, 1936 in the Winnipeg Free Press and entitled "Six beaver taken north in restocking venture," states that "forward looking plans for the restocking with beaver on a large expanse of fur bearing territory around Moose Lake, will be advanced with the departure by air plane from Stevenson Field of six beaver from New York State." The airplane pilot was again Tom Lamb. In the 1930s and 1940s beavers had nearly disappeared from northern Manitoba due to over trapping. In addition to this, beaver were live trapped in other areas south of Manitoba and translocated north by truck and aircraft (Manitoba, the keystone province 1948; Malaher, 1984). These measures proved to be successful, and beaver catches rose from 6361 pelts in 1939-1940 to 51 318 beavers in 1963-64 (Smith, 1976). Although we did not find further documentation on restocking in Moose Lake, this was probably one of many translocation targets in northern Manitoba.

In addition, contrary to what has been widely assumed, we found that only 20 beavers were released in a single introduction event in 1946. In this regard Lamb wrote in his letter "We only had three or four days of trapping when we got an inch of ice... I would watch beavers walk over our trap... however, we got 20 beaver when we would hardly get back to The Pas late October." This number of beavers is further confirmed in one of his stops on the way to Argentina in Miami, Florida (U.S.A.), the city from which the news published in the Schenectady Gazette comes from and is entitled "Twenty beavers migrate to Argentina." Moreover, the weekly newsreel "Sucesos Argentinos" highlights "Aiming to enrich our native fauna, the Secretary of the Navy bought from Canada

^b The local magazine Argentina Austral mentioned the introduction of beavers to Tierra del Fuego in its November 1946 edition, saying that "La Marina se encuentra negociando la compra de 50 castores" ("the Secretary of the Navy is in advanced negotiations to buy 50 beavers") and later (August 1960) published an article entitled "Vida de los castores en el río Claro: multiplicación de las diez parejas liberadas" ("Life of beavers in the Claro river: spread of the ten released pairs").

^c These authors cite Godoy (1963) as a primary or secondary literature source.

20 beavers..." and shows cinematographic recordings of the beaver release in TDF. Finally, Tom Lamb mentioned in his letter that he asked \$ 650 per beaver in addition to his expenses to transport the beavers from Montreal to Ushuaia, TDF, and he was paid 13 000 dollars for the catch. Taken together, the evidence we have presented puts into question the previous assertions about this introduction to southern Patagonia and provides substantial historical evidence to assert that it was 20 individuals with no reference to sex ratio from northern Manitoba.

The origin of the erroneous statement that 25 pairs of beavers were released was also identified. The original request of the Argentine government was for 50 beavers, as Tom Lamb notes in his letter "I think it was September 1945 when Dave Allan phoned me from his Indian department Office of Trusts and Annuities, Ottawa, asking me if I could deliver 50 live beaver to Peron Minister of Argentina." As mentioned before, Lamb could only trap 20 of the 50 requested beavers.

In conclusion, we present historical evidence that clarifies the origin of the beavers introduced to southern Argentina and refutes the general assertion that 25 pairs constituted the founder population. We additionally show that restocking was a common practice in northern Manitoba in the 1930s and 1940s. This means the founding TDF population could have higher genetic diversity than an equivalent sample from a long established population. In the largest genetic study of the TDF population conducted to date, Fasanella et al. (2010) could only identify 7 different haplotypes. Under the assumption that 25 pairs of beavers had been introduced, as many as 25 mitochondrial lineages could have founded the TDF population. The authors suggest that some of these lineages could have been lost due to demographic stochasticity or natural selection during the process of colonization and invasion. Nevertheless, the introduction of fewer (less than a half of what was previously thought) individuals may provide a more parsimonious explanation to these findings. Moreover, the particular features of the source population

in Manitoba reveal new challenges for genetic studies on the TDF beaver population.

A successful beaver introduction from few founding individuals was also reported in Europe. Only 7 North American beavers were the founders of a population of 12 500 beavers in Finland and northwest Russia (Parker et al., 2012). However, there are many reported cases of failed introductions of *C. canadensis* in Finland and unsuccessful reintroductions of its European relative (*Castor fiber*) in Europe (Nolet and Baveco, 1996; Parker et al., 2012). We do not believe this means beavers are not affected by the problems small populations face, but these examples do represent instances of extraordinarily successful biological invasions, initiated with a very low propagule pressure.

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