

Demography and Spread of Invasive Beavers in the Heterogeneous Landscapes of

Patagonia

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
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ABSTRACT

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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. Beavers have impacted enormously the biodiversity of the island of Tierra del Fuego, and they are now spreading northward on the continent, prompting the governments of Argentina and Chile to seek methods to control their spread. Beavers first established in forests, where they were initially introduced, but by the 1990s they began to establish in the adjacent steppe. In this dissertation, I study the biology of invasive beavers across the two major habitat types in Patagonia and attempt to develop modeling tools that might be useful to manage their spread.

In chapter one I studied the history of the beaver introduction in Patagonia and provide evidence that the 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.

In chapter two I studied the demography of invasive North American beavers in the two contrasting habitat types of the island of Tierra del Fuego, forest and steppe. Habitat differences can affect vital rates which may in turn impact the speed of the invasion, but this has been rarely addressed when managing the spread of invaders. I use repeated observations, mark-resight methods, telemetry and camera traps to

estimate colony size and vital rates of beavers in the two habitats. Colony size and the number of offspring (“kits”) produced per colony per year were higher in the steppe, contrary to the belief that forest is better habitat. Here I suggest this may be the result of the longer time since invasion in the forests of Tierra del Fuego and that the forest subpopulation is showing density dependent regulation. Beaver survival was high in all age classes and was higher than survival rates recorded in North America. My work shows that beaver plasticity and predator release have likely facilitated the invasion in Patagonia.

In chapter three, I investigated the more recent invasion of beavers in an area of the Patagonian steppe. I utilized repeated high resolution satellite images to identify beaver ponds, and used them to study changes in beaver abundance and habitat use over time. The number of beaver ponds increased 85 % between 2005 and 2014. During this period, beavers changed their habitat selection pattern, presumably as a response to increased density. Beavers established on small watercourses in canyons first, but as more canyons became occupied over time, beavers moved to less preferred watercourses in plains and U-shaped valleys. Potential new beaver colonies established close to existing beaver ponds, suggesting proximity to a beaver pond is an important determinant of beaver colonization. Identifying habitat preferred by beavers in the steppe could help to increase early detection of the invader at the invasion front. This

work highlights the importance of the use of high resolution remote sensing technologies to better understand and monitor biological invasions.

Finally, in chapter four, I built a spatially explicit individual-based model parameterized with data I collected in the field and use it to make management recommendations. Specifically I assessed the efficacy of a potential management strategy in which a “fire-break” (a zone beyond the current population front in which beavers are removed) perpendicular to the population front is instituted to attempt to prevent further northward spread of the beaver in continental Patagonia. I found that even a 100 km wide firebreak is insufficient to contain the spread of beavers, long dispersal events being the major cause of this failure. Further, I found that increasing the fraction of beavers culled within the firebreak does not decrease either the arrival time or the number of beavers that cross the firebreak. Counterintuitively, my model indicates that moderate levels of culling within the firebreak (rather than high) may be a more effective method to manage the invasion, likely as a result of inversely density dependent dispersal.

Dedication

To friends and friendship

Contents

| | |
|-------------------------------------------------------------------------------------------------------------------|-----|
| Abstract | iv |
| List of Tables..... | x |
| List of Figures | xi |
| Acknowledgements | xii |
| General introduction and overview | 1 |
| 1. Origin and history of the beaver introduction in South America..... | 5 |
| 2. The demography of invaders in heterogeneous landscapes: Beavers as a case study.. | 14 |
| 2.1 Introduction..... | 14 |
| 2.2 Methods | 18 |
| 2.2.1 Study sites..... | 18 |
| 2.2.2 Field sampling | 20 |
| 2.2.3 Statistical models to estimate colony size and number of kits..... | 21 |
| 2.2.4 Estimation using camera traps of the proportion of colonies producing kits .. | 25 |
| 2.2.5 Estimation of survival using mark-resight and telemetry..... | 26 |
| 2.2.6 Estimation of kit survival | 27 |
| 2.2.7 Estimation of survival of juveniles and adults..... | 28 |
| 2.2. 8 Parameter estimation | 29 |
| 2.3 Results | 29 |
| 2.4 Discussion..... | 36 |
| 3. Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe | 43 |

| | |
|-------------------------------------------------------------------------------------------------|-----|
| 3.1 Introduction..... | 43 |
| 3.2 Methods | 46 |
| 3.2.1 Study area..... | 46 |
| 3.2.2 Extraction of covariates | 47 |
| 3.2.3 Data analysis | 50 |
| 3.2.3.1 Resource selection functions | 50 |
| 3.2.4 Effect of proximity to existing colonies on establishment of potential new colonies | 53 |
| 3.3 Results | 55 |
| 3.4 Discussion..... | 61 |
| 4. Predicting and managing the spread of invasive beavers in Patagonia | 67 |
| 4.1 Introduction..... | 67 |
| 4.2 Methods | 72 |
| 4.2.1 Estimating dispersal parameters and fitting observed rates of spread | 77 |
| 4.2.2 Simulating management scenarios | 78 |
| 4.3 Results | 79 |
| 4.4 Discussion..... | 82 |
| Appendix A..... | 86 |
| Appendix B | 90 |
| References | 97 |
| Biography | 117 |

List of Tables

| | |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| Table 1: Number of beavers and origin of the individuals released in Tierra del Fuego, Argentina, according to different authors..... | 8 |
| Table 2: Mean litter sizes of beavers reported in scientific literature. | 34 |
| Table 3: Mean survival rates of juvenile and adult beavers using telemetry reported in scientific literature..... | 35 |
| Table 4: Five best ranked logistic models to study resource selection by beavers. Abbreviations: CA (catchment area), CO (vegetation cover), ELEV (elevation), LA (landform), SG (stream gradient), YR (year)..... | 56 |
| Table 5: Logistic models to study the establishment of potential new colonies. Models with $AIC < 2$ are presented. Abbreviations: CA (catchment area), COV (vegetation cover), ELEV (elevation), SG (stream gradient)..... | 60 |
| Table 6: Parameters of the SEIBM to fit the observed rates of spread of invasive beavers. | 76 |

List of Figures

| | |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| Figure 1: Location of the study sites in the forest (dark grey) and the steppe (light gray) in Tierra del Fuego, Argentina..... | 19 |
| Figure 2: Mean yearly colony size (\pm posterior SD) for the forest and the steppe | 30 |
| Figure 3: Mean yearly number of kits (\pm posterior SD) for the forest and the steppe..... | 32 |
| Figure 4: Bottom row: Detail of the study area, the triangle indicates location of the top row images. Top row: High resolution satellite images. No ponds are distinguished in 2005, but new ponds are formed in 2010 and 2014. | 46 |
| Figure 5: Increase in the number of beaver ponds for our entire study area (top) and for a subset of our study area (bottom). Numbers in parenthesis indicate the area in hectares flooded by beaver ponds..... | 55 |
| Figure 6: Interaction between catchment area and vegetation cover for 2005 (left) and 2014 (right). Solid lines indicate the probability of pond establishment at different levels of vegetation cover, dotted lines indicate 95 % confidence intervals | 57 |
| Figure 7: Relative likelihood of landform use (\pm SD) for 2005, 2010 and 2014. Relative likelihoods were calculated using a RSF where covariates were set at the median values. | 58 |
| Figure 8: (a) Distribution of the distances of potential new colonies to the closest pond at time t-1. (b) Probability of establishment of potential new colonies as a function of the distance to the closest pond. Probabilities were calculated from the best ranked logistic model that incorporated distance. | 60 |
| Figure 9: Spread of introduced beavers in Patagonia. The square indicates the site where the first 20 beavers were released. The circle represent the site in the continent where beavers arrived in 1976 according to the dendrochronological record. The triangle represent the northernmost point where a beaver has been captured (in 2013)..... | 71 |
| Figure 10: Arrival time of beavers on the opposite side of a firebreak when culling levels are 0.5 (left) and 0.8 (right) for a 100 km wide firebreak. | 81 |
| Figure 11: Mean number of beavers crossing the firebreak at three different widths. Dark bars indicate a culling fraction of 50 % and light bars indicate 80 % culling. | 81 |

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General introduction and overview

Introduction of non-native species is one of the greatest threats to biodiversity. Although we have significantly increased our knowledge of the biology of invasions in recent years, some areas remain poorly understood. For instance, we know the speed of biological invasions is affected by population growth and dispersal, but most work still assumes invaders spread in homogeneous habitat even when most landscapes are heterogeneous at some scale. In addition, we have a great deal of research attempting to predict what makes an invasion succeed or what the impacts of the invaders are at high densities, but we know very little about the role that density dependence plays in the spread of biological invasions and how density dependence can impact the final abundance and distribution of the invader.

Biological invasions are the most pressing threat to biodiversity in Patagonia. Numerous invaders have established in Patagonia over the last century, the North American beaver (*Castor canadensis*) probably being the best known. Beavers have impacted enormously the biodiversity of the island of Tierra del Fuego, and they are now spreading northward on the continent, prompted the governments of Argentina and Chile to seek methods to control their spread. In this dissertation, I study the biology of the North American beaver in the heterogeneous landscapes of Patagonia, and try to develop modeling tools that might be useful for managing its spread.

In chapter one of my dissertation, I used historical documentation to investigate the origin and history of the beaver introduction in South America. Propagule size especially, has been since long considered an important predictor of the success of biological invasions. Yet, information on the number and origin of the beavers introduced in Argentina has proven to be elusive in the last 70 years. In chapter one, I clarify the number released, site of origin, and historical details of the beaver introduction in Argentina. Chapter one has been published with Laura Fasola as the second author in the *Journal of Neotropical Mammalogy*. Readers less interested in the history of the introduction may wish to skip chapter one and move directly to the following chapters that concern the population biology of the invader and potential management strategies.

In chapter two I studied the demography of invasive beavers in the two major habitats of Patagonia: forest and steppe. In addition to relatively fixed habitat differences, these habitats differ in the time since they were invaded, with beavers spreading over the steppe more recently. I used mark-resight methods, radio-telemetry, repeated observations and camera traps to estimate colony sizes and vital rates of beavers in each habitat and compare them to the vital rates of beavers in North America. By comparing vital rates in Tierra del Fuego and North America, I also discuss whether predator release (which has been proposed as a major driver of the invasion) has occurred in Tierra del Fuego. Chapter two has been submitted for publication to

Ecological Applications and includes Julio Escobar, Laura Fasola, Ignacio Roesler and Adrian Schiavini as coauthors (in that order).

In chapter three, I studied post establishment changes in habitat selection using high resolution satellite images. Studying changes in habitat selection over time during a biological invasion can help to better target efforts to eradicate the invader by identifying currently preferred habitat. Beavers build dams that are easily discerned in high resolution images and I used those images to study changes in beaver abundance and habitat use over time in the steppe, and to ask if there is any sign of density dependence as the beaver population has increased. Chapter three has been published in *Biological Invasions* and includes Mariano González-Roglich as the second author.

Finally, in chapter four, I build a spatially explicit individual-based model parameterized with data I collected in the field and use it to make management recommendations. I first validated my model by fitting the observed rate of spread in Patagonia since introduction. Subsequently, I assessed the efficacy of a potential management strategy in which a “fire-break” (a zone beyond the current population front in which beavers are removed) perpendicular to the population front is instituted to attempt to prevent further northward spread of the beaver in continental Patagonia. I assess how the width of the fire-break and the fraction of beavers culled within the fire break influence whether it will stop or slow the invasion. Chapter four has not been submitted yet but I anticipate Gina Himes Boor and William Morris will be coauthors.

I would like to present my dissertation, not as a thesis on beaver biology, but rather, as a piece of research that studies the biology of an invader using beavers as a case study. Broadly speaking chapter one shows that propagule size was not a contributor to invasion success in the beaver spread on Patagonia. On the contrary, in chapter two, I show that predator release and plasticity have likely played a major role in the spread of the invasion. The enemy release hypothesis, in particular, has found strong support in plants but only a few studies have been conducted on other groups, such as vertebrates. In chapter two, we also found differences in the demography of the invaders between habitats although these are probably caused by negative density dependence in sites invaded a long time ago. Chapter three shows density dependent habitat selection in the steppe. Although invasions seem to be an excellent model to test these theories, I was surprised by how little research has been conducted in this area, perhaps because we have less data on what occurs at the intermediate stages of an invasion. Last, in chapter four, I show how difficult it can be to control the invasion of a species with high dispersal capabilities that search actively for mates.

1. Origin and history of the beaver introduction in South America

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, thereafter)

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.

Table 1: 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 ^c) |
| 50 | Alberta | 1 (Fasanella et al., 2010) |
| 20 ^{a,b} or 50 | Canada | 1 (Massoia and Chebez, 1993 ^c) |
| 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) |

^aMassoia and Chebez 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.

^bThe 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”).

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

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 a few km 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 51318 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 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 13000 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 12500 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.

2. The demography of invaders in heterogeneous landscapes: Beavers as a case study

2.1 Introduction

At a coarser or finer scale all habitats are heterogeneous and organisms often respond to that heterogeneity. Habitat differences can affect vital rates which will in turn determine distribution and abundance of a species across a heterogeneous landscape. Although studies on environment-specific demography are widespread in plants, such studies focused on animals have been comparatively scarce, perhaps due to difficulties posed by detection and animal movement that are only now being addressed (Royle et al. 2013). For biological invasions, habitat heterogeneity can affect population growth rates and dispersal at the invasion front, impacting the rate of spread (Shigesada et al. 1986, Dewhurst and Lutscher 2009). Thus, understanding the effect of habitat heterogeneity on demography is particularly important in predicting the spread of biological invasions. In this paper, we quantify differences in colony sizes and vital rates of introduced beaver in two very different habitats in Patagonia: forest and steppe.

In addition to relatively fixed differences between habitats, changes to a habitat after it has been invaded may impact vital rates, affecting both the growth and dynamics of local populations and the rate at which an invasion proceeds. In some population models (Skellam 1951, Kot et al. 1996), negative density dependence behind the invasion front (which may result from habitat degradation) does not influence the speed of the invasion. However, other models have shown that density dependence can generate

fluctuating rates of spread by increasing dispersal distance in areas where resources have been depleted (Dwyer and Morris 2006). When assessing effects of different habitats on invading species, we must acknowledge that differences between habitats in the time since invasion may be confounded with inherent differences in the quality of those habitats before they were invaded.

Beavers were introduced to the island of Tierra del Fuego (TDF) in 1946 to “enrich” native fauna and foster a fur trade, and have since spread throughout the archipelago. More recently, they began spreading in continental Patagonia (Graells et al. 2015). In southern Patagonia, beavers: negatively impact recruitment of *Nothofagus* spp., the dominant trees in riparian forests (Anderson et al. 2006b, Martínez Pastur et al. 2006); create entirely new habitats that allow establishment of other invasive species (Anderson et al. 2006b, Henn et al. 2014); and affect food webs of streams (Anderson and Rosemond 2007, Anderson and Rosemond 2010). Beavers first established in the forests in which they were initially introduced but by the 1990s began to establish in the adjacent steppe (Skewes et al. 2006, Anderson et al. 2009).

Beaver impacts on subantarctic forests have been well investigated, but no detailed studies on demography of invasive beavers in any habitats in Patagonia have been conducted to date. Demographic information can be useful to better understand and manage the ongoing beaver invasion. For instance, predator release has been suggested as a major driver of the invasion (Wallem et al. 2007); here we test this

hypothesis by comparing survival rates of beavers in Patagonia with those of beavers in North America. If predation is what regulates beaver populations in the native range, this comparison may give us information on the level of culling needed to control further spread of the invasion. Beavers are also known to adjust fecundity in response to habitat quality and increased density. Gunson (1970) found that beavers in low quality habitats show high frequency of resorption of embryos resulting in fewer offspring (“kits”) per female beaver. Bergerud and Miller (1977) and Payne (1984b) showed that mean litter size decreased as density increased in Canada, but high densities can also cause delayed reproduction of juveniles due to decreasing availability of new territories (Bergerud and Miller 1977, Busher and Lyons 1999). Differences in fecundity between habitats will likely affect the spread of the invasion in heterogeneous landscapes.

In Patagonia, successful establishment of beavers in the semiarid steppe has challenged previous studies assuming that steppe was unusable habitat. Lizarralde et al. (2004) and Wallem et al. (2007) suggested that low density of beaver colonies in the steppe could reflect poor habitat quality, although animal density can be a misleading indicator of habitat quality (Van Horne 1983, Battin 2004). Skewes et al. (2006) reported lower colony densities and assumed lower colony sizes in the steppe compared to the forest when estimating total abundance of beavers in TDF. Poor demography in the steppe could slow the spread of the invasion, but the few data reported on the rate of

spread suggest that it is at least as fast and perhaps faster in the steppe (Skewes et al. 2006), which could be due to differences in demography, movement, or both.

Heterogeneity within major habitat types can also affect vital rates. At the scale of individual beaver colonies, research in northern hemisphere forests has shown an association between food availability and colony size and recruitment. For example, Fryxell (2001) found higher colony sizes and more kits per colony in areas with high woody cover and aquatic vegetation. Within-habitat differences in vegetation variables can improve our understanding of what drives demographic differences between forest and steppe. On the other side of the coin, absence of difference within or between habitats can be a sign of invader plasticity, which has been cited as a major predictor of invasion success in mammals (González-Suárez et al. 2015).

The goal of this paper is to compare demography of invasive beavers within and between habitats in Patagonia, and between Patagonia and North America. To do this, we estimated: age-specific survival using mark-resight methods and telemetry; the proportion of breeding pairs producing kits using camera traps; and the mean number of kits produced per breeding pair and the overall trends for beaver colonies in the forest and steppe using repeated observations. We used these data to address four questions:

1. Do colony sizes and vital rates currently differ between forest and steppe habitats?

2. Can we identify features within these habitats that correlate with demographic variation?

3. How might the longer history of beaver presence in forests influence the current colony sizes and vital rates?

4. Do vital rates of beavers differ between Patagonia and North America?

2.2 Methods

2.2.1 Study sites

We defined four study sites on the main island of Tierra del Fuego, two in the forest and two in the steppe (Fig.1). Sites in the forest were separated at least 150 km from sites in the steppe. Forest is dominated by three tree species in the genus *Nothofagus*, and has an understory with low species richness. Annual precipitation in the forest sites ranges from 500 to 600 mm, and snow covers the ground typically between May and September. High cloud cover and proximity to the sea generate conditions of high relative humidity throughout the year and temperatures that vary between 4 and 15 °C in summer and -3 and 6 °C in winter (Martínez Pastur et al. 2006). Beavers have been present in our forest sites for at least 50 years and have impacted between 20 and 40% of the stream length (Anderson et al. 2014).

Sites in the steppe vary in cover of the dominant woody shrub *mata negra* (*Chilliostrichum diffusum*), used by beavers for food and dam construction. Annual precipitation ranges from 200 to 300 mm and snow rarely accumulates in winter.

Temperatures are similar to those of the forest sites, but strong winds and lower precipitation increase evapotranspiration and favor the growth of vegetation adapted to xeric conditions. First reports of beaver colonies in our study sites in the steppe were in the early 1990's (Lizarralde 1993).

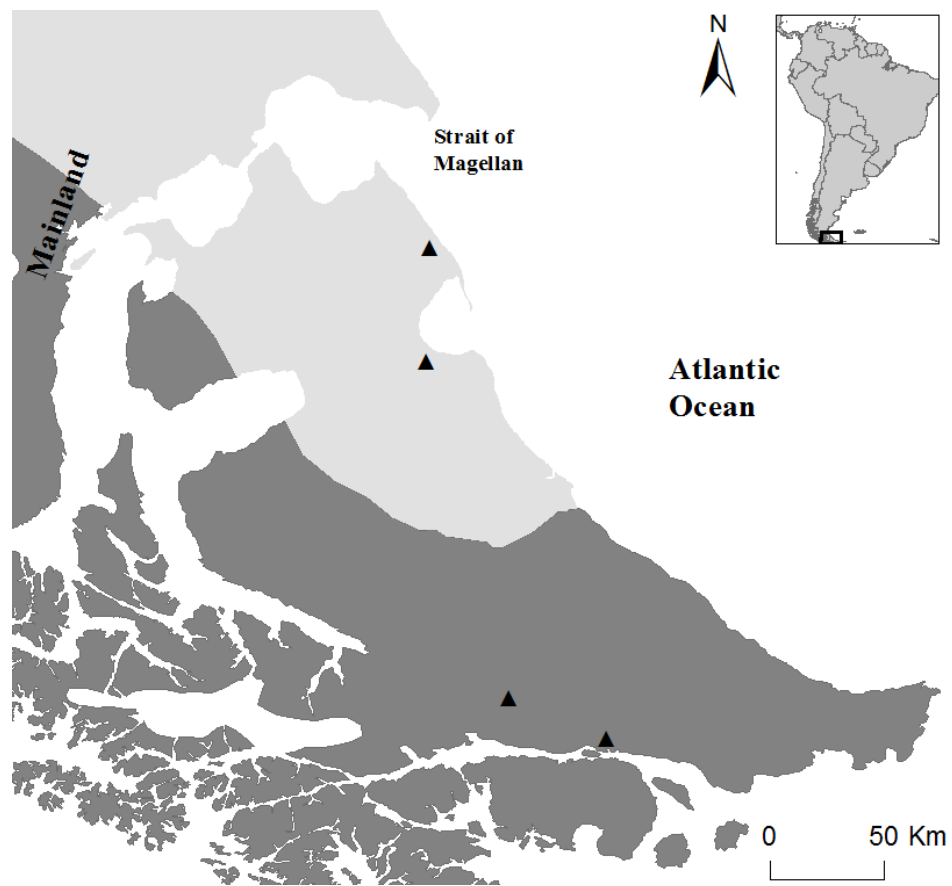


Figure 1: Location of the study sites in the forest (dark grey) and the steppe (light gray) in Tierra del Fuego, Argentina.

2.2.2 Field sampling

From 2011 to 2015 we studied 25 beaver colonies in each habitat type. At each site we observed a minimum of ten colonies, except for one of our sites in the steppe where we only had five colonies. A beaver colony usually consists of a breeding pair, newborn kits and juveniles born the previous year. Beaver kits are born around October in the southern hemisphere and juveniles may disperse after they are a year old to establish new colonies.

We conducted 2-3 repeated observations of each colony between mid-January and mid-April of each year for three years. Observations were performed with binoculars/monocular by a trained observer on non-rainy days for 2 hours before dusk, when beavers are active. Observation spots were selected to have good visibility of the focal lodge. In our study sites, hunting is rare and beavers are not wary and thus are easy to observe. We recorded the total number of individuals at each colony and the number of kits. Kits are easy to distinguish by size and behavior from juveniles and adults.

At each colony, we assessed food abundance by placing between four and six equally spaced 20 m transects perpendicular to the shoreline on the pond where the main lodge was located. Aquatic vegetation is scarce in streams in TDF and was therefore not considered in our sampling. We measured woody understory cover (in forest) and shrub cover (in steppe) by recording length and height of the vegetation

intercepted by the line transect. We estimated the proportion of vegetation cover as the total length covered by woody vegetation divided by 20.

We measured forest structure at our forest sites as follows. Centered at 7.5, 17.5, 27.5, 37.5, and 47.5 m along a 50m transect, we located 5x10m quadrats (with the 5m sides parallel to the transect). Beavers mostly forage within a 50 m distance from the pond (Fryxell 2001). At each quadrat we recorded the number of live trees higher than 150 cm, diameter of these trees at 20 cm above the ground, and number and diameter of dead trees cut by beavers.

2.2.3 Statistical models to estimate colony size and number of kits

We used N-mixture models to assess differences in colony size and number of kits per colony per year between and within habitats (Royle 2004, Kery et al. 2005). N-mixture models allow one to estimate abundance in spatially replicated populations using temporally repeated counts. Generally, the model consists of two parts, one to model the ecological state (abundance) and another to model the observation process (counts). In particular, we assume that

$$N_i \sim \text{Poisson}(\lambda) \quad \text{eq. 1} \quad \text{Ecological process}$$

$$y_{ij} | N_i \sim \text{Binomial}(N_i, p) \quad \text{eq. 2} \quad \text{Observation process}$$

where N_i is the true local abundance at colony i , drawn from a Poisson distribution with mean λ , y_{ij} is the number of individuals observed at site i at time j

(counts) and p is the probability of detection for each individual. In our case we used colony size as a measure of local abundance.

To account for temporal trends in colony size for each habitat, we simplified the model formulated by Kery et al. (2009). This is an open N-mixture model, in which changes in colony size may occur between years but we assume no changes within years so that counts within years provide information on the detection probability. We modeled λ and p as a function of covariates such that:

$$\log(\lambda_{ik}) = a_{\text{habitat}_i} + r_{\text{habitat}_i} \times (k - 1) \quad \text{eq. 3}$$

$$\text{logit}(p_i) = c_{\text{habitat}_i} \quad \text{eq. 4}$$

Equation 3 indicates that colony size can vary by habitat at site i and year k . a_{habitat_i} is an intercept that represents log colony size at year 1 in the habitat i , and r_i represents a constant annual population growth rate in habitat i . Equation 4 assumes detection probability p_i at colony i depends only on the habitat at colony i , as we did not have enough data to estimate a different detectability for each year. Specifically, c_{habitat_i} is the intercept that represents a constant probability of detection in habitat i . We applied this log-linear Poisson model to the colony size data to estimate habitat-specific average colony sizes, growth rates, and detectabilities.

Variables determining the size of a colony within habitats should have a consistent effect over time. To study how vegetation variables affected colony size within habitats we ran separate single- season N-mixture models for each year and habitat. For our models we chose to incorporate vegetation variables to predict colony size and we assumed a constant probability of detection p across sites. Assuming constant detectability was preferred as these models may be hard to fit with small sample sizes, particularly if the number of predictors is high, and we were more interested in determinants of colony size than of detectability. Models for the forest had the understory cover, its height, and the median tree diameter as potential predictors of colony size. Models for the steppe included shrub cover and height of the shrub cover as potential predictors.

To model the number of kits produced per colony per year, we again used N-mixture models, but assumed that the true number of kits varied among colonies according to a zero-inflated Poisson distribution. Under this model, colonies may have no kits as a consequence of both a Bernoulli process and a Poisson process. The hierarchical model has the structure

Level 1 (kits produced, colony i , year k) $z_{i,k} \sim \text{Bernoulli}(\Omega)$ eq.5

Level 2 (true number of kits, colony i , year k) $K_{i,k} \sim \text{Poisson}(z_{i,k}\kappa_k)$ eq. 6

Level 3 (observed number of kits, colony i , year k) $x_{i,k} \sim \text{Binomial}(K_{i,k}, p_i)$ eq. 7

where Ω is the probability that a colony will have one or more kits (assumed to be constant for all colonies and years in a given habitat), $z_{i,k}$ is a random variable indicating whether kits were ($z_{i,k} = 1$) or were not ($z_{i,k} = 0$) produced in colony i in year k , κ_k is the Poisson mean number of kits per colony in year k , $K_{i,k}$ is the true number of kits in colony i in year k (and includes the probability that a colony produces zero kits), p_i is the probability of detection of each kit in colony i (which only depends on the habitat type in colony i), and $x_{i,k}$ is the observed number of kits in colony i in year k . As before, we estimated each of the parameters using the appropriate link function. To model variation in the number of kits within habitats we took the same approach that we followed with colony sizes, so that only number of kits – not detectability - was modeled as a function of vegetation covariates.

2.2.4 Estimation using camera traps of the proportion of colonies producing kits

Although in principle we can estimate the proportion of colonies producing kits for each habitat, using eqs. 5 to 7, estimates of Ω can be biased especially when Poisson counts are low or the number of colonies is small. Therefore, we assumed Ω was the same for forest and steppe in our N-mixture models (eq. 5). To independently estimate the proportion of colonies producing kits, we used camera traps in the last year of our study. To do this, we selected 22 colonies (11 in each habitat) and placed camera traps for three consecutive nights in each colony. The number of colonies was limited by the presence of good sites to place camera traps. We selected sites to place camera traps after watching where beaver families spent more time in our repeated observations. We considered each night to be an observation, and we assigned a 1 to nights when kits were observed and 0 otherwise. We used an occupancy model corrected for detectability (MacKenzie et al. 2002) where occupancy is just the presence of kits in a colony:

$$z_i \sim \text{Bernoulli}(\Omega_c) \quad \text{eq. 8}$$

$$y_{i,j} | z_i \sim \text{Bernoulli}(z_i p) \quad \text{eq. 9}$$

Here z_i is the true occurrence ($z_i = 1$ if site i has kits and 0 otherwise) and is governed by Ω_c (probability of a colony having kits). Observations (or camera-trap nights) provide information about p , although p here refers to the probability of detection of at least one kit using camera traps. We modeled the probability of detection

and/or the proportion of colonies having kits as functions of habitat covariates as we did with N-mixture models before.

2.2.5 Estimation of survival using mark-resight and telemetry

Every year, between December and April we live-trapped beavers in the same beaver colonies we observed, using snares with a relaxing lock (McKinstry and Anderson 1998). After trapping, we waited at least three days before resuming repeated observations and camera trapping to allow the colony to resume normal activity. Snares were set the day before and were checked early in the morning to minimize the time beavers were held in the traps.

Captured beavers were manually restrained by two people without using anesthesia, and we covered their eyes to relieve stress. We placed uniquely colored ear-tags (Dalton ID) on captured beavers that can be seen with binoculars when observing colonies. Beaver ears were wiped prior to piercing with a diluted chlorhexidine solution to prevent infections. We used the repeated observations we detailed in the previous section to gather information on beaver survival through mark-resighting.

We attached beaver tail transmitters with a mortality sensor (Advanced Telemetry Systems, Isanti MN, USA) to juvenile and adult beavers (Arjo et al. 2008). Transmitters weighed 35 g and had a battery life of 500 days. Transmitters were fitted quickly by drilling a 5 mm hole with a cordless drill in the beaver's tail, offset from the center line where the tail is composed mainly of fatty tissue. We applied a solution of

sulfadiazine to the hole to avoid potential infections and facilitate healing. Beavers were sexed by palpation of the baculum (Osborn 1955) which was later corroborated using molecular methods with hair samples (Goldberg et al. 2011). We weighed beavers with a spring scale and released them at the site where capture occurred. All capture and handling protocols were approved by the Duke University Animal and Care Committee and the wildlife office of the province of Tierra del Fuego, Argentina.

We checked beaver survival using telemetry every two weeks between November and April in each habitat. When we detected a mortality signal we located the radio-transmitter to confirm death or tag loss. In addition to this, we flew over the study area in a small airplane equipped with a telemetry antenna at the end of each field season to relocate animals that may have dispersed.

2.2.6 Estimation of kit survival

Because only individuals heavier than 7 kg can be radio-tagged, we separately estimated survival of kits and survival of juveniles and adults. We used weight to define age classes and followed the criteria established by Feldman (2015), such that individuals that weighed more than 5 kg at the time of capture were considered juveniles older than a year. Kit survival was therefore assessed only through mark-resight. We used a Cormack-Jolly-Seber model with a robust design (Gimenez et al. 2007) to estimate kit survival. As the total number of captured kits was small ($N = 18$) we

pooled kits from forest (N = 5) and steppe (N = 13) and estimated yearly survival and detection assuming they did not differ by habitat.

2.2.7 Estimation of survival of juveniles and adults

We captured 91 adults and juveniles (forest N= 30, steppe N= 61) and radio-tagged 51 of them. As both juveniles and adults could have had either ear tags only or both ear tags and radio tags, we fitted a multistate capture-recapture model to estimate monthly survival (Lebreton et al. 2009). We transformed monthly survival to yearly survival and approximated the variance using the delta approximation (Powell 2007). Our data set was built by compiling individual encounter histories during 52 months of study. We defined 5 observation states for individual beavers: alive with radio tag, alive without radio tag (ear-tags only), dead with radio tag, dead without radio tag, and not observed. Details on the construction of our model are given in Appendix B. More generally the model included estimates of survival using telemetry, survival using mark-resight data, the probability of transitioning from the telemetry group to the mark resight group (i.e., transmitter stopped working or was lost), and habitat specific probabilities of detection. Because of limited sample size, we assumed survival was the same in forest and steppe, a reasonable assumption as adults and juveniles do not have known predators in either of these habitats in Tierra del Fuego.

2.2. 8 Parameter estimation

We adopted a Bayesian approach to fit all models in our study. We used vague, non-informative priors for our parameters. We fit our models using JAGS (Plummer 2003). To compute posterior distributions, we ran three chains of the MCMC algorithm for 300,000 iterations, discarded the first half, and thinned the remainder to one in 10 to obtain 15,000 samples of the posterior. We checked for convergence in our estimates such that all our parameters showed Gelman-Rubin statistics that were less than 1.1. In addition, we tested model adequacy of N-mixture models by conducting a posterior predictive check (Gelman and Meng 1996), and by visually inspecting plots of the discrepancy between the distribution of the chi-square statistic for actual and replicate data.

2.3 Results

Colony size in the steppe was larger than in the forest in all three years of the study (Fig. 2). Colony size remained relatively constant over years in the forest (mean growth rate r_{forest} , 95 % CRI; -0.04, -0.22-0.14), while there was a slight increase over time in colony size in the steppe (mean growth rate r_{steppe} , 95 % CRI; 0.12, -0.01-0.27). Probability of detection was higher in the steppe compared to the forest (p , 95 % CRI; forest, 0.49, 0.29-0.64; steppe, 0.57, 0.40-0.70).

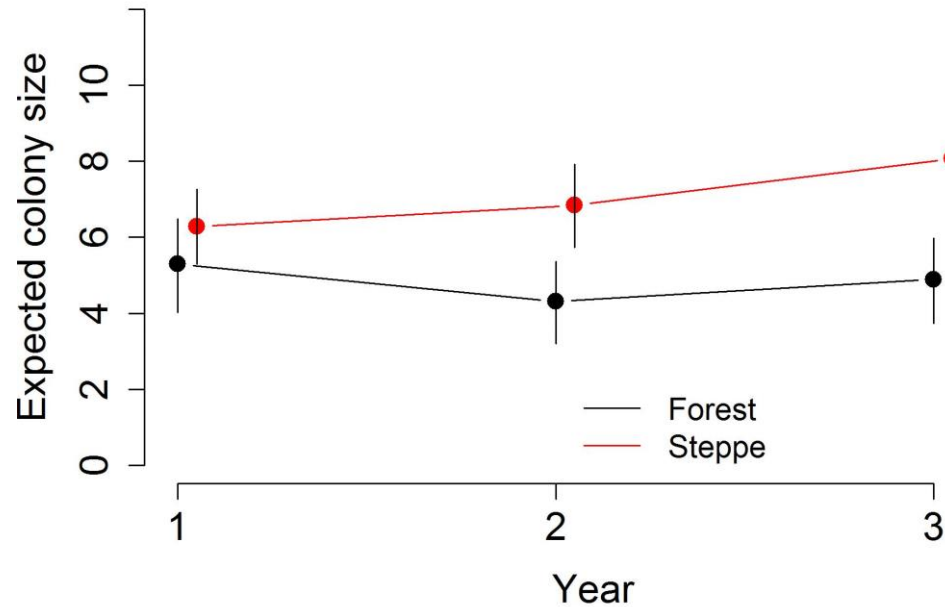


Figure 2: Mean yearly colony size (\pm posterior SD) for the forest and the steppe

Within-habitat heterogeneity impacted colony sizes differently in the forest and the steppe. In the forest only the median tree diameter was consistently negatively correlated with colony size across years, although the effect was close to 0 the second year (Table 1, Appendix A). Accordingly, cut trees were smaller in diameter than standing trees. In the steppe, none of the vegetation variables showed an important and consistent effect in our study (Table 2, Appendix A). Interestingly, we recorded some of the largest colony sizes in the steppe in areas with little or no shrub cover.

We also found a trend toward a higher number of kits per colony in the steppe compared to the forest (Fig.3). This model was run for 500,000 iterations to achieve better convergence estimates. The probability of detection of kits in the steppe was much higher than in the forest (p , 95% CRI; forest, 0.19, 0.04-0.49, steppe, 0.63, 0.29-1). We did not incorporate covariates to model Ω which was close to 0.8 (Ω , 95% CRI; 0.77, 0.6-0.91). Zero inflated Poisson models of the number of kits fitted for each year resulted in very imprecise coefficient estimates, probably because of the combination of small sample size and a high number of covariates (Tables 3 and 4, Appendix A). Thus, we were unable to assess the effect of within habitat heterogeneity on the number of kits. Overall, the mean litter size was similar to values reported by studies in the native range, with the number of kits in the forest falling in the lower end of the range (Table 2).

Camera traps helped us to assess with greater confidence whether the proportion of colonies with kits differed between habitats. Given we had a small data set and we could not fit covariates for both the proportion of colonies with kits and the probability of detection, we determined which model to fit as follows. We compared the fraction of colonies where kits were recorded at least once with the raw probability of detection. The raw probability of detection was calculated as the number of nights a kit was recorded by our camera traps divided by the total number of observations (camera trap nights). We found that the raw proportion of colonies producing kits did not vary as

much between habitats (forest, 0.72; steppe, 0.63) as the raw probability of detection (forest, 0.5; steppe, 0.76).

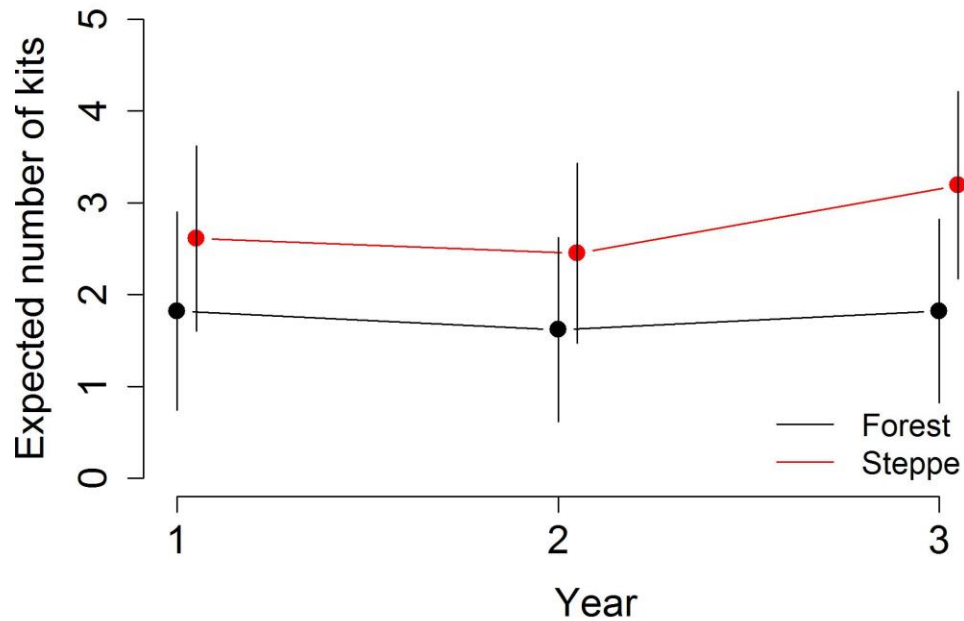


Figure 3: Mean yearly number of kits (\pm posterior SD) for the forest and the steppe.

Thus, we decided to fit an occupancy model where detection, but not the proportion of colonies with kits, varied by habitat. Under this model the corrected proportion of colonies with kits was 0.76 (95 % CRI; 0.68-1), while an estimation of the proportion of colonies producing kits using estimates of the zero inflated Poisson model was close to 0.69 . Detection (now of kits, not of all individuals as above) was again higher in the

steppe (p, 95% CRI; forest, 0.43, 0.24-0.65; steppe, 0.71, 0.42-0.9).

Estimates of kit survival were imprecise given the small sample size (mean survival, 95% CRI, 0.66, 0.39-0.94). An interesting detail of our data is that mortality sensors in the radio tags allow us to separate mortality from permanent emigration. Of our radio-tagged beavers only 5 died (2 in the forest and 3 in the steppe). Yearly survival derived from telemetry was very high (mean, SD, 0.97, 0.02) and apparent survival estimated from mark resight data (which includes permanent emigration) was much lower (mean, SD, 0.68, 0.06) suggesting permanent emigration was common, as one would expect in juveniles and young adults. Both kit survival and the pooled survival rate of adults and juveniles were much higher than survival rates estimated from radiotelemetry data in North America (Table 3).

Table 2: Mean litter sizes of beavers reported in scientific literature.

| Mean litter size | Location | Study |
|----------------------------|------------------------------|-------------------------------|
| 1.7-2.7 ¹ | Newfoundland (Canada) | Bergerud and Miller (1977) |
| 2.7 | Ohio (USA) | Svendsen (1980) |
| 1.5-2.7 ¹ | Newfoundland (Canada) | Payne (1984b) |
| 3.5 | Illinois (USA) | Bloomquist and Nielsen (2010) |
| 2.5 | Illinois (USA) | Havens et al. (2013) |
| 1.7 (forest)- 2.7 (steppe) | Tierra del Fuego (Argentina) | This study |

¹ Range reported over three years study

Table 3: Mean survival rates of juvenile and adult beavers using telemetry reported in scientific literature.

| | Survival juveniles | Survival adults | Location | Study |
|----|--------------------------|-----------------|------------------------------|--------------------------------|
| | 0.29-0.59 ^{1,2} | 0.29-0.59 | Illinois (USA) | Havens et al. (2013) |
| | 0.36 | 0.66 | Wyoming (USA) | McKinstry and Anderson (2002) |
| | 0.43 | | Illinois (USA) | McNew and Woolf (2005) |
| | 0.67 | | Wyoming (USA) | VanDeelen and Pletscher (1996) |
| 35 | 0.55-0.76 ³ | 0.76-0.87 | Illinois (USA) | Bloomquist and Nielsen (2010) |
| | 0.82 | 0.88 | Massachusetts (USA) | DeStefano et al. (2006) |
| | 0.89 | | Illinois (USA) | Cleere (2005) |
| | 0.97 ¹ | 0.97 | Tierra del Fuego (Argentina) | This study |

¹ Juveniles and adults were pooled to obtain a single survival estimate

² Estimates for the first and second year of the study.

³ Survival was estimated for females and males separately.

2.4 Discussion

In our study we used several robust statistical methods to best estimate colony sizes and vital rates of invasive beavers in different habitats in Patagonia. Colony size and the number of kits produced per colony were higher in the steppe compared to the forest, but we were unable to detect differences in all other vital rates between habitats. Survival of juvenile and adult beavers was very high relative to the native range, suggesting predator release may be a major driver of the invasion. In the coming paragraphs, we will discuss the main reasons for the success of the invasion examine the evidence for density-dependence and make recommendations based on our results, for how the beaver invasion in Patagonia should be managed.

Several factors explain why beavers have been so successful in Patagonia. First beavers are very plastic in the type of habitats they can use. The higher colony size and number of kits produced, along with a trend towards increasing colony sizes in the steppe, highlights not only that beaver populations can thrive in the steppe but that steppe can play an important role in the spread of the invasion. Trends in the number of kits are similar to those found for colony sizes and we believe that higher colony sizes in the steppe are at least partially related to a greater kit production there. Although Figure 3 is not conclusive regarding differences in the number of kits between forest and steppe two additional pieces of evidence confirm this trend. First, the number of kits captured in the steppe was almost 30 % higher than in the forest. Second, detection of kits in

highly conspicuous beaver trails using camera traps was also higher in the steppe and higher detection would suggest higher abundance (Royle and Nichols 2003).

The second reason for beaver's invasion success is that, as in North America, they have the ability to utilize the best location within habitat types, even when they can thrive under a range of conditions. The median of tree diameter was correlated (negatively) with colony size in the forest. Beavers usually selected smaller trees in the forest, as cutting down large trees represents a cost of both greater predation risk and higher provisioning time (Fryxell and Doucet 1993). Although we did not find any consistent predictors of colony size in the steppe, colony size and the number of kits produced per colony were high even in areas with no woody vegetation cover in the steppe, which suggests that beavers are extremely adaptable and can rely on herbaceous vegetation only. This may be particularly true in Tierra del Fuego where winters are milder than in northern Manitoba, where the beavers originally introduced into TDF were obtained (Pietrek and Fasola 2014). Other studies showed that the availability of woody vegetation cover does not necessarily correlate positively with site occupancy (Beier and Barrett 1987, Hartman 1996, Suzuki and McComb 1998). Phenotypic plasticity and more specifically habitat breadth have been cited as a main predictor of invasion success in mammals (González-Suárez et al. 2015). For invasive beavers in Patagonia, the ability to utilize diverse habitats has been an underappreciated contributor to invasion success.

The third reason for the beaver's invasion success is likely to be release from predators, and perhaps diseases as well. Survival of juveniles and adults was among the highest reported in the literature (Table 2). We argue this is probably a consequence of predator release. Another factor that often impacts beavers in their native habitat is the bacterial disease tularemia, but the only study on beaver diseases did not find tularemia in Patagonian beavers (Skewes 1999). Two out of the five deaths we reported in our study were the result of trapping of nuisance beavers or shooting, which is occasional in our study sites and has remained low in most of Tierra del Fuego. Pumas (*Puma concolor*) could prey upon beavers in continental Patagonia but it is hard to determine how this will impact beaver survival. In areas of their native range wolves and coyotes seem to be their main predators (Muller-Schwarze 2011).

Particularly for juveniles, an associated cost of dispersal is an increase in mortality (DeStefano et al. 2006, Muller-Schwarze 2011). Mortality can be caused by predation, human-beaver encounters or intraspecific encounters, among other causes. Human-beaver encounters occur (as we mentioned above), but probably at much lower rates than in populated areas in North America (DeStefano et al. 2006). We only found one beaver at one of our study sites in the steppe that presented injuries that may be ascribed to a conspecific fight. We did however find that survival was lower for kits than for juveniles and adults, as other studies report. Payne (1984a) found as low as 48% of beaver kits survive to the first six months, and Bloomquist and Nielsen (2010) reported

survival rates of 0.28 for the first 11 months. Although imprecise given the small size of our sample, estimates of kit survival were also higher in our study than these North American estimates. Beaver kits that venture far from the lodge could be preyed upon by foxes (*Lycalopex* spp.) or raptors in Tierra del Fuego, even though these predators are unlikely to be able to kill the larger juvenile and adult beavers.

Our study adds further evidence in favor of the enemy release hypothesis in vertebrates. Although frequently cited as a driver of invasion success, evidence supporting the enemy release hypothesis has been partial and overwhelmingly biased to plants studies (Keane and Crawley 2002, Colautti et al. 2004, Liu and Stiling 2006). In a recent review, Jeschke et al. (2012) revealed that five out of eight studies on vertebrates but 54 out of 106 studies on all species combined show some support to the enemy release hypothesis, suggesting that introduced vertebrates are in fact more likely to experience enemy release.

Classic invasion theory predicts that successful invaders should exhibit early reproduction and high fecundity, which will lead to high population growth rates (Pimm 1991). However, Sæther et al. (2004) found that longer reproductive lifespans are associated with higher establishment success in birds. According to this work, small populations are more prone to extinction because they are short-lived. In a recent paper, Capellini et al. (2015) showed that long lifespans and large litters are traits that characterize successful introduction and establishment of mammal invaders. Further,

their work showed that spread of mammal invaders after successful establishment can also be predicted by the age at the first reproduction. All these traits (potentially large litter sizes, long reproductive spans and early maturation) have been reported in beavers (Boyce 1981), and shed light on other factors that facilitated beaver spread in Patagonia.

Lower colony sizes and number of kits in the forest may be a sign of density dependent regulation in beaver populations. Colony density at our study sites in forest is certainly at the upper end of the highest densities recorded, and in contrast to the steppe (Pietrek and González-Roglich 2015), most suitable sites in the forest have been occupied. Our finding that larger tree diameters can negatively affect colony size in the forest combined with the absence of any vegetation effects in the steppe supports the hypothesis that because beavers have occupied the forest for a longer period of time, they are now experiencing negative density dependence there but not in the steppe. Observed speeds of invasion in the forests of continental Patagonia (Sanguinetti et al. 2014) suggest forest should have originally been at least as productive as the steppe now is. Lower litter sizes have been reported at high colony densities (Bergerud and Miller 1977, Payne 1984b). However, we did not observe differences between habitats in the proportion of colonies producing kits in the last year of our study.

In table 1 we compared litter sizes reported for beavers in North America with those in our study. We have here included only studies in North America that used observations or complete colony removal to estimate the number of newborns. Other

studies have looked at the number of embryos or placental scars in females, which overestimate the number of kits. The mean number of beaver kits we found in the steppe is consistent with most other work in North America. The lower number of kits in the forest agrees with the work of Payne (1984b) who reported mean litter sizes as low as 1.5 kits/colony at high densities.

Juvenile survival and fecundity are thought to be among the first vital rates to decline in response to density dependence in large mammals. Eberhardt (1977) proposed that in marine mammals increases in density should affect first early age survival, then fecundity and finally adult survival. Gaillard et al. (2000) confirmed that pattern using large ungulates as a model. Although we could not separate kit survival in forest and steppe, fecundity seems to be declining in forested areas invaded a longer time ago while survival of adults remains high in both habitats. Thus, beavers could be another instance of this general pattern found in larger mammals, but further study to get a better estimate of kit survival is needed to support this hypothesis.

Many studies on the spread of the invasions assume that negative density-dependence does not affect the speed of the invasion at the front. Although, we did not study vital rates at the front, more recently colonized areas showed better demography than areas invaded a longer time ago, suggesting that the influence of negative density-dependence is weaker near the front. While demography near the front may be the

major contributor to the speed of the invasion, changes in dispersal as a consequence of changes in density may also affect the speed of the invasion.

Our results have important implications for managing the spread of the beaver invasion in Patagonia. First, we should leave behind the traditional view of the steppe as suboptimal habitat that cannot support the invasion, and instead encourage active management, particularly in areas of the steppe that can be a source of propagules to mainland Patagonia. Moreover, as detectability is higher in the steppe, this may be a better place to monitor beavers and thus, to cull the population. Second, high survival is likely a major driver of the invasion. In previous work we have conducted using an integrodifference equation structured model (Neubert and Caswell 2000), we simulated the beaver invasion using vital rates of the species in North America. The speed of the invasion was highly sensitive to increase in adult survival and the increase in survival rates had a much higher impact on the invasion speed than the increase of the mean dispersal distance (Pietrek, unpublished). Third, all other things being equal, areas that were invaded longer ago will contribute proportionally less to the spread of the invasion than more recently invaded areas for two reasons: lower fecundity and lower proximity to the invasion front. Lastly, the new demographic data on beavers in Patagonia that we have presented here should be useful for parameterizing more realistic population models to better manage the ongoing beaver invasion in continental Patagonia.

3. Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe

3.1 Introduction

Much of the theory on ecological invasions has addressed the determinants of the speed of invasion (Skellam 1951, Kot et al. 1996, Hastings et al. 2005). These studies have focused on the invasion front, defined as the points in space where population density has reached a threshold level. But perhaps as important as the rate of movement of the invasion front are changes in the distribution and abundance of the invader behind the front, after the invader has become established. Demographic or behavioral responses behind the front may reflect density dependent feedback, and may shed light on the ultimate abundance toward which the established invader population may tend, as well as the ultimate fraction of the landscape that will be affected (Dwyer and Morris 2006, Pачepsky and Levine 2011, Ehrlén and Morris 2015).

Resources competition is one way in which density dependence can limit abundance and distribution of organisms. For instance, Pimm et al. (1985) found that blue-throated hummingbirds (*Lampornis clemenciae*) preferred high sucrose feeders rather than low sucrose feeders at low densities, but this preference vanished as density increased.

Changes in habitat selection patterns with increasing density have been found for mice, ants and fish, and have given rise to mechanistic theories of density dependent habitat selection (Fretwell and Lucas 1969, Rosenzweig 1981). Biological invasions are good models to study density dependent habitat selection, although this has been rarely

tested in animal invasions or reintroductions (Nummi and Saari 2003, Armstrong et al. 2005). At the initial stages of the invasion we might see individuals selecting optimal patches, but as optimal patches fill and resource availability changes, we expect to see a weakening in habitat selection.

Twenty American beavers (*Castor canadensis*) were introduced to southern Argentina in 1946 (Pietrek and Fasola 2014). Since then, they have spread throughout the archipelago of Tierra del Fuego and mainland Chile, where they were first detected in the early 1990s (Skewes et al. 2006). Beavers change the structure and composition of the *Nothofagus* riparian forests (Anderson et al. 2006a, Martínez Pastur et al. 2006), affect native fish and aquatic macroinvertebrate assemblages (Anderson and Rosemond 2007, Moorman et al. 2009), and impact food webs of Subantarctic streams (Anderson and Rosemond 2010). More importantly, beavers create entirely new habitats in the forests of Tierra del Fuego allowing the establishment of other invasive species (Anderson et al. 2006b). Thus understanding the post-invasion changes in habitat use by beavers is important for gauging their impacts on native species and ecosystems. In Tierra del Fuego, beavers first established in the forests in which they were introduced, but by the 1990s beavers began to establish in the adjacent steppe where very little research has been conducted to date (Lizarralde 1993, Skewes et al. 2006, Wallem et al. 2007). Factors affecting beaver settlement and dam building in North America include vegetation cover, stream gradient, bank slope and hydrological order among others

variables (Dieter and McCabe 1989, Barnes and Mallik 1997, Suzuki and McComb 1998). However, most of these studies have looked at native populations with a long settlement history. But near carrying capacity, beaver colonies could be settling in suboptimal sites that other beavers left unutilized. For instance, John et al. (2010) found reintroduced European beavers (*Castor fiber*) were more likely to settle in areas with steeper gradients, smaller watersheds, and closer to roads 12 years after their initial release. Recent spread of beavers in the Patagonian steppe sets up a unique scenario to test this hypothesis.

Another important factor that may influence the probability of beaver settlement is the proximity of established colonies. At a small scale beavers can expand their home range by impounding new areas nearby, but at a larger scale new ponds can provide insight into the dispersal distances of beavers. A study on beaver dispersal in New York State found that 88 % of the dispersers moved to a location within 5 km from their native colonies (Sun et al. 2000). What we do not know is what dispersal distances are in newly invaded regions, and whether those distances change post-establishment.

Our objectives in this paper were: 1) to quantify the increase in the number of ponds and the area impacted by beavers over time in an invaded area of the Patagonian steppe; 2) to identify what landscape features invasive beavers select at different stages of the invasion; and 3) to understand how the proximity of neighboring colonies affects the likelihood that a site will become colonized.

3.2 Methods

3.2.1 Study area

We selected a 500 km² area of mixed steppe in northern Tierra del Fuego, Argentina, based on high resolution satellite image availability (Figure 4). Annual rainfall ranges from 200 to 300 mm. Altitude varies from sea level close to the Atlantic, to 300 meters to the west of the study area. Shrub cover is dominated by the woody plant *mata negra* (*Chilliostrichum diffusum*) used by beavers for food and dam construction and ranges from 0 to 60 % shrub cover. Geomorphology has been shaped by glacial, marine, and glaciofluvial processes that established the canyons and valleys where the major watercourses flow (Rabassa et al. 2000).

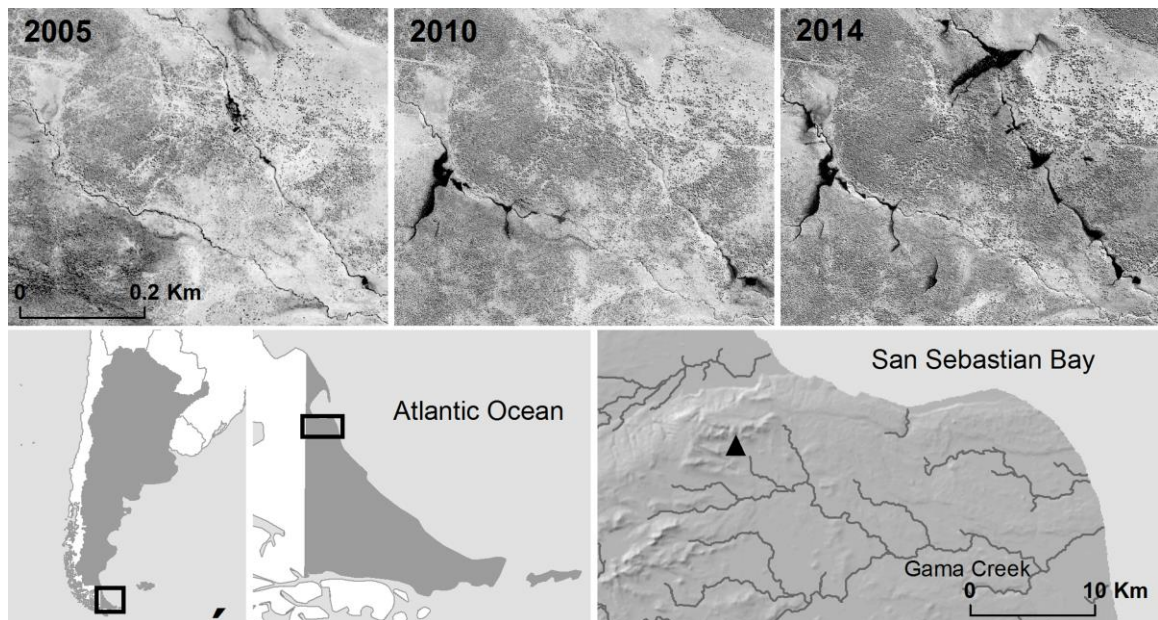


Figure 4: Bottom row: Detail of the study area, the triangle indicates location of the top row images. Top row: High resolution satellite images. No ponds are distinguished in 2005, but new ponds are formed in 2010 and 2014.

The study area is part of one of the largest private ranches in Argentina, *Estancia Sara* (53°25'59"S, 68°10'59"W"), which is mainly dedicated to sheep farming and oil and gas extraction. Beaver ponds were first detected here in the early 1990s (Carlos Mann, pers. comm., Lizarralde 1993) and beaver hunting and dam destruction is only occasional and restricted to nuisance beavers. From 2011 to 2015 we have been conducting demographic studies on beavers in this ranch and the area has been prospected by air and land repeatedly. One major water course, Gamma Creek, flows through our study area to the Atlantic and is fed by several smaller streams that depend primarily on local precipitation which is mainly concentrated in autumn-winter.

3.2.2 Extraction of covariates

Beavers are the quintessential ecological engineers, building dams that are easily discerned in high resolution images by their morphology (Meentemeyer and Butler 1995). This is particularly true in semiarid shrubby environments where tree interference is absent. Beavers can also dig bank holes in river slopes of high order rivers (Breck et al. 2001), not impounding water, but this is rare in stream systems (Barnes and Mallik 1997, Collen and Gibson 2001) such as our study area where beavers frequently build dams. For this study we used satellite images to determine beaver ponds location and extent over time. The images used were from October 2003 (Quickbird panchromatic, 60 cm),

August 2005 (Quickbird multispectral, 60 cm), March 2010 (Geoeye panchromatic, 50 cm), and March 2014 (Worldview panchromatic, 50 cm). Images were already georeferenced, and since no major alignment errors were identified, no correction was needed. Upon visual inspection of the images (scale 1:3,000), ponds were identified and a polygon hand-drawn to delineate each one using ArcGIS 10.2.2 (ESRI 2014). From this dataset we estimated the number of ponds per year and their total area. As images from 2003 covered only half of the study area, we separately analyzed the increase of the number of ponds for half of the study area between 2003 and 2014 and for the entire study area between 2005 and 2014. Likewise, we only used years 2005, 2010, and 2014 for the analysis of habitat selection and establishment of potential new colonies.

Topographic features determine water movement along the landscape, and can consequently affect beaver dispersion and establishment in the Patagonian steppe. We used a 30 m digital elevation model (DEM) from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER-GDEM V2) (Tachikawa et al. 2011) to derive a set of covariates which could affect pond establishment. A 30 m pixel size was considered appropriate for this study, given that it approximately matches the mean size of beaver ponds (~850 m²). Due to the lack of a detailed hydrologic map of the study area, we used the DEM to develop a stream dataset based on the accumulation of upstream cells using Spatial Analyst hydrology tools in ArcGIS (ESRI 2014). All cells with an accumulated flow of at least 100 units were classified as streams. As we did not have

an actual measurement of stream flow we used catchment area as a proxy to flow and likelihood of flooding which are arguably important features for pond establishment. Catchment area of each pixel in the stream network was defined as the up-stream area draining through that particular pixel, and was determined using the flow accumulation raster. Stream gradient was estimated for each cell in the stream network as mean percent change in elevation for a 120 m long section, 60 m upstream and 60 m downstream of the corresponding cell.

We considered available habitat to be all stream cells, including areas occupied by ponds. For that, we converted the hand digitized polygons to pixels matching the 30 by 30 m cells of the DEM used to create the stream network. All pixels in contact with a polygon identified as a pond in a particular year were considered used.

To describe the topographic position of each cell in the stream network (i.e. the relative position of each cell relative to its surroundings) we calculated landforms as suggested by Weiss (2001) . Of the 10 available landform types, we removed all cells with land form types with less than 3 % representation in the stream network and where use was a rare event, leaving only 4 classes: 1) Canyons and deeply incised streams (17 %), 2) U-shaped valleys (36 %), 3) Plains (30 %), and 4) Open slopes (9 %), these landforms accounted for 92 % of the available pixels in the study area.

Vegetation cover is a key attribute affecting ecosystem functioning, from water movement to the availability of resources beavers need to feed and build dams. To

estimate woody cover in the vicinity of ponds, we used the panchromatic satellite images from 2014. Using a combination of texture analysis (3 by 3 window variance) and ISODATA unsupervised classification (Ge et al. 2006); we created a land cover map with two classes: woody or non-woody. From this map we estimated percent woody cover at an aggregated scale of 1m. For each pixel of available habitat woody cover was estimated as the mean woody plant cover of a 60 m radius circular buffer around each cell. Sixty meters is along the longest distances from ponds beavers are known to forage (Fryxell 1992, Muller-Schwarze 2011). Correlation among covariates was generally low, except for vegetation cover and elevation (0.59) and therefore all variables were kept for the analyses.

3.2.3 Data analysis

3.2.3.1 Resource selection functions

We used resource selection functions (RSF) to study the variables affecting pond establishment by beavers (Boyce and McDonald 1999, Manly et al. 2002). Resource selection functions describe the relative probability of use of habitat features by animals and have been widely used in ecology (Keating and Cherry 2004, Johnson et al. 2006, Lele and Keim 2006, Northrup et al. 2013). We followed a used-availability design in which all suitable parts of the landscape are assumed to be available to the individuals but some units are preferred over others. Beavers can travel long distances (we have

recorded a 19 km dispersal event in this area using radio-telemetry) (and see Leege 1968, VanDeelen and Pletscher 1996, Sun et al. 2000), so they are likely to be able to sample all suitable units in the landscape. We decided to take all pixels occupied by watercourses in our study area as the landscape available to beavers.

As this is a non-equilibrium population, where new ponds form every year, and we wanted to understand what habitat features beavers select over time, we made availability time specific. Thus, used units at time t were not available for colonization at time $t+1$. Likewise, we defined used units at time t to be only newly occupied pixels. We set 2005 as our first year and all beaver ponds identified in 2005 defined our first used units.

To build the dataset for our analysis we sampled without replacement 5 % of the available landscape for each year and added all the used units for the corresponding year. To avoid unit overlap we removed units contained in both the available and used sample from the used sample as suggested by Manly et al. (2002). We also discarded repeated units among the available sample at different years for the analysis. In the final dataset across all years, the available sample representing 13 % of all available pixels. Used units were only 4 % of the units in the study area and ranged from 365 to 467 pixels per year.

We ran 16 logistic regression models to elucidate what variables predict beaver pond establishment (Manly et al. 2002). The dependent variable was use (1 = used, 0 = non-

used) of landscape units as previously defined. The simplest model contained all landscape variables (catchment area, elevation, landform, stream gradient, vegetation cover) and a year effect. Two more complex models included either an interaction of catchment area with stream gradient or catchment area with vegetation cover and were included based on biological grounds. Areas with little vegetation cover may not provide enough material for dam construction at high flows which can be caused by high catchment areas or steeper gradients. All other models were variants of the first three that included an interaction of year with each predictor variable for the simplest model, and an additional three way interaction with year for the other two.

We ranked models using Akaike Information Criteria (AIC)(Burnham and Anderson 2002). For the best model we estimated a RSF using the exponential function:

$$P(y = 1|\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)$$

eqn 1

where the betas represent the coefficients of the logistic regression and the x's represent the landscape variables under study. Equation 1 allowed us to estimate relative likelihoods of use, and variances of the estimators were calculated as using a Taylor's series approximation as suggested by Manly et al. (2002).

We assessed goodness of fit of our RSF function using k-fold validation (Boyce et al. 2002, Johnson et al. 2006). We used Huberty's rule of thumb to determine the optimal

training to testing ratio (Fielding and Bell 1997) and we determined a testing ratio of 20 % based on the number of model parameters. We divided the data into fifths, estimated the parameters of logistic models using 4/5 of the data and used the remaining group as the testing dataset. We repeated this analysis five times, each time computing the Spearman's rank correlation between the area adjusted frequency of cross validated points within individual bins and the bin rank. Area adjusted frequencies were simply the frequencies of cross validated points divided by the frequency of the RSF values within the bin across the study area. Predictions were divided in ten equal sized bins and rare bins occurring at the tail of the RSF scores were merged for the analysis.

3.2.4 Effect of proximity to existing colonies on establishment of potential new colonies

We were interested in making inferences about dispersal patterns in beavers based on establishment of new ponds over time. New ponds can result from expansion of preexisting beaver colonies or from the founding of new colonies. For this analysis we considered all ponds mapped between 2005 and 2014 using high resolution images. Based on the minimal distance we found between neighboring colonies in the field (Pietrek in prep.) and in the scientific literature (Bergerud and Miller 1977), we defined a potential new colony to be a pond or set of ponds at time $t+1$ that is separated at least 200 m from the closest pond at time t . Potential new colonies were only added to the dataset if they were closer to another beaver pond than to the edge of the satellite image,

as the occurrence of other ponds outside of the image could affect the probability of establishment of a potential new colony. We placed a 60 meter buffer around the center of a new colony, and we extracted the same landscape covariates used in previous analysis. For continuous variables we assigned the mean value over all the pixels included in buffers, and for landforms we assigned the habitat that overlapped more than 50 % of the pixels. The final set of landscape variables included catchment area, elevation, landform, stream gradient and vegetation cover.

We used a control-case design (Hosmer and Lemeshow 2005) in which 60 m radius buffers around the centers of potential new colonies were the sampling units and were matched to an equal sized sample of randomly located areas that did not contain beaver ponds. We built logistic regression models with all 30 possible combinations of variables and ranked models using AIC corrected for small sample size (AICc). As the number of potential new colonies was small, we combined potential colonies from 2010 and 2014 in the analysis. We added the variable Euclidean distance from ponds formed at time $t+1$ to the nearest pond at time t to the best model, and estimated the probability of a potential new colony establishment as a function of distance to the nearest pond. All analyses were performed using R version 3.1.

3.3 Results

The number of beaver ponds and the area covered by ponds increased over time in our study area (Figure 5). Analysis of the area that included an image from 2003 showed a rapid increase from 2003 to 2005, followed by a more or less linearly increase from 2005 to 2014. Overall, the number of ponds increased 85 % from 2005 (N = 117) to 2014 (N = 217) in our study area.

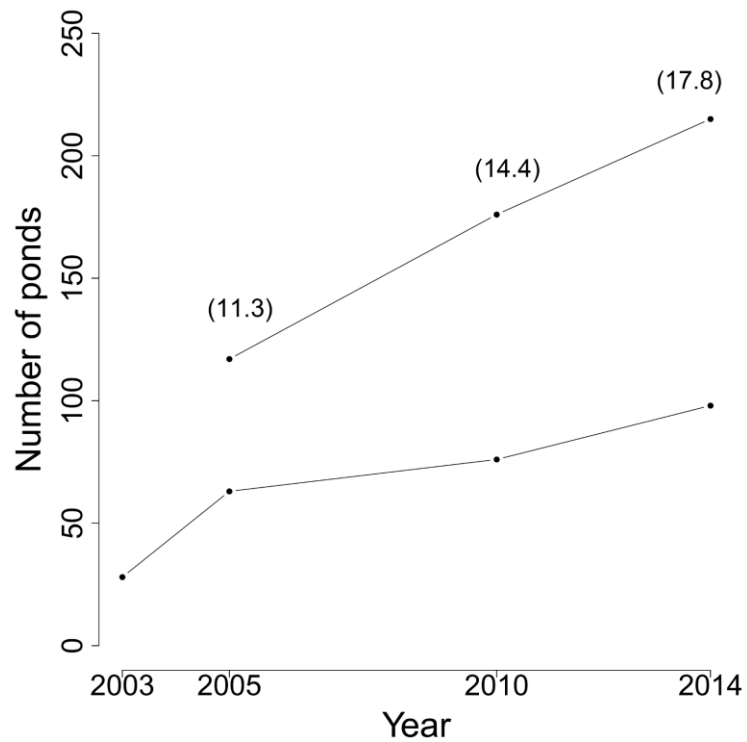


Figure 5: Increase in the number of beaver ponds for our entire study area (top) and for a subset of our study area (bottom). Numbers in parenthesis indicate the area in hectares flooded by beaver ponds.

The full model that included all variables, a two-way interaction between landform and year, and a three-way interaction between vegetation cover, catchment

area and year was ranked first among competing models (Table 4). All other models ranked at least 14 AIC units below the best model. The interaction between landform and year was selected twice among the 5 best ranked models. This suggests that habitat selection of beavers changed over time.

Table 4: Five best ranked logistic models to study resource selection by beavers. Abbreviations: CA (catchment area), CO (vegetation cover), ELEV (elevation), LA (landform), SG (stream gradient), YR (year)

| Model | K | AIC | Δ AIC | AIC Cum | |
|--------------------------------------|----|---------|--------------|---------|--------|
| | | | | wt | weight |
| CA+ CO+ELEV+SG+LA+YR+CA*CO*YR+YR*LA | 16 | 4879.81 | 0 | 1 | 1 |
| CA+ CO+ELEV+SG+LA+YR+CA*CO*YR+YR*SG | 14 | 4894.65 | 14.84 | 0 | 1 |
| CA+ CO+ELEV+SG+LA+YR+CA*CO*YR | 13 | 4897.28 | 17.46 | 0 | 1 |
| CA+CO+ELEV+SG+LA+YR+CA*CO*YR+YR*ELEV | 14 | 4899.28 | 19.47 | 0 | 1 |
| CA+CO+ELEV+SG+LA+YR+SG*CO*YR+YR*LA | 16 | 4914.71 | 34.9 | 0 | 1 |

We fit logistic models for each year to better analyze the interaction between vegetation cover and catchment area. Beavers preferred areas with low vegetation cover when watercourses were small, but at high catchment area, the probability of pond establishment increased as vegetation cover increased in 2005 (Figure 6). We found little or no difference in the probability of pond establishment at low catchment area with different levels of vegetation cover for 2010 and 2014. Smaller watercourses probably are easier to manage for beavers and vegetation cover is not as needed to build ponds as higher water flows may demand.

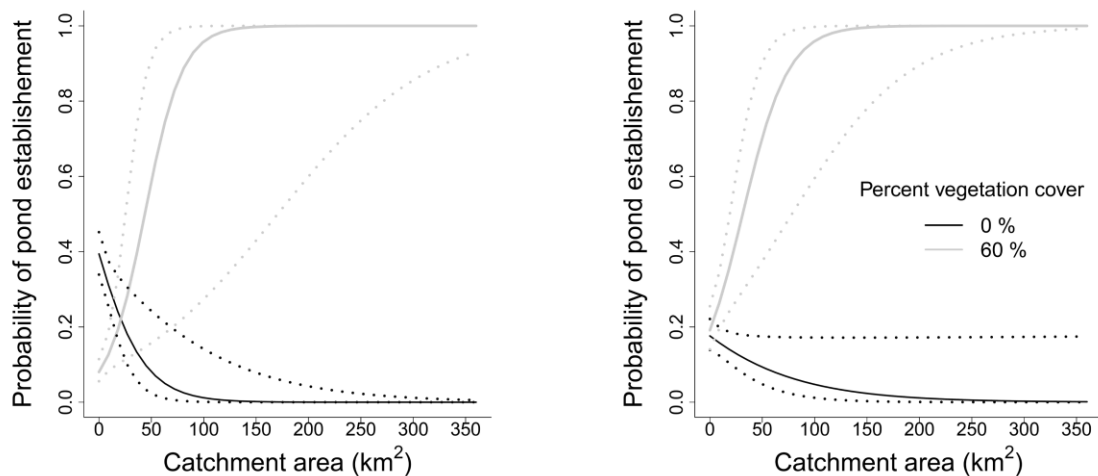


Figure 6: Interaction between catchment area and vegetation cover for 2005 (left) and 2014 (right). Solid lines indicate the probability of pond establishment at different levels of vegetation cover, dotted lines indicate 95 % confidence intervals

To understand how beavers used the landscape we calculated a relative likelihood of landform use using a RSF fitted with the parameters of the best ranked

model. Based on proximity, similar geomorphology and use by beavers we merged open slopes and plains into one category called plains. Beavers used canyons more frequently at the first years of our study, but the likelihood of canyon use decreased with time (Figure 7). Conversely, beavers increased use of both plains and U-shaped valleys in 2010 and 2014, although watercourses in U-shaped valleys were preferred over those in plains.

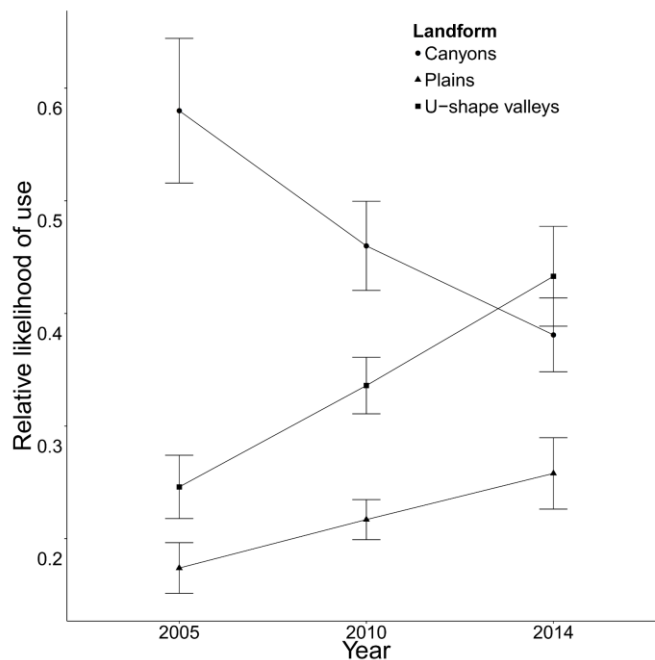


Figure 7: Relative likelihood of landform use (\pm SD) for 2005, 2010 and 2014. Relative likelihoods were calculated using a RSF where covariates were set at the median values.

We tested predictive performance of the best RSF. Correlations between area adjusted-frequencies and bin ranks were high and ranged between 0.82 and 0.93. A

Spearman's rank correlation for mean frequency values by bins was also high (0.93) confirming the model predicted used locations well.

Twenty six potential new colonies were founded in 2010 and 2014. The small sample size of colony foundation events unfortunately prevented us from asking if dispersal distances changed over time. Distances to the closest pond at t-1 ranged from 258 m to 3246 m (Figure 8a). The median distance to the nearest colony was 618 m and the mean was 864 m. Incorporation of distance to nearest pre-existing pond improved the best ranked logistic regression model by 7 AIC units (Table 5). The best ranked model included catchment area, elevation, stream gradient and distance. We used the best ranked model to estimate the probability of establishment of potential new colonies as a function of the distance to the closest pre-existing pond (Figure 8b). The probability of new colonies declined slowly with distance, consistent with the high dispersal distances observed for beavers.

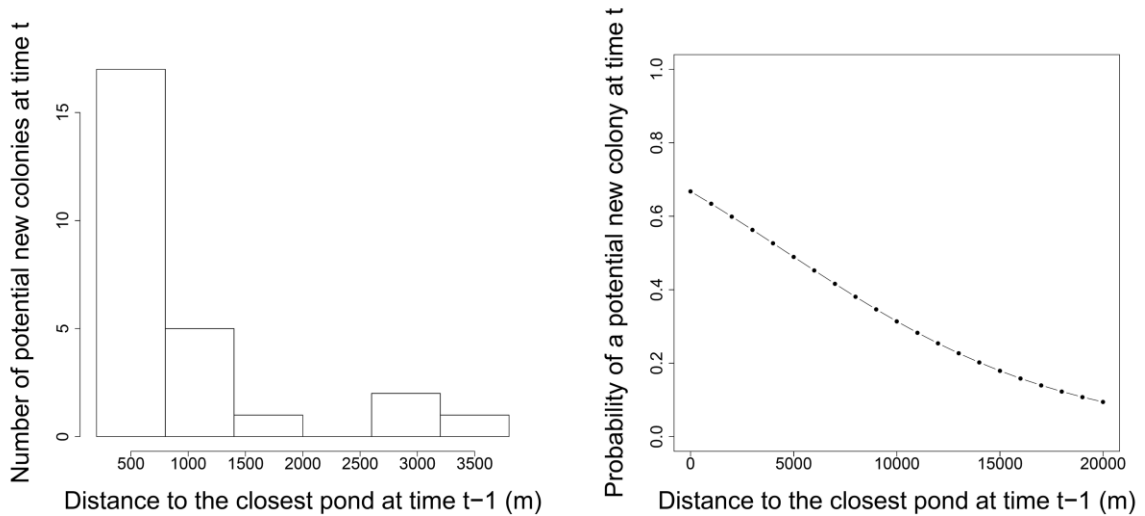


Figure 8: (a) Distribution of the distances of potential new colonies to the closest pond at time t-1. (b) Probability of establishment of potential new colonies as a function of the distance to the closest pond. Probabilities were calculated from the best ranked logistic model that incorporated distance.

Table 5: Logistic models to study the establishment of potential new colonies. Models with AIC < 2 are presented. Abbreviations: CA (catchment area), COV (vegetation cover), ELEV (elevation), SG (stream gradient).

| Model | K | AIC | Δ AIC | AIC | |
|----------------|---|-------|--------------|------|--------|
| | | | | wt | Cum |
| | | | | wt | weight |
| CA+ELEV+SG | 4 | 60.52 | 0 | 0.28 | 0.28 |
| CA+SG | 3 | 61.3 | 0.78 | 0.19 | 0.47 |
| CA+ CO+ELEV+SG | 5 | 62.3 | 1.91 | 0.11 | 0.57 |

3.4 Discussion

High resolution imagery provides information about both population increase and habitat selection of beavers in our study area. By studying both processes simultaneously, we were able to assess how changes in population density affected patterns of habitat selection. Beavers settled on watercourses in canyons in the beginning of our study and used other habitats that were initially less preferred as the number of beaver ponds in the study area increased. Images can also shed light on the dispersal capabilities of an invader in a recently colonized landscape. As we now discuss, understanding both density dependent habitat selection and dispersal can be of critical importance for controlling invasions in general and for beaver management in Patagonia in particular.

Although the time scale of the study was relatively short (11 years) we could easily discern an increase in the number of beaver ponds and in the area affected over time. This increase was particularly high in the first years of our study, suggesting high rates of population growth. In a study conducted during a period of beaver population expansion between 1940 and 1986 in Minnesota, Johnston and Naiman (1990) found that 75 % of the ponds were established in the first twenty years. Moreover, they found this increase to be linearly related to the increase in the number of colonies, confirming that the number of ponds is likely a good indirect measure of abundance.

Aerial photographs have been used to identify beaver ponds (Naiman et al. 1988, Johnston and Naiman 1990, Meentemeyer and Butler 1995, Cunningham et al. 2006), but high resolution satellite images offer new possibilities. They can be used over extended areas in remote locations and, unlike photographs, their quality is relatively constant over space and time (Gergel et al. 2010). High resolution images for our study area are only available from 2003 and later, which prevented us from studying the first years of the invasion. However, the high increase in the number of ponds since 2003 suggests beaver settlement in the area is recent. First records of beaver ponds in Estancia Sara go back to the early 1990s but beaver remains were found in systematic searches by cetacean biologists in San Sebastian Bay (Fig. 4) in the early 1980s (N. Goodall Pers. Comm). Lags between invaders' first detection and population spread are frequent in biological invasions (Sakai et al. 2001, Crooks 2005) and can be a consequence of exponential growth starting from low population numbers.

Beavers first selected canyons to establish their ponds. Streams located in canyons often occurred close to headwaters and are not very deep nor wide, facilitating dam construction (Barnes and Mallik 1997). Johnston and Naiman (1987) proposed that deeply incised streams can also facilitate access to resources from the pond and escape from predators compared to broad riparian valleys. In a study we are conducting in this area, we found colony densities along some of these canyons to be 1.5 colonies per km of stream length, among the highest densities ever recorded for beavers (Muller-Schwarze

2011). Use of canyons declined over time, and beavers increased the use of watercourses in plains and U-shaped valleys in recent years. Streams located in canyons represented 17 % of the pixels in our study area while watercourses on plains and U-shaped valleys comprised 75 % of the total landscape. Our study highlights the importance of geomorphology for beaver settlement in the steppe in agreement with other studies (Johnston and Naiman 1987, Hartman 1996, Suzuki and McComb 1998, Coronato et al. 2003).

High rates of population growth combined with reduced availability of preferred habitat can cause organisms to shift their habitat selection over time. Such density-dependent habitat selection has been very well studied in rodents (Morris 1989, Messier et al. 1990, Halama and Dueser 1994), and RSFs have been increasingly used to study density dependent habitat selection (McLoughlin et al. 2010, van Beest et al. 2014). John et al. (2010) studying the expansion of a reintroduced population of the European Beaver did also observed changes in habitat selection over time. Still, those changes were related to vegetation features rather than geomorphology as we show in this study.

Here we argue that high resolution data on the spread of invasions can not only help us to better understand density dependent habitat selection, but shed light on the mechanisms affecting invasion success. Rapid behavioral and population responses to increased density can promote invader persistence (Human and Gordon 1999, Duckworth and Badyaev 2007, Sol et al. 2013). As beavers fill up watercourses in

canyons (as suggested by very high densities and RSFs), they begin to use other, less preferred habitats. For beavers, streams in plains often have higher flows as they collect water from headwaters, making dam construction and water management more difficult. Yet once most canyon sites were occupied, beavers in the landscape we studied demonstrated the behavioral flexibility to use streams in plains. We do not know however whether their demography is poorer in such sites, which might eventually slow the rate of population increase.

For small streams, we did not expect to see differences in pond establishment as a function of vegetation cover, as mud can suffice as a building material to manage running water. Interactions between shrub vegetation cover and catchment area showed that areas with less vegetation cover in smaller watercourses were preferred over those with higher vegetation cover in 2005. Shrubs usually grow in drier areas on river banks and the absence of woody vegetation can be ascribed to the presence of meadows that are easier to flood and to excavate for dam construction material. Contrary to what many beaver biologists may believe, we think woody material is mainly used to build dams and its importance as forage may be less relevant for individuals in the steppe than previously thought (Beier and Barrett 1987, Hartman 1996, Suzuki and McComb 1998). Models that included an interaction of vegetation cover with stream gradient ranked poorly. This is probably a consequence of relatively low gradients in the steppe. We believe as we move closer to the Andes higher water flows and gradients will make

stream gradient a more important variable for beaver habitat selection (Coronato et al. 2003).

Distance to the nearest pre-existing pond was an important predictor of establishment of potential new colonies. This is not surprising as other studies in the native range found juveniles dispersed close to their natal colonies (VanDeelen and Pletscher 1996, Sun et al. 2000). The mean distance of a potential new colony to the nearest pond was 864 m, substantially less than the mean distance other studies on beaver dispersal have recorded. If we use the distribution in Fig. 8a to represent dispersal distances, we are assuming that dispersers came from the nearest colony, which is not necessarily true. Beavers can disperse much longer distances, and measuring long-distance dispersal events requires a larger study area. For instance, using telemetry we detected a 19 km dispersal event of a juvenile residing in the study area (A. Pietrek, pers. obs.). Such events are likely to become more frequent as habitats fill up.

Most population models assume the speed of the invasion is governed by constant dispersal and a density independent growth rate at the wave front (see Hastings et al. 2005 for a review), but few have investigated how declining vital rates and an increase in dispersal distance behind the front affects the speed of the invasion. Dwyer and Morris (2006) found that an increase in the dispersal distance as result of resource depletion can lead to fluctuating rates of spread. Consequences of this can be

profound and may turn our attention to the areas behind the invasion front to better manage the invasion. At a more practical level, our research may provide a guideline to better target search efforts and beaver detection in the continental steppe. Although there may be some differences between steppe habitats on the mainland (where beavers are now invading) and on the island of Tierra del Fuego (where we conducted our study), our results suggest that geomorphological features are important in beaver habitat selection. Patagonia still harbors remote areas hardly accessible by road, and use of high resolution satellite images can be an important tool to more efficiently detect beaver activity. Furthermore, at the initial stages of the invasion stronger habitat selection can increase chances of detecting the invader if the preferred habitat is identified.

4. Predicting and managing the spread of invasive beavers in Patagonia

4.1 Introduction

Biological invasions are a major threat to biodiversity worldwide. There is consensus that invasions have detrimental effects ranging from the population to the ecosystem levels. By increasing the number of introductions, the increase of international commerce and transportation menaces native biodiversity in the most remote places on earth (Mack et al. 2000, Levine and D'Antonio 2003). Given the vast number of invasive species already established, it is critical to design better strategies to slow or stop the spread of the invaders. Control and eradication of biological invasions have proven to be challenging, particularly when time and economic resources allocated to management are limited (Manchester and Bullock 2000, Simberloff 2009). Realistic models can be a useful tool to more efficiently evaluate proposed strategies to stop or slow the spread of an invasion. Here, we construct a spatially explicit individual based model of the spread of introduced beavers in Patagonia and use it to evaluate one control strategy.

Twenty North American beavers were introduced to the island of Tierra del Fuego in 1946 (Pietrek and Fasola 2014). Currently at least 100,000 beavers populate the Fuegian archipelago (Choi 2008). In Tierra del Fuego beavers are responsible for the most drastic landscape alteration that has occurred in the Holocene, impacting between

20 and 40 % of stream length (Anderson et al. 2014). Beavers cause changes in the structure and composition of *Nothofagus* forests (Martínez Pastur et al. 2006), impact fish and aquatic macroinvertebrate assemblages (Anderson and Rosemond 2007, Moorman et al. 2009) and affect stream food webs (Anderson and Rosemond 2010). More importantly perhaps, beavers create entirely new habitats (beaver meadows) that allow establishment of many invasive plant species and require active restoration to return to their original state (Anderson et al. 2006a, Henn et al. 2014).

Beavers were reported in mainland Chile in the early 1990s, but recent studies suggest beavers may have arrived on the continent between the late 1960s and early 1970s (Graells et al. 2015). In 2013 a beaver was detected close to the city of Puerto Natales (Sanguinetti et al. 2014) (Figure 9). This has highlighted the urgent need to control further northward spread of beavers and has prompted the governments of Argentina and Chile to design a binational strategy to slow or stop the invader from continuing to spread northward in continental Patagonia. One potential strategy, similar to one that was proposed to control the spread of rabies in foxes (Murray et al. 1986) and raccoons (Russell et al. 2005) is to place a “firebreak” just beyond the invasion front. A firebreak would be a longitudinal strip of some width perpendicular to the direction of spread within which a fraction of beavers are removed. Further, to allocate economic resources more efficiently, we would like to know the narrowest width of the

firebreak and the lowest culling levels within the firebreak that are compatible with achieving control of the invasion.

Traditional modelling approaches to study the spread of invasions have ranged from correlational species distribution models (Beaumont et al. 2009, Elith et al. 2010, Uden et al. 2015) to more mechanistic models of spread that account for population dynamics and dispersal (Andow et al. 1990, Kot et al. 1996, Hastings et al. 2005). Simple diffusion models demonstrate that the rate of spread is influenced by both the rate of movement of individuals (represented by the diffusion rate) and by the rate of population growth at low density (Fisher 1937, Skellam 1951). More recent developments of invasion models have attempted to increase the predictive power of these models by incorporating: 1) more complex patterns of movement through the use of non-normal dispersal kernels (Kot et al. 1996, Clark 1998, Krkosek et al. 2007); and 2) differences in demography and movement among life stages (Kot et al. 1996, Neubert and Caswell 2000). Yet, most of these models assume a homogeneous continuous habitat and deterministic dynamics.

These limitations of traditional invasion models and greater computational power have led to increased use of individual-based models, (IBMs) also called agent-based models (ABMs)(Grimm et al. 2005, Grimm and Railsback 2013) to model biological invasions. IBMs describe the behavior of individuals in space and time and allow for interactions with other agents and with their environment. Population-level

patterns arise as an emergent property of the behavior of individuals in relation to their local environment. The appeal of individual-based models is that they can easily incorporate a wide range of behaviors and traits that analytical models cannot. Further, the parallel development of geographic information systems (GIS), has led to an explosion of so-called spatially explicit individual-based models (SEIBMs) that more realistically represent the interaction of individuals across space (Travis et al. 2011).

While a disadvantage of SEIBMs is that they can require a large amount of data to estimate their many parameters, they are especially appropriate to model the spread of beavers in Patagonia for two reasons. First, beavers move mainly through watercourses and dispersing juveniles will select only certain sites to settle based on geomorphology, vegetation cover and vicinity to other beavers (Muller-Schwarze 2011). All these features can be easily incorporated into a GIS layer within an SEIBM but cannot easily be captured with a diffusion or integro-difference equation model. Second, IBMs can incorporate stochasticity relatively more easily than can analytical invasion models. For instance, population growth near the front, where density is low, can be affected by demographic stochasticity. Also, the few established beaver families in the invasion front may or may not increase the speed of the invasion in a given year, as by chance juveniles produced may disperse backward toward already occupied territory rather than beyond the invasion front.

The main aim of this paper is to build a realistic SEIBM of beaver spread and use it to help make management decisions based on sound science. To achieve this, we parameterized our model with vital rates derived from data collected in Tierra del Fuego and estimated the dispersal parameters that matched observed rates of spread of beavers in Patagonia. Subsequently, we use this model to ask what the most effective combination of width of the firebreak and culling levels is to prevent further spread of beavers in mainland Patagonia.

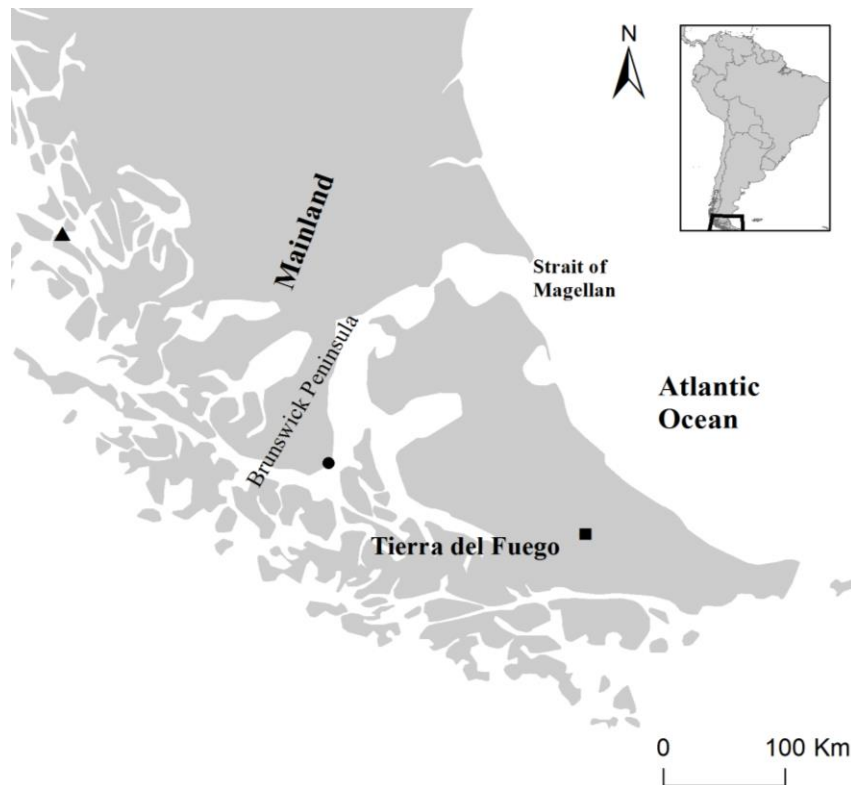


Figure 9: Spread of introduced beavers in Patagonia. The square indicates the site where the first 20 beavers were released. The circle represent the site in the continent where beavers arrived in 1976 according to the dendrochronological record. The triangle represent the northernmost point where a beaver has been captured (in 2013).

4.2 Methods

We built a spatially explicit individual-based model (SEIBM) in Netlogo 5.2.0 (Wilensky 1999) which is emerging as the dominant platform for SEIBMs in ecology. Netlogo is a multiagent programmable environment that incorporates a graphical user friendly interface much more accessible to educators or stakeholders. The model describes the position of each beaver each year on a two dimensional landscape. Because beavers depend primarily on water, watercourses defined the potential breeding sites in our simulations. Thus, we constructed detailed hydrological maps (90 m cell size) using a Digital elevation model (DEM) of our study area that included only streams below the tree line (600 m) located on slopes of less than 20 degrees, where beavers will more likely settle (Allen et al. 1983, Coronato et al. 2003).

We refer to a beaver family that shares a common territory as a colony. Colony composition usually varies from a single pair of adults to a family composed of the adult pair, the kits born that year and 2 or more additional offspring of the parents born in previous years. Juveniles generally disperse when they are 2 years old to found new colonies, but some can remain longer in their natal colony. For simplicity, we assumed beavers always dispersed at two years of age in our model. Thus, we defined 4 beaver age classes in our simulation: kits, yearlings (between one and two years old), juveniles (2 years old) and adults (three years and older). Colonies were defined by the presence of an adult female and an adult male at a site. New colonies are founded by one

dispersing juvenile male and one dispersing juvenile female arriving at the same site, but existing colonies may persist after the death of one of the parents if a juvenile of the opposite sex from the surviving parent arrives. Once forming a colony, adults stay together for the rest of their lives and rarely disperse.

At each one-year time step in the model, beavers aged or died, reproduced, and potentially moved, in that order. Using age specific vital rates we determined the fate of each beaver (survive and move to the next age class or die) stochastically using a Bernoulli distribution, and then determined which sites had two adults (i.e., were colonies). Only colonies can produce kits. Therefore, for each colony we first determined stochastically whether they would have kits and if so, we drew a number of kits from a Poisson distribution. All demographic parameters were based on empirical estimates obtained for beavers in Tierra del Fuego for two habitats: forest and steppe (Pietrek et al. chapter 2) (Table 1 to see model parameters). As population growth at low, rather than high, density determines the speed of the invasion, the number of kits produced per colony in our simulations was the mean number of kits per colony in the steppe, which has been more recently colonized and is likely less affected by density dependence (Pietrek et al. in review).

After survival and reproduction (which occurs in spring), juvenile beavers disperse to found new colonies. Although some studies have shown that the probability of beaver dispersal is inversely related to colony density (Bergerud and Miller 1977,

Busher and Lyons 1999) we assumed every juvenile dispersed. We think this is a fair assumption since we were especially interested in predicting rates of spread which are determined by low density conditions at the invasion front, which increase the probability of dispersing.

Juvenile beavers cannot disperse to cells already occupied by a colony. However, they can disperse to a cell occupied by a lone juvenile or adult of the opposite sex. Chemical communication through scent mounds and visual communication through cut and gnawed trees and damming are signals dispersing beavers can use to assess the presence of other beavers (Muller-Schwarze 2011) . In our simulation, beavers cannot establish a colony closer than 700 m from an existing colony. This defines what the highest densities of beavers behind the wave are and are based on the highest estimates of colony density reported in the literature. As singletons attract floating dispersers, we simulated dispersal as follows. Juveniles will first attempt to move to cells occupied by juveniles or adults of the opposite sex that do not have a mate (this can include cells that previously contained a colony, but one of the members of the pair died). Given the ability of dispersers to detect potential mates over quite large distances, and to move over large areas while searching, we assumed that any site with a compatible mate within a maximum distance was equally likely to be chosen by a dispersing juvenile. We did not include an effect of distance effect in this first step of the dispersal process, as adding distance-dependent mate search significantly reduced the speed of the simulated

invasion and made it difficult to match the observed rate of spread. However, if no mates were available within the search radius, beavers moved a distance (with an error) randomly draw from a Weibull distribution. For simplicity we will assume this is an exponential distribution. If a beaver does not find a suitable cell at the randomly chosen distance with its error, it will move first to the next available cell closest to that is less than the randomly chosen dispersal distance and secondarily to the next available cell beyond the randomly chosen dispersal distance.

Table 6: Parameters of the SEIBM to fit the observed rates of spread of invasive beavers.

| Parameter | Value | Distribution | Description |
|-------------------------------|---------|--------------|---------------------------------------------------------------------------------|
| Beaver propagule size | 20 | - | Numbers of beavers released according to Pietrek and Fasola 2014 |
| Initial location of beavers | - | Uniform | Randomly placed in a radius that matched the radius to search for mates |
| Proportion of colonies w/kits | 0.7 | Bernoulli | Mean proportion of colonies with kits according to Pietrek et al. in review |
| Number of kits per colony | 2.75 | Poisson | Mean number of kits produced per colony according to Pietrek et al. in review |
| Annual survival of kits | 0.66 | Bernoulli | Mean survival of kits produced per colony according to Pietrek et al. in review |
| Annual survival of yearlings | 0.97 | Bernoulli | Mean survival of yearlings according to Pietrek et al. in review |
| Annual survival of juveniles | 0.97 | Bernoulli | Mean survival of juveniles according to Pietrek et al. in review |
| Annual survival of adults | 0.97 | Bernoulli | Mean survival of adults according to Pietrek et al. in review |
| Minimum dispersal distance | 0.72 km | | Based on inter-colony distances at high densities reported |
| Mean dispersal distance | - | Weibull | |
| Distance error | 1.5 km | | Distance error of the distances drawn from the Weibull distribution |
| Radius to search for mates | - | Uniform | Beavers mate with a random unpaired beaver within this radius |

4.2.1 Estimating dispersal parameters and fitting observed rates of spread

As we mentioned above some of the population parameters were estimated from field data but we lacked good data on beaver dispersal. Thus, we fitted our dispersal parameters using the observed speed of invasion and used the fully parameterized model to ask our management questions.

The observed rate of spread was estimated using dendrochronological data (Graells et al. 2015). Beavers were first introduced to the Cami Lake on the island of Tierra del Fuego in 1946 and earliest dates of occupancy on mainland Chile go back as far as 1968 (Fig. 9). The three oldest sites dated by Graells correspond to 1968 (1) and 1976 (2). We chose the site that showed a higher correlation value between the sample of live trees used to date the trees cut by beavers (Rio Yumbel, $r = 0.78$) and is therefore, the most precise estimate of beaver arrival to the continent. The mean observed rate of spread was 7.66 km/year. To simulate the spread of beavers we used a rectangular strip of our landscape running southeast to northwest 250 km long by 50 km wide that included the release point at Cami Lake in southeastern Tierra del Fuego at the bottom right corner of the rectangle and the sites first invaded on the continent at the top of the rectangle. At time 0 we placed twenty beavers (the original propagule size) (Pietrek and Fasola 2014) at the release point in Cami Lake and we assumed beavers paired up in ten colonies. Although we do not exactly know the sex ratio of the first twenty beavers,

genetic studies suggest it was close to one (Fasanella et al. 2010). To make the simulation feasible with our available computing power and allow beavers to move freely, we allowed beavers to leave the right edge of the landscape and reemerge on the left edge and vice versa (i.e., our simulated landscape represented a cylinder) . We let our simulations run for 20 years. We calculated the speed of the simulated invasion as the distance from the release point to the beaver farthest from that point divided by the number of time steps (years) since simulation initiation. To determine what starting conditions could best match the observed speed of the invasion we varied two parameters in our simulations: the radius within which beavers can detect potential mates and the mean dispersal distance for beavers who do not find mates within this radius. After exploring the parameter space, we chose the combination of these two parameters that best approximated the observed annual rate of spread, and we ran 100 simulations of the fully parameterized model.

4.2.2 Simulating management scenarios

Once we found a set of dispersal parameters that reproduced the observed speed of the invasion, we simulated six different management scenarios on the continent. We used three different widths for the firebreak (25, 50 and 100 km) and two different culling rates within the firebreak. Each eaver within the firebreak, regardless of its age, faced a probability of 0.5 or 0.8 of being culled each year.

We ran our model on a rectangular strip from southeast (Brunswick Peninsula) to northwest 300 km long by 50 km wide that included the northernmost point where a lone beaver was recorded in 2013. As the greatest challenge to the success of the firebreak will occur when beavers have attained high colony density right up to the edge of the firebreak, we placed the beginning of the firebreak at 10 km and we filled all suitable sites behind with beaver colonies. The proportion of lone beavers and colony composition in the new landscape was constructed using results from our previous simulation. We ran 50 simulations for each scenario (each simulation was 5 years long) and we recorded the time of the first arrival to the other side of the firebreak and the cumulative number of beavers that crossed the firebreak in 5 years.

4.3 Results

The lowest value for the mate search radius and for the mean dispersal distance when mates were not found that yielded the historical invasion speed was 19km for both parameters. Other combinations of higher dispersal distance and lower search radius also produced the observed rate of spread, but we decided to stick to mean dispersal rates similar to the highest reported in the literature (Beer 1955). The mean rate of spread predicted by the fully parameterized model was 7.68 ± 0.46 km/year.

Results of the management scenarios showed an interesting pattern. Regardless of culling levels, the time to arrival to the other side of the firebreak was one year in all

simulations when the firebreak was 25 km wide and 1 year in 97% of the cases when the firebreak was 50 km wide. With a 50km firebreak, the only three cases in which the first beaver did not arrive until the second year occurred when the culling fraction was 0.5. A 100 km wide firebreak resulted in an increase of the time of arrival (Figure 10). Yet, in 34 % of the simulations, beavers crossed the firebreak the first year (at both culling fractions). Nevertheless, the percentage of simulations in which the time of first crossing was 5 years or longer was higher when the fraction of beavers removed was lower (34 % vs 12 %)(Figure 10).

The mean number of beavers that crossed over a 5 year period decreased substantially with firebreak width (Fig. 11). However, the fraction of beavers culled did not have much effect, although there was also a trend towards fewer beavers crossing at lower culling. Fig. 11 shows the numbers crossing the firebreak as a whole. Over the entire firebreak, 1.5 beavers/km crossed when the firebreak was 25 km wide, 0.41 beavers/km did so when it was 50 km wide and only 0.04 beavers crossed when it was 100 km wide.

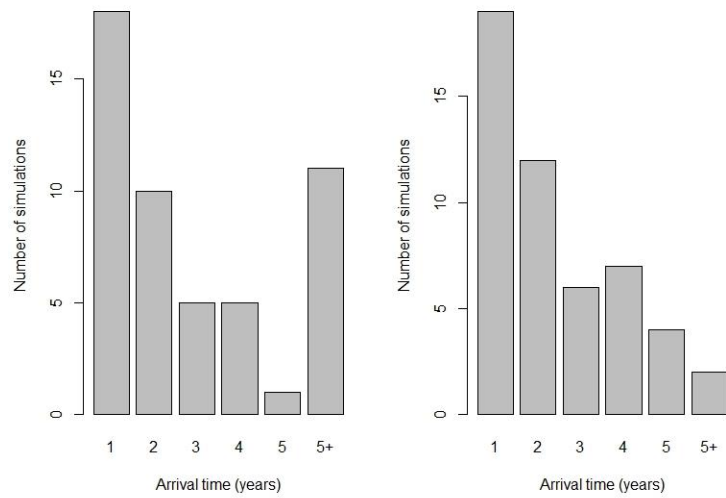


Figure 10: Arrival time of beavers on the opposite side of a firebreak when culling levels are 0.5 (left) and 0.8 (right) for a 100 km wide firebreak.

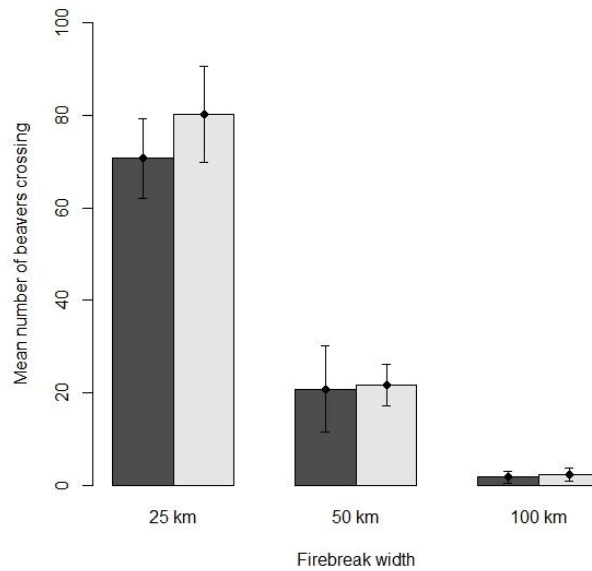


Figure 11: Mean number of beavers crossing the firebreak at three different widths. Dark bars indicate a culling fraction of 50 % and light bars indicate 80 % culling.

4.4 Discussion

We here simulated a potential strategy to contain the northward spread of beavers in Patagonia. Our study shows that even a 100 km wide firebreak can be breached in only a single year. Interestingly, we found that a higher fraction of beavers culled did not decrease either the mean number of individuals crossing the firebreak or the time it took the first beaver to arrive to the other side of the firebreak. Therefore removing a lower fraction of beavers within the firebreak can be a better strategy. In the next paragraphs, we will discuss these results and try to provide some guidance to manage the beaver invasion in Patagonia.

The mean number of beavers that crossed the firebreak decreased as the width of the firebreak increased. As expected, a 25 km wide firebreak did very little to prevent the northward spread of beavers. Beavers can travel long distances. Saveljev et al. (2002) reported a beaver that migrated more than 500 km in Russia. Beer (1955) found a mean dispersal distance of 17 km in Minnesota, close to the mean dispersal distance we used in our models. Out of 10 beavers we have radio-tracked in both forest and steppe in Patagonia we recorded one beaver that dispersed 19 km, and we believe our ability to relocate other beavers after dispersing was often constrained by the long distances they move. Long-distance dispersal events have been one of the main factors driving the spread of rabies in raccoons in Ohio, where a strategy (a cordon sanitaire) similar to the firebreak strategy we explored here was found to be unsuccessful (Russell et al. 2005).

Long distance dispersal is also an important determinant of the speed of biological invasions and longer moves in the front of the invasion can accelerate the rates of spread as shown by Lindstrom et al. (2013). The decrease in the number of beavers that made it through the firebreak was however, quite abrupt. Only 0.02 beavers/km crossed the firebreak when it was 100 km wide compared to 1.5 beavers/km when it was 25 km wide. This nonlinear response implies that for each dollar invested in increasing the width of the firebreak the return (measured as the inverse of the number of individuals crossing the firebreak) will increase.

Unexpectedly, higher culling rates increased the number of beavers that crossed the firebreak and decreased the arrival time, potentially reducing the cost of managing the invasion within the firebreak. We think this is a consequence of density dependent dispersal as an emergent property of our model. If a beaver does not find a suitable site with a potential mate nearby (as may happen at the low density generated by high culling rates), it will choose a dispersal distance from the exponential distribution which sometimes results in long distance moves. Negative density-dependent dispersal may occur as a consequence of conspecific attraction or to emigrate out of low density areas that may cause an Allee effect (Kuussaari et al. 1998). Dispersers rapidly occupy sites where juveniles of the opposite sex established or where one of the pair members dies. This suggests negative density dependent dispersal may occur although there are few cases well documented with mammals (Matthysen 2005). Travis et al. (2009) showed that

accelerating invasion rates may result from the evolution of density dependent dispersal. Bergerud and Miller (1977) and Busher and Lyons (1999) suggested that removal of colonies can increase the probability of juvenile dispersal by increasing the availability of sites for recolonization, although we did not incorporate this process in our model.

Very little is known in general on how beavers, and other animals, move and find mates at low densities. Thus, it is hard to predict how realistic our model is. Studies attempting to understand how density impacts the probability of dispersal and/or the distance dispersers' travel are scarce but very much needed to manage invasions and to conserve endangered species. Allee effects are generally expected to decrease the speed of the invasion, but the high success of numerous invaders suggests these species rarely experience it.

Here we analyzed how a human barrier could slow the spread of beavers but assumed the landscape was otherwise permeable to beavers. Movement along basins is probably more frequent than movement between basins. However, in areas with relatively high drainage density (such as the one we studied), beavers can easily move between basins. In Tierra del Fuego, three out of 10 radio-tagged beavers show some sort of inter-basin movement. Beavers in Wisconsin moved as far as 11 km from the nearest body of water suggesting they can travel long distances on the ground (Muller-Schwarze 2011). Terrestrial dispersal could have facilitated spread in Tierra del Fuego,

where sub-adult beavers do not have any predators, thus allowing them to disperse longer distances over land. Beavers have also colonized mainland Chile and several of the islands in the archipelago of Tierra del Fuego by swimming across the sea, demonstrating their extraordinary dispersal capabilities.

In conclusion, even a 100 km firebreak will not contain the beaver spread in Patagonia. This is particularly true in the light of previous successful invasions starting from a small number of individuals (Parker et al. 2012, Pietrek and Fasola 2014). Although, we simulated conditions of high density behind the firebreak our results can be considered conservative as the work from Graells et al. (2015) suggests beavers may have arrived on the continent before 1976, thus resulting in a higher invasion speed and more frequent long distance dispersal. Future studies that incorporate dispersal data at varying densities and habitats may improve models of beaver management in Patagonia.

Appendix A

Table 1. Parameter estimates for colony size in the forest based on summaries of the marginal posterior distributions of binomial mixture models fitted to counts in years 1, 2 and 3.

| | | Posterior mean | Posterior SD | 95 % CRI |
|--------|----------------------|----------------|--------------|---------------|
| | Intercept | 2.2 | 0.55 | -0.92, 2.96 |
| | Understory cover | 0.004 | 0.012 | -0.02, 0.02 |
| Year 1 | Height of understory | -0.005 | 0.007 | -0.02, 0.01 |
| | Median of tree size | -0.006 | 0.003 | -0.01, 0.001 |
| | p | 0.65 | 0.11 | 0.38, 0.83 |
| | Intercept | 2.1 | 0.69 | 0.4, 2.96 |
| | Understory cover | 0.007 | 0.01 | -0.02, 0.03 |
| Year 2 | Height of understory | 0.006 | 0.009 | -0.02, 0.01 |
| | Median of tree size | -0.001 | 0.003 | -0.008, 0.007 |
| | p | 0.34 | 0.12 | 0.12, 0.59 |
| | Intercept | 2.26 | 0.53 | 1.02, 2.96 |
| | Understory cover | -0.005 | 0.012 | -0.03, 0.02 |
| Year 3 | Height of understory | -0.004 | 0.008 | -0.02, 0.01 |
| | Median of tree size | -0.004 | 0.003 | -0.01, 0.003 |
| | p | 0.51 | 0.12 | 0.25, 0.72 |

Table 2. Parameter estimates for the colony size in the steppe based on summaries of the marginal posterior distributions of binomial mixture models fitted to counts in years 1, 2 and 3.

| | | Posterior mean | Posterior SD | 95 % CRI |
|--------|-----------------------|----------------|--------------|--------------|
| Year 1 | Intercept | 2.16 | 0.44 | 1.24, 2.92 |
| | Shrub cover | -0.008 | 0.009 | -0.02, 0.01 |
| | Height of shrub cover | 0.006 | 0.009 | -0.01, 0.02 |
| | p | 0.4 | 0.13 | 0.17, 0.64 |
| Year 2 | Intercept | 2.16 | 0.33 | 1.49, 2.82 |
| | Shrub cover | 0.012 | 0.009 | -0.005, 0.03 |
| | Height of shrub cover | -0.012 | 0.009 | -0.03, 0.006 |
| | p | 0.67 | 0.11 | 0.4, 0.84 |
| Year 3 | Intercept | 2.16 | 0.33 | 1.48, 2.81 |
| | Shrub cover | 0.012 | 0.009 | -0.004, 0.03 |
| | Height of shrub cover | -0.012 | 0.01 | -0.03, 0.006 |
| | p | 0.68 | 0.1 | 0.42, 0.83 |

Table 3. Parameter estimates for number of kits in the forest based on summaries of the marginal posterior distributions of binomial mixture models fitted to counts in years 1, 2 and 3.

| | | Posterior mean | Posterior SD | 95 % CRI |
|--------|----------------------|----------------|--------------|-------------|
| Year 1 | Intercept | 0.76 | 1.64 | -2.65, 2.92 |
| | Understory cover | 0.04 | 0.15 | -0.21, 0.36 |
| | Height of understory | -0.001 | 0.04 | -0.08, 0.09 |
| | Median of tree size | -0.006 | 0.01 | -0.03, 0.03 |
| | Ω | 0.54 | 0.18 | 0.22, 0.92 |
| | p | 0.34 | 0.18 | 0.04, 0.72 |
| Year 2 | Intercept | -0.49 | 1.63 | -2.89, 2.69 |
| | Understory cover | 0.006 | 0.1 | -0.13, 0.26 |
| | Height of understory | -0.12 | 0.15 | -0.43, 0.17 |
| | Median of tree size | 0.06 | 0.08 | -0.08, 0.22 |
| | Ω | 0.45 | 0.2 | 0.13, 0.76 |
| | p | | | |
| Year 3 | Intercept | -0.01 | 1.75 | -2.86, 2.84 |
| | Understory cover | 0.19 | 0.25 | -0.22, 0.69 |
| | Height of understory | -0.02 | 0.05 | -0.14, 0.07 |
| | Median of tree size | 0.01 | 0.02 | -0.02, 0.05 |
| | Ω | 0.51 | 0.16 | 0.23-0.89 |
| | p | 0.15 | 0.11 | 0.004-0.42 |

Table 4. Parameter estimates for the number of kits in the steppe based on summaries of the marginal posterior distributions of binomial mixture models fitted to counts in years 1, 2 and 3.

| | | Posterior mean | Posterior SD | 95 % CRI |
|--------|-----------------------|----------------|--------------|-------------|
| Year 1 | Intercept | 1.12 | 0.95 | -0.68, 3.18 |
| | Shrub cover | -0.01 | 0.02 | -0.05, 0.03 |
| | Height of shrub cover | 0.004 | 0.02 | -0.03, 0.04 |
| | Ω | 0.73 | 0.14 | 0.44-0.97 |
| | p | 0.41 | 0.18 | 0.07, 0.63 |
| Year 2 | Intercept | 1.51 | 0.87 | -0.16, 3.34 |
| | Shrub cover | -0.003 | 0.02 | -0.05, 0.05 |
| | Height of shrub cover | 0.001 | 0.02 | -0.04, 0.04 |
| | Ω | 0.59 | 0.13 | 0.33, 0.87 |
| | p | 0.29 | 0.14 | 0.05-0.57 |
| Year 3 | Intercept | 1.48 | 0.83 | -0.01, 3.34 |
| | Shrub cover | -0.01 | 0.01 | -0.03, 0.01 |
| | Height of shrub cover | 0.01 | 0.01 | -0.01, 0.04 |
| | Ω | 0.81 | 0.09 | 0.6-0.97 |
| | p | 0.3 | 0.14 | 0.05-0.58 |

Appendix B

Data manipulation

We compiled individual encounter histories for each of the 91 individuals over the 52 months of our study (from now on “y” matrix). Every month we recorded an observation state for each beaver. The observation states were:

- 1) Alive with radio
- 2) Alive no radio
- 3) Dead with radio
- 4) Dead no radio
- 5) Not seen

We combined bi-weekly telemetry events into one monthly occasion. If a radio-tagged individual was found dead on the second recording event, we assigned the state “Dead with radio” to that month. Although radio-tagged individuals had both transmitters and colored ear-tags we gave priority to telemetry recordings over sightings while the transmitter was working.

Individuals were censored a) after they died, b) if the colony was abandoned and individuals were not found anywhere else in our study sites or c) if we recorded individuals outside our study sites in our overflights. One marked beaver died as the result of a recapture and we decided to censor it the month before that occurred.

Model structure

We fit a multi-state model in the Bayesian framework to analyze our data. Multi-state models describe the probability of transition between true states as a Markovian process with an observation model that links observation and true states. The true states were:

- 1) Alive with radio
- 2) Alive no radio
- 3) Dead with radio
- 4) Dead no radio

We built a state matrix to model the transition of an individual from true state A at time t to true state B at time $t+1$. The state transition matrix can be described as follows:

$$\begin{bmatrix} Sr_{i,t}(1 - \psi_{i,t}) & Sr_{i,t} \psi_{i,t} & (1 - Sr_{i,t})(1 - \psi_{i,t}) & (1 - Sr_{i,t})\psi_{i,t} \\ 0 & Snr_{i,t} & 0 & 1 - Snr_{i,t} \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Where $Sr_{i,t}$ is the probability of the radioed individual i survived from occasion t to occasion $t+1$, $Snr_{i,t}$ is the probability the non-radioed individual i survived from occasion t to occasion $t+1$, and $\psi_{i,t}$ is the probability of the radioed individual i at time t to transition to a non-radioed state at time $t+1$ (i.e. transmitter was lost or stopped working).

The observation matrix links the true and observed states (as defined above). We defined the true states at time t as the rows of the matrix and the columns as the observed states at time t . The observation matrix can be described as follows:

$$\begin{bmatrix} Pr_{i,t} & 0 & 0 & 0 & 1 - Pr_{i,t} \\ 0 & Pnr_{i,t} & 0 & 0 & 1 - Pnr_{i,t} \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Where $Pr_{i,t}$ is the probability of detection of the radioed individual i at time t and $Pnr_{i,t}$ is the probability of detection estimated from mark-resight data of the non-radioed individual i at time t . As state four was never observed in our dataset, we set all transition probabilities to 0 on that column.

We set the probability of detection of radioed beavers to one, as we tracked individuals during the day while they were resting in their lodges and they were detected every single time if present. Given telemetry surveys were performed only 6 months a year, we set the probability of detection to 0 the months surveys were not conducted. To incorporate this information on sampling occasions we built a $i \times t$ matrix (from now on “sample” matrix) in which we assigned a 1 to an individual if telemetry was conducted that month and 0 otherwise.

We modeled the probability of detection using mark-resight data by habitat. To do this we constructed a $i \times t$ matrix (from now on “habitat” matrix) in which we assigned a 1 to mark resight occasions of individuals in the forest, 2 to mark resight occasions of individuals in the steppe and we set to 0 the probability of detection the months colonies were not sampled.

Here is the JAGS code for the model:

```
model {  
  
  # Priors and constraints  
  
  for (t in 1:(n.occasions-1)){  
    phiR[t]<-mean.phi[1]    # Prior for survival radioed individuals  
    phiNR[t]<-mean.phi[2]   # Prior for survival non-radioed individuals  
    psiRNR[t]<-mean.psi     # Prior for tag loss  
  }  
  
  for (u in 1:2){
```

```

    mean.phi[u]~dunif(0,1)
  }
  mean.psi~dunif(0,1)

  for (i in 1:nind){
    for (t in f[i]:last[i]){
      pRi[i,t]<-R[sample[i,t]]
    }
  }
  R[1]<-1 #sampled
  R[2]<-0 # not sampled

  for (i in 1:nind){
    for (t in f[i]:last[i]){
      p[i,t]<-beta[habitat[i, t]]
    }
  }

  beta[1]~dunif(0,1) # Detection in the forest
  beta[2]~dunif(0,1) # Detection in the steppe
  beta[3]<-0 # not sampled

# Define state-transition and observation matrices
for (i in 1:nind){
  # Define probabilities of state S(t+1) given S(t)
  for (t in f[i):(last[i]-1)){
    ps[1,i,t,1] <- phiR[t] * (1-psiRNR[t])
    ps[1,i,t,2] <- phiR[t] * psiRNR[t]
    ps[1,i,t,3] <- 1-phiR[t]* (1-psiRNR[t])
    ps[1,i,t,4] <-(1-phiR[t])*psiRNR[t]
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- phiNR[t]
    ps[2,i,t,3] <- 0
    ps[2,i,t,4] <- 1-phiNR[t]
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1
    ps[3,i,t,4] <-0
    ps[4,i,t,1] <- 0

```

```

ps[4,i,t,2] <- 0
ps[4,i,t,3] <- 0
ps[4,i,t,4] <- 1

# Define probabilities of O(t) given S(t)
po[1,i,t,1] <- pRi[i,t+1]
po[1,i,t,2] <- 0
po[1,i,t,3] <- 0
po[1,i,t,4] <- 0
po[1,i,t,5] <- 1-pRi[i,t+1]
po[2,i,t,1] <- 0
po[2,i,t,2] <- p[i,t+1]
po[2,i,t,3] <- 0
po[2,i,t,4] <- 0
po[2,i,t,5] <- 1-p[i,t+1]
po[3,i,t,1] <- 0
po[3,i,t,2] <- 0
po[3,i,t,3] <- 1
po[3,i,t,4] <- 0
po[3,i,t,5] <- 0
po[4,i,t,1] <- 0
po[4,i,t,2] <- 0
po[4,i,t,3] <- 0
po[4,i,t,4] <- 0
po[4,i,t,5] <- 1

} #t
} #i

# Likelihood
for (i in 1:nind){
  # Define latent state at first capture
  z[i,f[i]] <- y[i,f[i]]
  for (t in (f[i]+1):last[i]){
    # State process: draw S(t) given S(t-1)
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
    # Observation process: draw O(t) given S(t)
    y[i,t] ~ dcat(po[z[i,t], i, t-1,])
  } #t
} #i
} # model

```

The data needed to run this model are the capture-history matrix y , the “sample” matrix that accounts for sampling/not sampling with radiotelemetry, and the “habitat” matrix that accounts for habitat-specific observations and not sampling. In addition to this, we need two vectors, “first” indicates the first time the individual was captured and marked and “last” which indicates when the individual was censored from the sample.

References

- Allen, A. W., W. Energy, and L. U. Team. 1983. Habitat suitability index models: beaver. Western Energy and Land Use Team, Division of Biological Service, Research and Development, Fish and Wildlife Service, US Department of the Interior.
- Anderson, C., C. Griffith, A. Rosemond, R. Rozzi, and O. Dollenz. 2006a. The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biol Conserv* 128:467 - 474.
- Anderson, C. B., C. R. Griffith, A. D. Rosemond, R. Rozzi, and O. Dollenz. 2006b. The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile - Do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biological Conservation* 128:467-474.
- Anderson, C. B., G. M. Pastur, M. V. Lencinas, P. K. Wallem, M. C. Moorman, and A. D. Rosemond. 2009. Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. *Mammal Review* 39:33-52.
- Anderson, C. B., and A. D. Rosemond. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154:141-153.
- Anderson, C. B., and A. D. Rosemond. 2010. Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. *Hydrobiologia* 652:349-361.
- Anderson C.B., N. Soto, J.L. Cabello, G. Martínez Pastur, M.V. Lencinas, P.K. Wallem, D. Antúnez and E Davis. 2011. *Castor canadensis* Kuhl (North American Beaver) Building effective alliances between research and management to mitigate the impacts of an invasive ecosystem engineer: Lessons from the study and

control of *Castor canadensis* in the Fuegian archipelago. Pp 347-359, in: A handbook of Global Freshwater Invasive Species (Fancys R.A., ed.). Earthscan Publishing, London.

Anderson, C. B., M. Vanessa Lencinas, P. K. Wallem, A. E. J. Valenzuela, M. P. Simanonok, and G. Martínez Pastur. 2014. Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. *Diversity and Distributions* 20:214-222.

Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* 4:177-188.

Argentina Austral. 1946. La cría del castor. November, p 40.

Argentina Austral. 1960. Vida de los castores en el Río Claro: Reproducción de las diez parejas iniciales. August, p 13-15.

Arjo, W. M., R. E. Joos, C. O. Kochanny, J. L. Harper, D. L. Nolte, and D. L. Bergman. 2008. Assessment of transmitter models to monitor beaver *Castor canadensis* and *C. fiber* populations. *Wildlife Biology* 14:309-317.

Armstrong, D. P., R. S. Davidson, J. K. Perrott, J. O. N. Roygard, and L. E. N. Buchanan. 2005. Density-dependent population growth in a reintroduced population of North Island saddlebacks. *Journal of Animal Ecology* 74:160-170.

Barnes, D. M., and A. U. Mallik. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. *Journal of Wildlife Management* 61:1371-1377.

- Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482-1491.
- Beaumont, L. J., R. V. Gallagher, W. Thuiller, P. O. Downey, M. R. Leishman, and L. Hughes. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* 15:409-420.
- Beer, J. R. 1955. Movements of tagged beaver. *J. Wildl. Manage* 19:492-493.
- Beier, P., and R. H. Barrett. 1987. Beaver Habitat Use and Impact in Truckee River Basin, California. *Journal of Wildlife Management* 51:794-799.
- Bergerud, A. T., and D. R. Miller. 1977. Population-dynamics of Newfoundland beaver. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 55:1480-1492.
- Bloomquist, C. K., and C. K. Nielsen. 2010. Demography of Unexploited Beavers in Southern Illinois. *Journal of Wildlife Management* 74:228-235.
- Boyce, M. S. 1981. Beaver life-history responses to exploitation. *Journal of Applied Ecology* 18:749-753.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268-272.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281-300.

- Breck, S. W., K. R. Wilson, and D. C. Andersen. 2001. The demographic response of bank-dwelling beavers to flow regulation: a comparison on the Green and Yampa rivers. *Canadian Journal of Zoology* 79:1957-1964.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* 2nd edition. Springer-Verlag.
- Busher, P. E., and P. J. Lyons. 1999. Long-Term Population Dynamics of The North American Beaver *Castor Canadensis* on Quabbin Reservation, Massachusetts, and Sagehen Creek, California. Pages 147-160 *Beaver protection, management, and utilization in Europe and North America*. Springer.
- Capellini, I., J. Baker, W. L. Allen, S. E. Street, and C. Venditti. 2015. The role of life history traits in mammalian invasion success. *Ecology Letters*, in press.
- Choi, C. 2008. Tierra del Fuego: the beavers must die. *Nature News* 453:968-968.
- Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204-224.
- Cleere, E. A. 2005. *Natal dispersal of beaver in the Embarras River Watershed in central Illinois*. Eastern Illinois University, Charleston, USA.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-733.
- Collen, P., and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. *Reviews in Fish Biology and Fisheries* 10:439-461.

- Coronato, A., J. Escobar, C. Mallea, C. Roig, and M. Lizarralde. 2003. Características geomorfológicas de ríos de montaña colonizados por *Castor canadensis* en Tierra del Fuego, Argentina. *Ecologia Austral* 13:15-26.
- Crooks, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12:316-329.
- Cunningham, J. M., A. J. K. Calhoun, and W. E. Glanz. 2006. Patterns of beaver colonization and wetland change in Acadia National Park. *Northeastern Naturalist* 13:583-596.
- Daciuk, J. 1978. Notas faunísticas y bioecológicas de Península Valdés y Patagonia, IV. Estado actual de las especies de mamíferos introducidos en la Región Araucana (Rep. Argentina) y grado de coacción ejercido en algunos ecosistemas surcordilleranos. *Anales de Parques Nacionales* 14:105-130.
- DeStefano, S., K. K. G. Koenen, C. M. Henner, and J. Strules. 2006. Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population. Pages 434-441. Blackwell Publishing.
- Dewhurst, S., and F. Lutscher. 2009. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. *Ecology* 90:1338-1345.
- Dieter, C. D., and T. R. McCabe. 1989. Factors Influencing Beaver Lodge-site Selection on a Prairie River. *American Midland Naturalist* 122:408-411.
- Duckworth, R. A., and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* 104:15017-15022.

- Dwyer, G., and W. F. Morris. 2006. Resource-dependent dispersal and the speed of biological invasions. *American Naturalist* 167:165-176.
- Eberhardt, L. L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. *Environmental Conservation* 4:205-212.
- Ehrlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters* 18:303-314.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1:330-342.
- ESRI. 2014. ArcGIS Desktop: Release 10.2.2. Environmental Systems Research Institute, Redlands, CA.
- Fabro, E. 1989. Fauna autóctona e introducida de la Tierra del Fuego. Dirección de Recursos Naturales, Boletín N°2, Departamento de Fauna Silvestre, Ministerio de Economía y Hacienda del Territorio Nacional de la Tierra del Fuego, Antártida e Islas del Atlántico Sur, Tierra del Fuego.
- Fasanella, M., S. Poljak, and M. S. Lizarralde. 2010. Invasive North American beaver (*Castor canadensis*): The Distribution of mitochondrial variation across the archipelago of Tierra del Fuego. *Mastozoología Neotropical* 17:43-52.
- Feldman, M. J. 2015. Ecología de castores invasores en diferentes hábitats de Tierra del Fuego. Universidad CAECE, Buenos Aires, Argentina.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38-49.

- Fisher, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355-369.
- Fitzpatrick, B.M., J.A. Fordyce, M.L. Niemiller, and R.G. Reynolds. 2012. What can DNA tell us about biological invasions? *Biological Invasions* 14:245-253.
- Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds part 1 theoretical development. *Acta Biotheoretica* 19:16-36.
- Fryxell, J. M. 1992. Space use by beavers in relation to resource abundance. *Oikos* 64:474-478.
- Fryxell, J. M. 2001. Habitat suitability and source-sink dynamics of beavers. *Journal of Animal Ecology* 70:310-316.
- Fryxell, J. M., and C. M. Doucet. 1993. Diet Choice and the Functional Response of Beavers. *Ecology* 74:1298-1306.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367-393.
- Ge, S., R. Carruthers, P. Gong, and A. Herrera. 2006. Texture Analysis for Mapping *Tamarix parviflora* Using Aerial Photographs along the Cache Creek, California. *Environmental Monitoring and Assessment* 114:65-83.
- Gelman, A., and X.-L. Meng. 1996. Model checking and model improvement. Pages 189-201 *Markov chain Monte Carlo in practice*. Springer.

- Gergel, S. E., N. C. Coops, and J. L. Morgan. 2010. Aerial Photography: A Rapidly Evolving Tool for Ecological Management. *Bioscience* 60.
- Gimenez, O., V. Rossi, R. Choquet, C. Dehais, B. Doris, H. Varella, J.-P. Vila, and R. Pradel. 2007. State-space modelling of data on marked individuals. *Ecological Modelling* 206:431-438.
- Godoy J.C. 1963. Fauna Silvestre. Evaluación de los Recursos Naturales de Argentina. CFI, Buenos Aires.
- Goldberg, C. S., K. Woodruff, R. Toldness, and L. P. Waits. 2011. Robust molecular sex identification of beaver (*Castor canadensis*) from non-destructive samples. *Conservation Genetics Resources* 3:729-731.
- González-Suárez, M., S. Bacher, and J. M. Jeschke. 2015. Intraspecific Trait Variation Is Correlated with Establishment Success of Alien Mammals. *The American Naturalist* 185:737-746.
- Goodall R.N.P. 1979. Tierra del Fuego. Ediciones Shanamaim, Buenos Aires.
- Graells, G., D. Corcoran, and J. Aravena. 2015. Invasion of North American beaver (*Castor canadensis*) in the province of Magallanes, Southern Chile: comparison between dating sites through interviews with the local community and dendrochronology. *Revista Chilena De Historia Natural* 88:3.
- Grimm, V., and S. F. Railsback. 2013. Individual-based modeling and ecology. Princeton university press.

- Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H. H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* 310:987-991.
- Gunson, J. R. 1970. Dynamics of beaver of Saskatchewan's northern forest. M.S. Thesis. University of Alberta.
- Halama, K. J., and R. D. Dueser. 1994. Of mice and habitats: tests for density-dependent habitat selection. *Oikos*:107-114.
- Hartman, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *Journal of Zoology* 240:317-325.
- Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, M. Holland, J. Lambrinos, U. Malvadkar, B. A. Melbourne, K. Moore, C. Taylor, and D. Thomson. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8:91-101.
- Havens, R. P., J. C. Crawford, and T. A. Nelson. 2013. Survival, Home Range, and Colony Reproduction of Beavers in East-Central Illinois, an Agricultural Landscape. *American Midland Naturalist* 169:17-29.
- Henn, J. J., C. B. Anderson, G. Kreps, M. V. Lencinas, R. Soler, and G. M. Pastur. 2014. Determining Abiotic and Biotic Factors that Limit Transplanted *Nothofagus pumilio* Seedling Success in Abandoned Beaver Meadows in Tierra del Fuego. *Ecological Restoration* 32:369-378.
- Hosmer, D. W., and S. Lemeshow. 2005. Logistic Regression for Matched Case-Control Studies. Pages 223-259 *Applied Logistic Regression*. John Wiley & Sons, Inc.
- Human, K. G., and D. M. Gordon. 1999. Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Sociaux* 46:159-163.

- Jaksic, F.M., J.A. Iriarte, J.E. Jiménez, and D.R. Martínez. 2002. Invaders without frontiers: cross-border invasions of exotic mammals. *Biological Invasions* 4:157-173.
- Jeschke, J., L. Gómez Aparicio, S. Haider, T. Heger, C. Lortie, P. Pyšek, and D. Strayer. 2012. Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14:1-20.
- John, F., S. Baker, and V. Kostkan. 2010. Habitat selection of an expanding beaver (*Castor fiber*) population in central and upper Morava River basin. *European Journal of Wildlife Research* 56:663-671.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347-357.
- Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. *Landscape Ecology* 1:47-57.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic Patch Creation in Relation to Beaver Population Trends. *Ecology* 71:1617-1621.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17:164-170.
- Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat selection studies. *Journal of Wildlife Management* 68:774-789.
- Kery, M., R. M. Dorazio, L. Soldaat, A. van Strien, A. Zuiderwijk, and J. A. Royle. 2009. Trend estimation in populations with imperfect detection. *Journal of Applied Ecology* 46:1163-1172.

- Kery, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications* 15:1450-1461.
- Kot, M., M. A. Lewis, and P. v. d. Driessche. 1996. Dispersal Data and the Spread of Invading Organisms. *Ecology* 77:2027-2042.
- Krkosek, M., J.-S. Lauzon-Guay, and M. A. Lewis. 2007. Relating dispersal and range expansion of California sea otters. *Theoretical Population Biology* 71:401-407.
- Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*:384-392.
- La Prensa Austral. 2013, Sep 2. Capturan castor que era intensamente buscado en Ultima Esperanza. URL:www.laprensaaustral.cl/cronica/capturan-castor-que-era-intensamente-buscado-en-ultima-esperanza-30267 (accesed October 15, 2013).
- Lebreton, J. D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spendelov. 2009. Modeling individual animal histories with multistate capture–recapture models. *Advances in ecological research* 41:87-173.
- Leege, T. A. 1968. Natural Movements of Beavers in Southeastern Idaho. *The Journal of Wildlife Management* 32:973-976.
- Lele, S. R., and J. L. Keim. 2006. Weighted distributions and estimation of resource selection probability functions. *Ecology* 87:3021-3028.
- Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17:322-326.

- Lindstrom, T., G. P. Brown, S. A. Sisson, B. L. Phillips, and R. Shine. 2013. Rapid shifts in dispersal behavior on an expanding range edge. *Proceedings of the National Academy of Sciences of the United States of America* 110:13452-13456.
- Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions* 8:1535-1545.
- Lizarralde, M.S., G. Bailliet, S. Poljak, M. Fasanella, and C. Giullivi. 2008. Assessing genetic variation and population structure of invasive North American beaver (*Castor Canadensis* Kuhl, 1820) in Tierra del Fuego (Argentina). *Biological Invasions* 10:673-683.
- Lizarralde, M., J. Escobar, and G. Deferrari. 2004. Invader species in Argentina: A review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. *Interciencia* 29:352-356.
- Lizarralde, M. S. 1993. Current status of the introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. *Ambio* 22:351-358.
- Lockwood J.L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20:223-228.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248-2255.
- Malaher, G. 1984. *The North I Love*. Hyperion Press Ltd., Winnipeg.

- Manchester, S. J., and J. M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* 37:845-864.
- Manitoba, the keystone province. 1948. Air Service Issue, Vol. 3, Issue 1. Travel and Publicity Bureau, Winnipeg.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, W. P. Erickson, B. F. J. Manly, L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition.
- Martínez Pastur, G., M. Lencinas, J. Escobar, P. Quiroga, L. Malmierca, and M. Lizarralde. 2006. Understorey succession in *Nothofagus* forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. *Appl Veg Sci* 9:143 - 154.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403-416.
- Massoia, E. and J.C. Chébez. 1993. Mamíferos silvestres del Archipiélago Fueguino. Ediciones L.O.L.A., Buenos Aires.
- McKinstry, M., and S. H. Anderson. 1998. Using snares to live-capture beaver, *Castor canadensis*. *Canadian Field-Naturalist* 112:469-473.
- McKinstry, M. C., and S. H. Anderson. 2002. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. *Canadian Field-Naturalist* 116:60-68.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology* 79:4-12.

- McNew, L. B., and A. Woolf. 2005. Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. *American Midland Naturalist* 154:217-228.
- Meentemeyer, R., and D. Butler. 1995. Temporal and spatial changes in beaver pond locations, eastern Glacier National Park, Montana, USA. *Geogr. Bull* 37:97-104.
- Messier, F., J. Virgl, and L. Marinelli. 1990. Density-dependent habitat selection in muskrats: a test of the ideal free distribution model. *Oecologia* 84:380-385.
- Moorman, M. C., D. B. Eggleston, C. B. Anderson, A. Mansilla, and P. Szejner. 2009. Implications of Beaver *Castor canadensis* and Trout Introductions on Native Fish in the Cape Horn Biosphere Reserve, Chile. *Transactions of the American Fisheries Society* 138:306-313.
- Morris, D. W. 1989. Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology* 3:80-94.
- Muller-Schwarze, D. 2011. *The beaver: its life and impact*. Cornell University Press, Ithaca, New York.
- Murray, J., E. Stanley, and D. Brown. 1986. On the spatial spread of rabies among foxes. *Proceedings of the Royal Society of London B: Biological Sciences* 229:111-150.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North-American streams by beaver. *Bioscience* 38:753-762.
- Navas J. 1987. Los vertebrados exóticos introducidos en la Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, *Zoología* 14:7-38.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613-1628.

- Nolet, B.A., and J.M. Baveco. 1996. Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. *Biological Conservation* 75:125-137.
- Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456-1463.
- Nummi, P., and L. Saari. 2003. Density-dependent decline of breeding success in an introduced, increasing mute swan *Cygnus olor* population. *Journal of avian biology* 34:105-111.
- Osborn, D. J. 1955. Techniques of sexing beaver, *Castor canadensis*. *Journal of Mammalogy* 36:141-142.
- Pachepsky, E., and J. M. Levine. 2011. Density Dependence Slows Invader Spread in Fragmented Landscapes. *American Naturalist* 177:18-28.
- Parker, H., P. Nummi, G. Hartman, and F. Rosell. 2012. Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. *Wildl Biol* 18:354 - 365.
- Payne, N. F. 1984a. Mortality Rates of Beaver in Newfoundland. *The Journal of Wildlife Management* 48:117-126.
- Payne, N. F. 1984b. Reproductive rates of beaver in Newfoundland. *Journal of Wildlife Management* 48:912-917.
- Pietrek, A. G., and L. Fasola. 2014. Origin and history of the beaver introduction in South America. *Mastozoologia Neotropical* 21:355-359.

- Pietrek, A. G., and M. González-Roglich. 2015. Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe. *Biological Invasions*:1-11.
- Pimm, S. L. 1991. *The balance of nature? Ecological issues in the conservation of species and communities*. Univ. of Chicago Press, Chicago. Pimm *The balance of nature*.
- Pimm, S. L., M. L. Rosenzweig, and W. Mitchell. 1985. Competition and food selection - field-tests of a theory. *Ecology* 66:798-807.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20-22 *in* Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). March.
- Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949-954.
- Rabassa, J., A. Coronato, G. Bujalesky, M. Salemme, C. Roig, A. Meglioli, C. Heusser, S. Gordillo, F. Roig, A. Borrromei, and M. Quattrocchio. 2000. Quaternary of Tierra del Fuego, Southernmost South America: an updated review. *Quaternary International* 68-71:217-240.
- Rosenzweig, M. L. 1981. A Theory of Habitat Selection. *Ecology* 62:327-335.
- Royle, J. A. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60:108-115.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. *Spatial capture-recapture*. Academic Press.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777-790.

- Russell, C. A., D. L. Smith, J. E. Childs, and L. A. Real. 2005. Predictive spatial dynamics and strategic planning for raccoon rabies emergence in Ohio. *Plos Biology* 3:382-388.
- Sæther, B.-E., Steinar Engen, Anders P. Møller, Henri Weimerskirch, Marcel E. Visser, Wolfgang Fiedler, and Erik Matthysen. 2004. Life-History Variation Predicts the Effects of Demographic Stochasticity on Avian Population Dynamics. *The American Naturalist* 164:793-802.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305-332.
- Sanguinetti, J., L. Buria, L. Malmierca, A. E. Valenzuela, C. Núñez, H. Pastore, L. Chauchard, N. Ferreyra, G. Massaccesi, and E. Gallo. 2014. Manejo de especies exóticas invasoras en Patagonia, Argentina: Priorización, logros y desafíos de integración entre ciencia y gestión identificados desde la Administración de Parques Nacionales. *Ecologia Austral* 24:183-192.
- Saveljev, A., M. Stubbe, A. Stubbe, V. Unzhakov, and S. Kononov. 2002. Natural movements of tagged beavers in Tyva. *Russian Journal of Ecology* 33:434-439.
- Schenectady Gazette. 1946. Twenty beavers migrate to Argentina. October 25, p. 5.
- Shigesada, N., K. Kawasaki, and E. Teramoto. 1986. Traveling periodic waves in heterogeneous environments. *Theoretical Population Biology* 30:143-160.
- Sielfeld W., and C. Venegas. 1980. Poblamiento e impacto ambiental de *Castor canadensis* Kuhl en Isla Navarino, Chile. *Anales del Instituto de la Patagonia* 2:247-257.

- Simberloff, D. 2009. The role of propagule pressure in biological invasions. *Annual Review Ecology, Evolution and Systematics* 40:81-102.
- Simberloff, D. 2009. We can eliminate invasions or live with them. Successful management projects. *Biological Invasions* 11:149-157.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196-218.
- Skewes, O., F. Gonzalez, R. Olave, A. Avila, V. Vargas, P. Paulsen, and H. E. König. 2006. Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. *European Journal of Wildlife Research* 52:292-296.
- Skewes, O. G., F. ; Rubilar, L. ; Quezada, O.M. ; Olave, R.R.; Vargas, V. ; Avila A.C. 1999. Investigación, aprovechamiento y control del castor, islas Tierra del Fuego y Navarino, Servicio de Gobierno Regional XII Región, Magallanes y Antártica Chilena, Punta Arenas, Chile.
- Smith H.P. 1976. The Solomon of the Traplins. *Manitoba Pageant*. Winter 1976.
- Sol, D., O. Lapiedra, and C. Gonzalez-Lagos. 2013. Behavioural adjustments for a life in the city. *Animal Behaviour* 85:1101-1112.
- Sucesos Argentinos N 432. Viaje al Sur. Buenos Aires: Noticiero cinematográfico Sucesos Argentinos, 1946, video.
- Sun, L. X., D. Muller-Schwarze, and B. A. Schulte. 2000. Dispersal pattern and effective population size of the beaver. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78:393-398.

- Suzuki, N., and W. C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon coast range. *Northwest Science* 72:102-110.
- Svendsen, G. E. 1980. Population parameters and colony composition of beaver (*Castor canadensis*) in southeast Ohio. *American Midland Naturalist* 104:47-56.
- Tachikawa, T., M. Hato, M. Kaku, and A. Iwasaki. 2011. Characteristics of ASTER GDEM version 2. Pages 3657-3660 *in* Geoscience and Remote Sensing Symposium (IGARSS), 2011 IEEE International. IEEE.
- Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. *Methods in Ecology and Evolution* 2:477-488.
- Travis, J. M. J., K. Mustin, T. G. Benton, and C. Dytham. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. *Journal of Theoretical Biology* 259:151-158.
- Uden, D. R., C. R. Allen, D. G. Angeler, L. Corral, and K. A. Fricke. 2015. Adaptive invasive species distribution models: a framework for modeling incipient invasions. *Biological Invasions* 17:2831-2850.
- Valenzuela A.E.J., C.B Anderson, L. Fasola, and J.L. Cabello. 2014. Linking invasive exotic vertebrates and their ecosystem impacts in Tierra del Fuego to test theory and determine action. *Acta Oecologica* 54:110-118.
- van Beest, F. M., A. Uzal, E. Vander Wal, M. P. Laforge, A. L. Contasti, D. Colville, and P. D. McLoughlin. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology* 83:147-156.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*:893-901.

VanDeelen, T. R., and D. H. Pletscher. 1996. Dispersal characteristics of two-year-old Beavers, *Castor canadensis*, in Western Montana. *Canadian Field-Naturalist* 110:318-321.

Wallem, P. K., C. G. Jones, P. A. Marquet, and F. M. Jaksic. 2007. Identifying the mechanisms underlying the invasion of *Castor canadensis* (Rodentia) into Tierra del Fuego archipelago, Chile. *Revista Chilena De Historia Natural* 80:309-325.

Weiss, A. 2001. Topographic position and landforms analysis. Pages 200-200 *in* Poster presentation, ESRI User Conference, San Diego, CA.

Winnipeg Free Press. 1936. Six beavers taking north in restocking venture. April 9, p. 4.

Biography

Alejandro Pietrek was born in Buenos Aires, Argentina in May of 1979. He graduated in 2004 with a Bachelor of Science with a major in Biology from the Universidad de Buenos Aires, Argentina. In 2009, he obtained a degree of Master of Science in Wildlife Ecology and Conservation from the University of Florida, US. His scientific publications include: *Susceptibility of lizards to predation under two levels of vegetative cover*, *Native plantations as an important element for biodiversity in vanishing forested landscapes: a study of the near threatened Araucaria Tit Spinetail*, *Origin and history of the beaver introduction in South America*, and *Post-establishment changes in habitat selection by an invasive species: beavers in the Patagonian steppe*. During his graduate studies Alejandro obtained several grants and awards including a Fulbright Scholarship in 2006.