

UCH-FC  
MAG - EBE  
S 586  
C. 1

**BEAVER PONDS AS WATERBIRD HABITAT IN  
TIERRA DEL FUEGO**

**Tesis**

**Entregada A La  
Universidad De Chile  
En Cumplimiento Parcial De Los Requisitos  
Para Optar Al Grado De**

**Magíster en Ecología Y Biología Evolutiva**



**Facultad De Ciencias**

**Por**

**Claudia Alejandra Silva Pinochet**

**Julio, 2010**

**Director de Tesis Dr: Irma Vila**

**FACULTAD DE CIENCIAS  
UNIVERSIDAD DE CHILE**

**INFORME DE APROBACION  
TESIS DE MAGISTER**

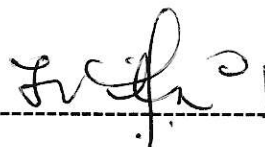
Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Magíster en Ciencias Biológicas con Mención en Ecología y Biología Evolutiva, presentada por la candidata:

**CLAUDIA ALEJANDRA SILVA PINOCHET**

Ha sido aprobada por la Comisión de Evaluación de la Tesis como requisito para optar al Grado de Magíster en Ciencias con mención en Ecología y Biología Evolutiva, en el examen de Defensa de Tesis rendido el día 15 de Junio de 2010.

**Directora de Tesis:**

Dra. Irma Vila P.

-----  


**Comisión de Evaluación de la Tesis:**

Dr. Javier Simonetti Z.

-----  


Dr. Michel Sallaberry A.

-----  




## Agradecimientos



Agradezco a WCS-Chile por facilitarme los datos sobre materia orgánica y macroinvertebrados y a todo el staff de WCS-Chile, en especial a quienes hicieron tan gratos mis terrenos: Dani, Claudio, Cristóbal, Maca y Fiore. También agradezco a mis ayudantes en terreno Soledad Gárate y Alejandra Bahamondez.

Agradezco el apoyo y gestión de las funcionarias de la Secretaría de Postgrado, en especial de Janet Guzmán.

Este trabajo fue financiado con la Beca Karukinka para Tesis en Tierra del Fuego, entregada por WCS-Chile.



## Indice de Materias

Introduction.....	1
Materials and methods.....	5
Results.....	13
Discussion.....	25
Conclusion.....	32
References.....	33
Appendix.....	38



## Lista de Tablas



Table 1. Waterbirds and terrestrial birds that occur in the study area .....	11
Table 2. Benthic organic matter and macroinvertebrates.....	15
Table 3. Correlation analysis for benthic organic matter and macroinvertebrates...	15
Table 4. List of macroinvertebrate taxa.....	16
Table 5. List of birds observed during surveys.....	18
Table 6. List of birds that use beaver ponds in Nort America.....	18



## Lista de Figuras

Figure 1. Map of the tierra del Fuego Archipelago.....	6
Figure 2. Maps of study sites.....	10
Figures 3-5. Rarefaction curves for carnivorous birds at the different habitat types.....	19
Figures 6-8. Rarefaction curves for shoreline carnivorous birds at the different habitat types.....	20
Figures 9-11. Rarefaction curves for omnivorous birds at the different habitat types.....	21
Figure 12. Rarefaction curve for herbivorous birds at beaver ponds.....	22
Figure 13. Rarefaction curve for piscivorous birds at beaver ponds.....	22
Figure 14. Density of omnivorous and shoreline carnivorous birds at beaver ponds and streams.....	23
Figure 15. Conceptual model of the effect of beavers in aquatic birds .....	24

## Resumen

El castor (*Castor canadensis*) fue introducido al archipiélago de Tierra del Fuego en 1946. En su hábitat nativo, la riqueza y abundancia de especies de aves acuáticas en pozones de castor es mucho mayor que en arroyos y lagunas cercanas. Un potencial mecanismo explicativo para el mayor uso de los pozones por aves acuáticas es un aumento en la disponibilidad de alimento resultante de procesos *bottom-up* gatillados por el embalsamiento del arroyo por el castor. En este estudio se investigó la relación entre aves acuáticas y pozones de castor y se comparó con la de los cuerpos de agua nativos.

La riqueza de especies de aves acuáticas fue mayor en pozones que en los hábitats nativos para tres de cinco grupos aviares de forrajeo definidos *a-priori*: herbívoros, omnívoros y piscívoros. En contraste, la riqueza de aves carnívoras no difirió entre hábitats y la de carnívoros de orilla fue mayor en arroyos. El análisis de materia orgánica bentónica que complementó las observaciones de aves mostró mayor disponibilidad en pozones que en arroyos, pero no hubo diferencias significativas con lagunas. No se detectaron diferencias en riqueza o densidad de macroinvertebrados entre los distintos hábitats.

Este estudio provee evidencia de que la introducción de castor en Tierra del Fuego ha tenido un efecto significativo sobre las aves. Se predice que los efectos tróficos *bottom-up* del castor en los arroyos resultantes en un aumento en la disponibilidad de alimento para las aves acuáticas serán de relativamente corta duración. En el contexto de un proyecto de erradicación de castores, es poco probable que la eliminación de pozones resulte en una reducción de la disponibilidad de hábitat para las aves acuáticas, al contrario, la erradicación podría aumentar la disponibilidad de hábitat al permitir el restablecimiento de los arroyos.

## Abstract

Beavers (*Castor canadensis*) were introduced to Tierra del Fuego in 1946. In their native habitat, waterbird richness and abundance in beaver ponds is much higher than in the adjacent rivers and than in concurrent lagoons. A potential explanatory mechanism for the higher use of beaver ponds by waterbirds is an increase in food resources resulting from trophic bottom-up processes triggered by beaver river damming. In this study I assessed the relationship between waterbirds and beaver ponds in Tierra del Fuego and compare it to that of native water bodies.

Bird species richness was higher in ponds than in native limnic habitats for three of the five avian foraging groups defined *a-priori*: herbivores, omnivores and piscivores. In contrast, richness of carnivorous birds did not differ between habitats and richness of shoreline carnivorous birds was higher in streams. Data on benthic organic matter that complemented the bird surveys showed higher stocks in ponds as compared to streams, but no significant difference was detected when compared to lagoons. No differences were detected between habitats for density or richness of macroinvertebrates.

This study provides evidence that beaver introduction into the Tierra del Fuego Archipelago has had significant effects on aquatic birds. Bottom-up trophic effects of beaver establishment in streams resulting in increased abundance of food resources for aquatic birds are expected to be relatively short-lasting. In the context of a project of beaver eradication in the Archipelago, the elimination of ponds is unlikely to reduce habitat availability for aquatic birds, on the contrary, eradication could render increased habitat availability by allowing the reestablishment of streams.



## Introduction

Beavers (*Castor canadensis* Kuhl, 1820) have historically been exploited for their fur, and this was both the cause for their near extinction in North America (Rosell *et al.* 2005), as well for their introduction to the Argentinean side of the Tierra del Fuego Archipelago (hereinafter TdF), in 1946. The Fuegian landscape offered a suitable combination of wetlands, woodlands and absence of predators for the successful establishment of beavers and, while a fur industry failed to develop in the area, the 25 initial beaver couples gave way to the spread and establishment of the species throughout nearly the entire Archipelago (Lizarralde 1993, Anderson *et al.* 2009 ). A survey carried out over a decade ago estimated over 100,000 individuals and a mean density of 1 beaver colony per km of stream only on the Chilean side of TdF (Skewes *et al.* 2006).

Judging from their habitat engineering capacity and the effects they have on their native range, it is predicted that beavers have the potential to cause significant effects at all levels of the ecological hierarchy in TdF, however only a fraction of those potential effects have been studied and confirmed (Crooks 2002, Silva & Saavedra 2008). Studies carried out so far show that the impact of beavers on riparian vegetation, aquatic macroinvertebrates and fish are similar in magnitude and direction to those on their native range (Vila *et al.* 1999, Anderson *et al.* 2006, Anderson & Rosemond 2007, Anderson *et al.* 2009, Arismendi 2009). In this context, the present study aims to

contribute to the understanding of beaver effects on the Fueguian ecosystem, this time focusing on the response of aquatic birds to the changes brought by beavers on the freshwater ecosystems of TdF.

Beavers build dams on rivers and streams, creating ponds. In North America, their range of origin, waterbird richness and density in beaver ponds is significantly higher than in adjacent rivers and than expected from habitat availability (Grover & Baldassarre 1995, Merendino *et al.* 1995, McCall *et al.* 1996, Rempel *et al.* 1997, McKinstry *et al.* 2001). Furthermore, waterbird presence in beaver ponds is higher than in concurrent lagoons of geological origin (Peterson & Low 1977, Bulluck & Rowe 2006, Longcore *et al.* 2006, Nummi & Hahtola 2008). A potential explanatory mechanism for the higher use of beaver ponds by waterbirds is an increase in food resources resulting from trophic bottom-up processes triggered by beaver river damming. River damming obstructs flow, increasing retention of sediments. This, together with the extra input of allochthonous material to the water body such as leaves and bark from beaver foraging activities, result in increased availability of organic matter for detritivorous macroinvertebrates and of nutrients for producers (Naiman & Melillo 1984, Francis *et al.* 1985, McDowell & Naiman 1986, Naiman *et al.* 1986; Devito & Dillon 1993). The bottom-up hypothesis predicts that productivity in the producer and decomposer trophic levels is limited by resources, and thus an increase in these resources will result in an increment in the biomass produced at these levels that will be transmitted up the food chain, although with decreasing strength since some energy will be lost in every link of the chain (Hairston *et al.* 1960, Fretwell 1987, Herenden 1995, Lampert & Sommer 1997). Following this reasoning, in beaver ponds the increment in resources for macrophytes, phytoplankton and detritivore macroinvertebrates resulting from river damming will boost productivity in these levels, and this effect will be transmitted up the

trophic chain, reaching aquatic birds sooner or later depending on their position in it (primary, secondary or tertiary consumers). Several empirical studies in the Northern Hemisphere support this prediction by reporting increases in biomass and/or density of various aquatic assemblages as a result of beaver activity (e.g. Hanson & Campbell 1963, McDowell & Naiman 1986, Margolis *et al.* 2001, Ray *et al.* 2001, Longcore *et al.* 2006, Anderson & Rosemond 2007, Krylov *et al.* 2007; reviewed in Collen & Gibson 2001 and Rosell *et al.* 2005).

In TdF, freshwater bodies of glacial origin are a common feature in the landscape. Their oligotrophic nature of these habitats means that their productivity is likely to be at least partially limited by nutrient availability, making them good candidates for the expression of the described trophic effect of beaver establishment (Smith 1985, Iturraspe & Urciolo 2000, Arismendi 2009). In addition, Anderson & Rosemond (2007), studying the impact of beavers in Navarino Island (part of TdF), found that beaver ponds had a higher standing crop of basal resources for detritivores (wood and benthic organic matter) and higher macroinvertebrate biomass than undisturbed stream reaches, and Arismendi (2009) showed that beaver ponds held a higher density of macroinvertebrates, while introduced fish (*Salmo trutta* Linnaeus, 1758) had a higher growth rate and higher relative weight in beaver ponds than in streams, and he concluded that the higher availability of resources (macroinvertebrates) seemed the most likely mechanism explaining the improvement in trout fitness. The results of both these studies are coherent with what is expected from a bottom-up trophic effect of beavers in Fuegian waterbodies.

So far, no study in TdF has assessed whether beaver ponds provide suitable habitat for waterbirds, less whether they are preferred over 'natural' water bodies. In this study I assess the relationship between waterbirds and beaver ponds and compare it to that of



native water bodies. Since it is proposed that the effects of beavers on aquatic birds will mainly result from a change brought by the species upon the trophic chain, I base my analysis on avian foraging groups. I compare species richness and density of avian foraging groups in beaver ponds in relation to undisturbed streams and lagoons of similar size. If an increment in basal resources and nutrients in beaver ponds is resulting in greater availability of food resources for birds in TdF, each avian foraging group should be richer in species and have a higher density of individuals in beaver ponds as compared to undisturbed streams and lagoons. The analysis of a data set on aquatic macroinvertebrates and benthic organic matter complements the bird observations, being expected that the availability of these resources increases as a result of the same mechanisms acting upon the birds.



## Methods

### *Study site*

Tierra del Fuego is an archipelago located at the southernmost tip of South America (54-56°S). This study took place on the Chilean side of the main island, *Isla Grande* (Fig. 1). This Island has a very marked environmental gradient that runs from NE to SW. In the northern part the terrain is flat and precipitations are scarce (250 mm $y^{-1}$ ). To the south, mean altitude increases towards the Darwin Mountain Range, precipitation also increases (400 mm  $y^{-1}$ ) and becomes more seasonally homogenous (Moore 1983, Iturraspe & Urciolo 2000).

This study took place in two areas of the forest-steppe ecotone (Figs. 1 & 2), within Karukinka Natural Park, a 300 ha private protected area managed by the Wildlife Conservation Society. Permanent and temporary water bodies of glacial origin are a widespread feature throughout the landscape. The watersheds of the study sites are located in the transition towards the Andean hydrogeographic zone, with the drainage network still retaining to a significant degree the gentle slope and limited flow of the steppe zone (Iturraspe & Urciolo 2000). As a result, water bodies are relatively shallow. Native streams and lagoons in a mixture of native steppe vegetation are characterized by grasses, sedges and shrubs, and forests, dominated by tree species of the genus *Nothofagus* (Moore 1983). On the other hand, vegetation in the vicinity of beaver ponds is a meadow rich in forbs and grasses that results from the foraging activities of these rodents, where any initial tree canopy cover is reduced up to 30 m from the water edge (Anderson *et al.* 2006).

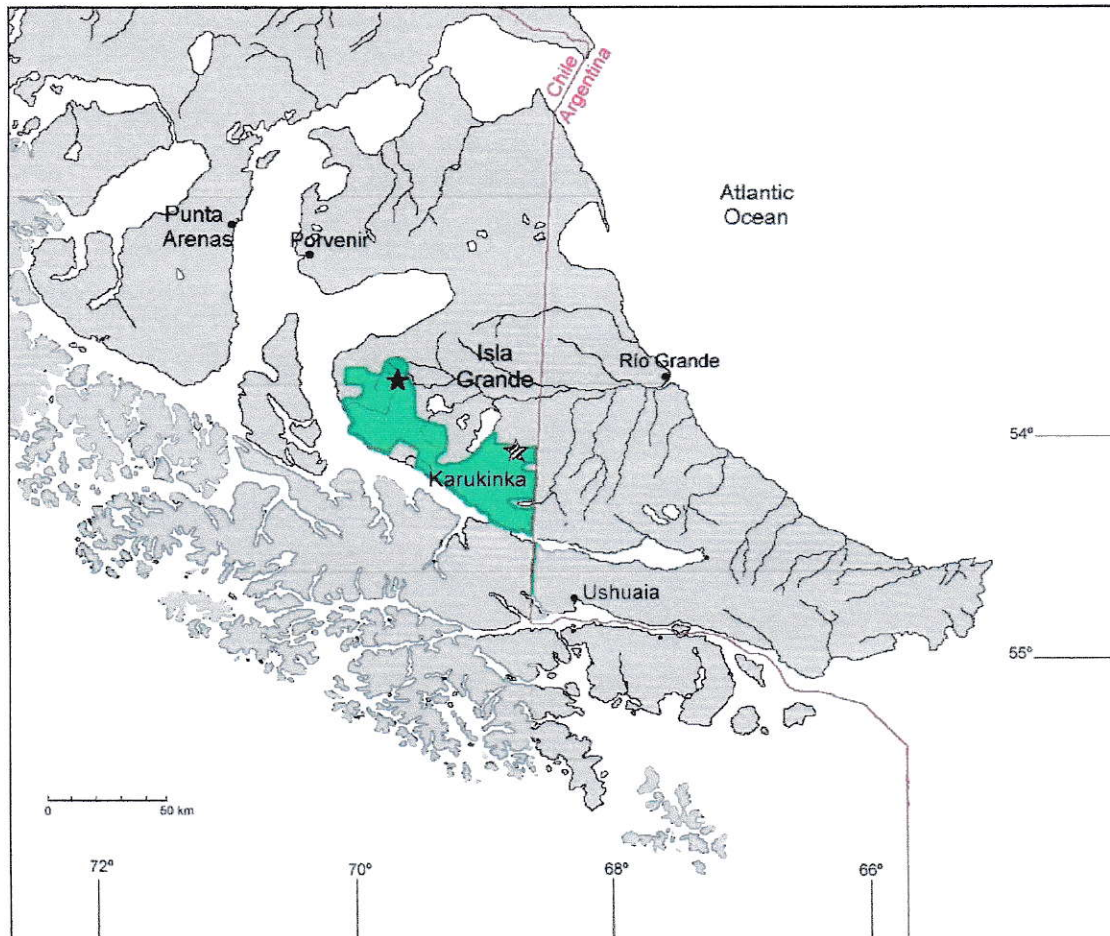


Figure 1. The Tierra del Fuego Archipelago. Main human settlements are identified with their names. Karukinka Natural Park is delimited in green. A black and a striped star indicate each of the two study sites (see Fig. 2 for detailed maps of study sites).

### *Organic matter and aquatic macroinvertebrates*

I analyzed a dataset on benthic organic matter and macroinvertebrates that was collected between October and November 2006 by Dr. Christopher Anderson, as part of a private consultancy to WCS. Raw data was provided as a result of this consultancy, but no analysis has so far been conducted on them. Although the bird surveys were carried out in 2008-2009, the macroinvertebrate community composition and abundance in New Zealand streams, which are similar to those of TdF in geological

origin, climatic conditions and nutrients, has been considered to be interannually stable in the long term, as long as no extreme variations in climate occur (Scarsbrook 2002, Collier 2007), which has not been the case for the 2006-2008 period (Arismendi 2009). The methods used to collect these data are as follows: benthic organic matter samples were taken with a core-sampler (0.7 m<sup>2</sup>) from beaver ponds, free-flowing streams (not paired with ponds) and lagoons in the surroundings of Vicuña base camp (marked with a striped star in Fig 1.). Three sub-samples were taken per replicate. Samples were passed first through a sieve of 1mm mesh size to separate coarse benthic organic matter (CBOM) and then through one of 250µm mesh size to separate fine benthic organic matter (FBOM). Samples were dried at 60°C and ashed at 500°C to determine ash-free dry mass (AFDM).

Samples of macroinvertebrates were taken with the same core sampler on the same sites for benthic organic matter samples, with three sub-samples on each site. They were passed through a sieve of 250 mesh size and stored in ethanol. In the laboratory, macroinvertebrates were separated from detritus under the microscope and identified to the lowest possible taxonomic level according to Fernández and Domínguez (2001) and Anderson (2004).

#### *Avian foraging groups and habitat use*

A preliminary list of the waterbirds that occur in our study area was made based on field guides (Venegas 1994, Couve & Vidal 2003). For the purpose of this study, we considered waterbirds to be those who live and feed in association to inland wetland habitats, as described in Victoriano *et al.* (2006) and Vilina *et al.* (2006). Additionally, we also considered for this study those terrestrial birds that do not live in the water, but



who are usually found in the surroundings of wetlands and feed on riparian aquatic resources (see Table 1). Birds were classified into foraging groups, according to the diet and feeding behavior described in Johnson & Goodall (1965), Fjeldså & Krabbe (1990), Del Hoyo *et al.* (1992), Fry & Fry (1992) and Todd (1996) (Table 1).

Waterbird surveys were conducted on beaver ponds, free-flowing rivers (not paired with ponds) and lagoons from 6.30 to 12.00 a.m. in November 2008 (1<sup>st</sup>-15<sup>th</sup>) and January 2009 (14<sup>th</sup>-29<sup>th</sup>). Beaver ponds and lagoons were censused using flush-counts, followed by 10-minutes point-counts with a period of adaptation of 5 minutes. Free-flowing rivers were censused using flush-counts along linear transect counts of 500 m along the river course (Gregory *et al.* 2004). Census were suspended on days of heavy rain. Sampled sites were selected in a random manner based on maps, aerial photographs and exploratory walks, but also subject to accessibility. In order to avoid species-area effects, I excluded ponds/lagoons considered too large for one point-counts. Each site was surveyed only once, and sites were separated from each other by at least 1 km to prevent double-counting of birds. In order to allow comparison between habitats, bird richness and abundance were standardized by area of surface water surveyed. Hectares were used as the basic surface unit because it is frequently used for bird surveys on lentic water bodies (e.g. Merendino *et al.* 1995). Although it is a counterintuitive unit for streams, it allows comparison between habitat types (for visualization purposes it might help to think that a 500 m stretch of a 20 m wide stream would approx. span 1 hectare of water surface). Area was estimated by assuming an elliptical shape of ponds/lagoons and measuring the transverse and conjugate diameters with a Rangefinder. For rivers, we assumed a rectangular shape and measured average width of the stream using the Rangefinder.

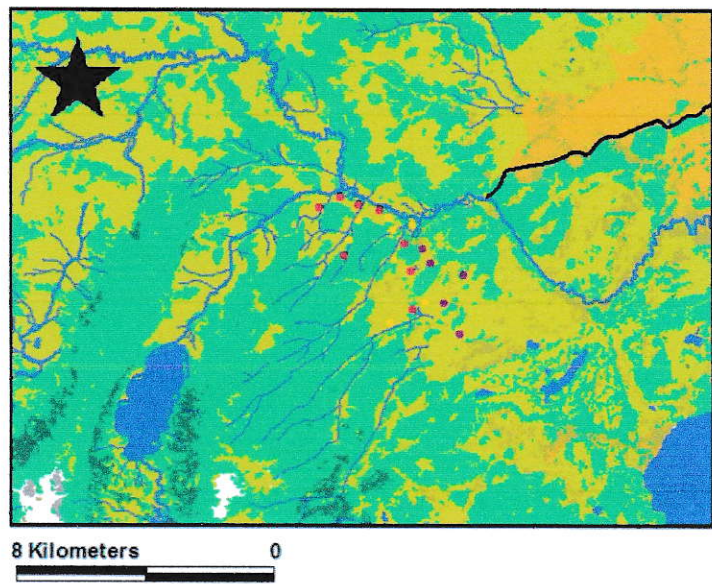
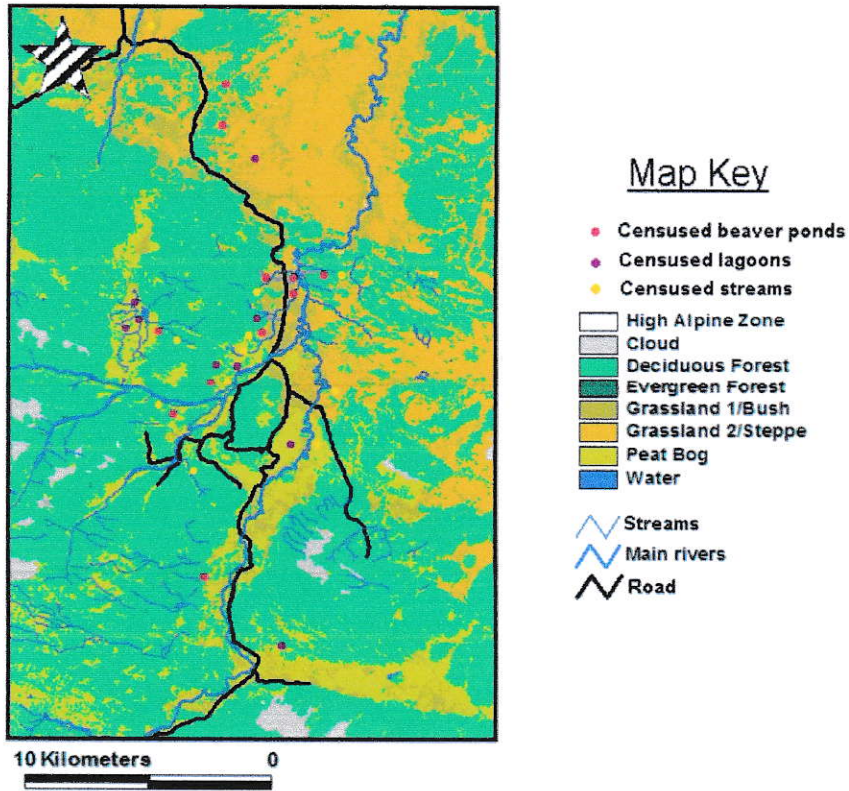


Figure 2. Maps of study sites. Location of bird surveys are indicated with colored dots (see map key). Striped star: Vicuña base camp and surrounding area. Black star: Lago Escondido base camp and surrounding area.

To allow comparison between the effects of beavers on their native and introduced ranges, a list of those waterbirds that prefer beaver ponds in North America was made. Finally, based on the bibliography and the results obtained, a conceptual model of the effect of beaver on Fuegian streams is proposed.

Table 1. Waterbirds and terrestrial birds closely associated to wetlands that occur in the study area.

<b>Herbivores</b>	<b>Shoreline carnivores</b>
<i>Anas sibilatrix</i> <sup>2</sup> Poeppig, 1829 <i>Fulica armillata</i> <sup>1</sup> Vieillot, 1817	<i>Nycticorax nycticorax</i> <sup>1,2,5</sup> Linnaeus, 1758 <i>Calidris bairdii</i> <sup>2</sup> Coues, 1861 <i>Calidris fuscicollis</i> <sup>2</sup> Vieillot, 1819
<b>Carnivores</b>	<i>Gallinago paraguaiiae</i> <sup>3*</sup> Vieillot, 1816 <i>Vanellus chilensis</i> <sup>1*</sup> Molina, 1782 <i>Pardirallus sanguinolentus</i> <sup>1</sup> Swainson, 1838 <i>Cinclodes fuscus</i> <sup>1*</sup> Vieillot, 1818 <i>Cinclodes oustaleti</i> <sup>1*</sup> Scott, 1900
<i>Lophonetta specularioides</i> <sup>1,5</sup> King, 1828 <i>Tachyeres patachonicus</i> <sup>1,2,5</sup> King, 1831 <i>Rollandia rolland</i> <sup>3</sup> Quoy & Gaimard, 1824	<i>Cinclodes patagonicus</i> <sup>1*</sup> Gmelin, 1789 <i>Cistothorus platensis</i> <sup>2*</sup> Latham, 1790 <i>Lessonia rufa</i> <sup>1*</sup> Gmelin, 1789
<b>Piscivores</b>	
<i>Podiceps major</i> <sup>1,2</sup> Boddaert, 1783 <i>Megaceryle torquata</i> <sup>1,4</sup> Linnaeus, 1766 <i>Phalacrocorax brasilianus</i> <sup>3,5</sup> Gmelin, 1789	
<b>Omnivores</b>	
<i>Anas flavirostris</i> <sup>2</sup> Vieillot, 1816 <i>Anas georgica</i> <sup>1,5</sup> Gmelin, 1789 <i>Anas platalea</i> <sup>5</sup> Vieillot, 1816 <i>Anas specularis</i> <sup>1,2</sup> King, 1828	

References for foraging groups: <sup>1</sup>Johnson and Goodall (1965), <sup>2</sup>Del Hoyo et al. (1992), <sup>3</sup>Fjeldsá & Krabbe (1990), <sup>4</sup>Fry & Fry (1992), <sup>5</sup>Todd (1996).

\* Terrestrial birds.



### *Data analyses*

Data on standing crops of total benthic organic matter (BOM), CBOM and FBOM, macroinvertebrate taxa richness and density, and bird abundance did not comply with the assumptions of normality and homocedasticity, so differences between habitat types were assessed using the non-parametric Kruskal-Wallis one-way analysis of variance by ranks and Mann-Whitney U tests. The Least Significance Difference in ranks was used as a post-hoc test to determine the source of significant differences. Correlation between standing stocks of organic matter in the different fraction sizes and macroinvertebrate density and richness was assessed using Spearman's correlation coefficient. The software Minitab© was used to perform all the afore mentioned statistical analyses. The software PAST© (Hammer *et al.* 2001) was used to generate rarefaction curves to allow comparison of species richness between sets of observations with different sample size. Finally, Moran's I was calculated to test for random spatial distribution of the data (see Appendix 1).

## Results

Standing stocks of BOM, CBOM and FBOM were all significantly higher (3-5 times) in beaver ponds compared to streams, and values in lagoons did not differ from those in either of the other two habitats (Table 2).

In total, thirty-three macroinvertebrate taxa were identified (Table 4). There was no significant difference between density of macroinvertebrate in ponds, streams and lagoons. Macroinvertebrate richness had similar values among the three habitat types (Table 2).

A significant positive correlation was found between BOM, CBOM and FBOM and macroinvertebrate density. The magnitude of the correlation decreased with decreasing fraction size (Table 3). Macroinvertebrate richness was not correlated to organic matter standing stock in any fraction size (Table 3).

(Table 5). No spatial autocorrelation was found between the variables studied (Appendix 1), but the lack of a vehicle and difficult accessibility of the area significantly limited the number of sites that could be located and reached, resulting in an unequal final sample size for the different habitats (14, 19 & 19 for lagoons, ponds and streams respectively). The species accumulation curves for each habitat did not level off with the number of sites sampled (data not shown), so rarefaction curves were constructed to compare species richness in each habitat for the smallest sample size (14 sites). At this sample size, there were no differences between habitats for carnivorous birds (Figs. 3-5). For shoreline carnivores richness was significantly higher in streams, followed by



lagoons and then by ponds (Figs. 6-8). In contrast, omnivore bird species richness was higher at ponds, followed by lagoons and then by streams (Figs. 9-11). Finally, no herbivores or piscivores were observed at streams nor lagoons, while species richness for these two groups was low, but greater than zero in ponds (Figs. 12 & 13).

Density of birds could not be compared between the three habitat types since there is no equivalent procedure to rarefaction for estimating species density for smaller sample sizes. Thus, only pond and stream habitats were compared for this variable. Omnivore abundance was greater in beaver ponds than streams, while there were no significant differences for shoreline carnivore density (Fig. 14). For the other foraging groups no significant differences could be tested because their scarce presence in the surveys (only one or two sightings per habitat type) did not allow statistical comparison.

Twenty species of birds were identified as occupying beaver ponds in a higher proportion to availability in North America (Table 6). The North American waterbird community had one foraging group that is not present in TdF, namely that of shoreline omnivores. Herbivores and shoreline carnivores were the most species-rich groups in North America, while in TdF the group of shoreline carnivores was the most species-rich, and herbivores were only comprised by one confirmed species (Tables 5 & 6). The omnivore group in ponds was composed by three species of dabbling ducks of the genus *Anas* both in the native and the introduced ranges of the beaver, but while in North America this is the group with a low relative number of species, in TdF the group is the richest of the strict waterbird species (i.e. excluding shoreline carnivores). In contrast, the also species-poor groups of carnivores and piscivores in North American ponds maintain this position in Fuegian ponds (Tables 5 & 6).

The conceptual model of the effect of beaver establishment on Fuegian streams on waterbirds is presented in Figure 15.

Table 2. Standing stocks (g AFDM/m<sup>2</sup>) of BOM, CBOM and FBOM and macroinvertebrate density (n° ind./m<sup>2</sup>) and richness (n°taxa/m<sup>2</sup>). Values correspond to median, first and third quartiles are in parenthesis. Differences between habitats were assessed using a Kruskal-Wallis analysis of variance by ranks, followed by a post-hoc LSD test. H Statistic, degrees of freedom (Df) and significance value (*p*) for KW are shown. Different capital letters indicate significant differences between habitats\*.

	<b>Beaver pond</b> (n=8)	<b>Stream</b> (n=10)	<b>Lagoon</b> (n=3)	<b>H</b>	<b>Df</b>	<b>p</b>
<b>BOM</b>	1.12 (0.93-1.4) A	0.30 (0.24-0.51) B	0.80 (0.49-1.4) AB	12.92	2	0.002
<b>CBOM</b>	0.52 (0.4-0.67) A	0.10 (0.08-0.16) B	0.32 (0.20-1.03) AB	12.00	2	0.002
<b>FBOM</b>	0.64 (0.53-0.77) A	0.20 (0.16-0.36) B	0.39 (0.21-0.40) AB	13.19	2	0.001
<b>Macroinvertebrate density</b>	253.6 (140.0-578.5)	100.5 (21.9-199.0)	279.0 (186.7-422.9)	5	2	0.067
<b>Macroinvertebrate richness</b>	12.6 (10.9-12.9)	10.7 (6.2-13.5)	10.5 (10.5-13.3)	0.75	2	0.721

\*A power test for ANOVA was used to obtain a conservative estimate of the power of the KW for this data set (Mahoney & Magel 1996). The power of the test was high (>0.8) for n=10 and 8 (ponds and streams) but lower (<0.4) for n=3 (lagoons). Lack of significant differences between lagoons and other habitats should thus be interpreted with caution.

Table 3. Correlation between benthic organic matter in its different fraction sizes and macroinvertebrate density and richness. The t statistic and p value for Spearman's correlation is given.

		<b>Spearman's ρ</b>	<b>t</b>	<b>p</b>
BOM	Density	0.648	3.709	<<0.01
	Richness	0.235	1.052	0.306
CBOM	Density	0.595	3.225	<0.01
	Richness all	0.166	0.074	0.471
FBOM	Density	0.583	3.129	<0.01
	Richness	0.296	1.351	0.193

Table 4. List of the macroinvertebrate taxa found on Vicuña base camp and their occurrence in the three different habitat types.

								Ponds	Streams	Lagoons		
Class	Subclass	Order	Suborder	Sub cohort	Family	Subfamily	Genus					
Arachnida	Acari	Acariformes	Prostigmata	Hydrachnidia				x	x	x		
Bivalvia	Heterodonta	Veneroida			Sphaeriidae		<i>Pisidium</i>	x	x			
Branchiopoda		Diplostraca	Cladocera					x	x	x		
Clitellata	Oligochaeta							x	x	x		
Entognatha	Collembola	Entomobryomorpha							x			
Gastropoda					Lymnaeidae		<i>Lymnaea</i>		x			
Hirudinea								x	x			
Insecta		Coleoptera			Dysticidae			x	x	x		
					Hydrophilidae			x	x			
					Scirtidae				x			
			Diptera			Ceratopogonidae			x	x	x	
						Chironomidae	Orthoclaadiinae			x	x	x
							Podonominae				x	
							Tanypodinae			x	x	x
							Chironominae	<i>Chironomus</i>		x	x	x
						Simuliidae		<i>Gigantodax</i>			x	
						Tabanidae					x	
Tipulidae					x	x	x					
		Ephemeroptera			Baetidae		<i>Andesiops</i>		x			



				Leptophlebiidae	Massartellopsis			X		
					Meridialaris	X		X		
	Plecoptera			Gryopterygidae	Antarctoperla			X		
					Limnoperla			X		
					Rhithroperla			X		
								X		
	Trichoptera			Hydroptilidae				X		
				Limnephilidae				X		
					Monocosmoecus			X		
				Hydrobiosidae					X	
				Hyalellidae					X	
Malacostraca	Amphipoda					X				
Maxillopoda	Calanoida					X		X		
	Cyclopoida					X		X		
	Harpacticoida					X		X		
Ostracoda						X		X		

Table 5. List of birds observed during the surveys and their occurrence the different habitats.

	Pond	Stream	Lagoon
<b>Herbivores</b>			
<i>Anas sibilatrix</i>	X		
<b>Omnivores</b>			
<i>Anas flavirostris</i> **	X	X	X
<i>Anas georgica</i> **	X		X
<i>Anas specularis</i>	X		
<b>Carnivores</b>			
<i>Lophonetta specularioides</i>		X	X
<i>Tachyeres patachonicus</i>	X		
<b>Piscivores</b>			
<i>Phalacrocorax brasilianus</i>	X		
<b>Shoreline carnivores</b>			
<i>Nycticorax nycticorax</i>		X	
<i>Calidris fuscicollis</i>			X
<i>Cinclodes fuscus</i>	X	X	X
<i>Cinclodes sp.*</i>		X	
<i>Gallinago paraguaiae</i>		X	
<i>Lessonia rufa</i>	X	X	X
<i>Vanellus chilensis</i>	X	X	X

\*Due to the difficulty of differentiating between *C. oustaleti* and *C. patagonicus* from the distance, they were recorded together.

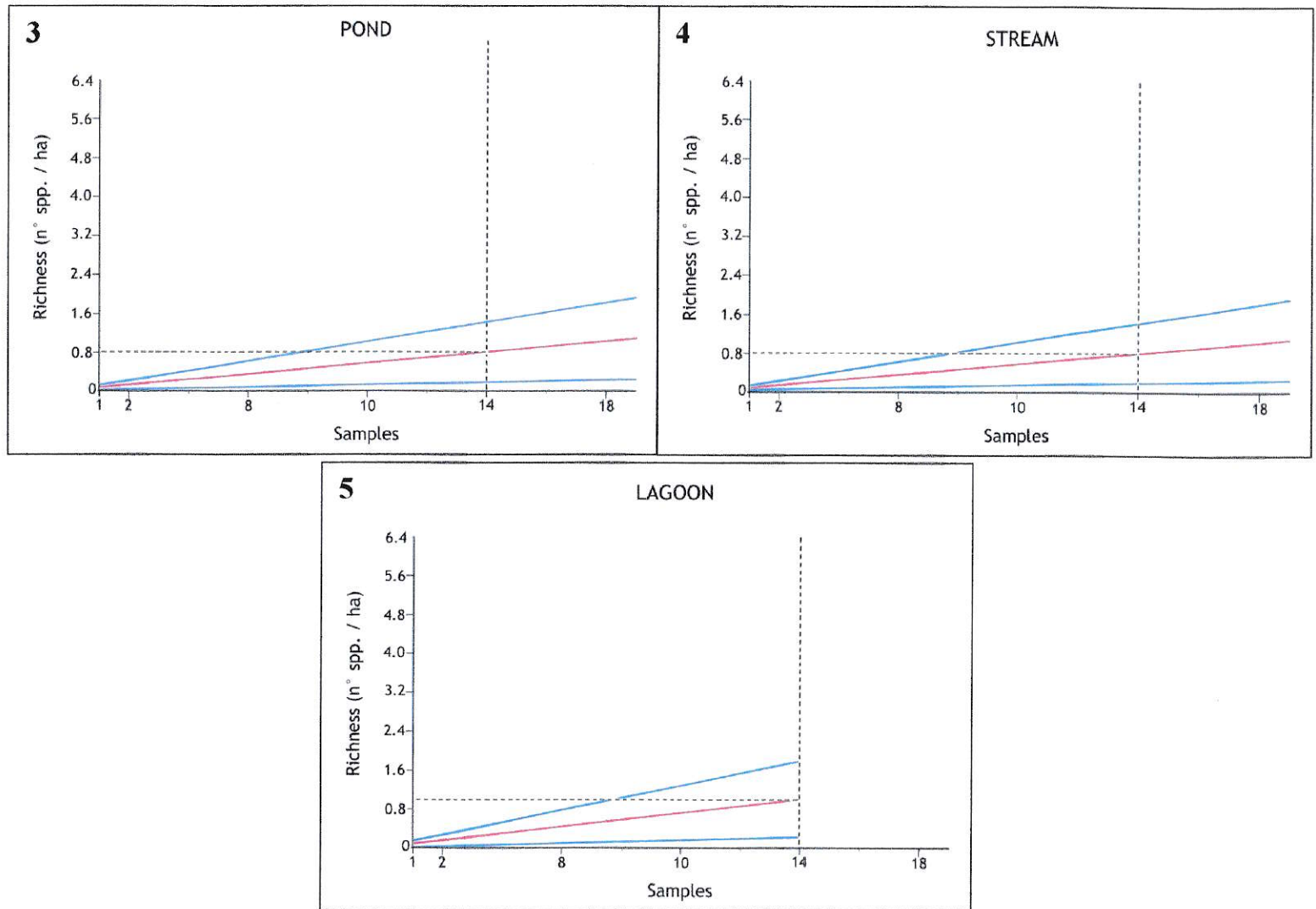
\*\*These species are herbivores but switch to an omnivore diet during the breeding season, when this study was conducted (Del Hoyo *et al.* 1992, Todd 1996).

Table 6. List of the birds that have been recorded using beaver ponds in a higher proportion to their availability in the landscape in North America.

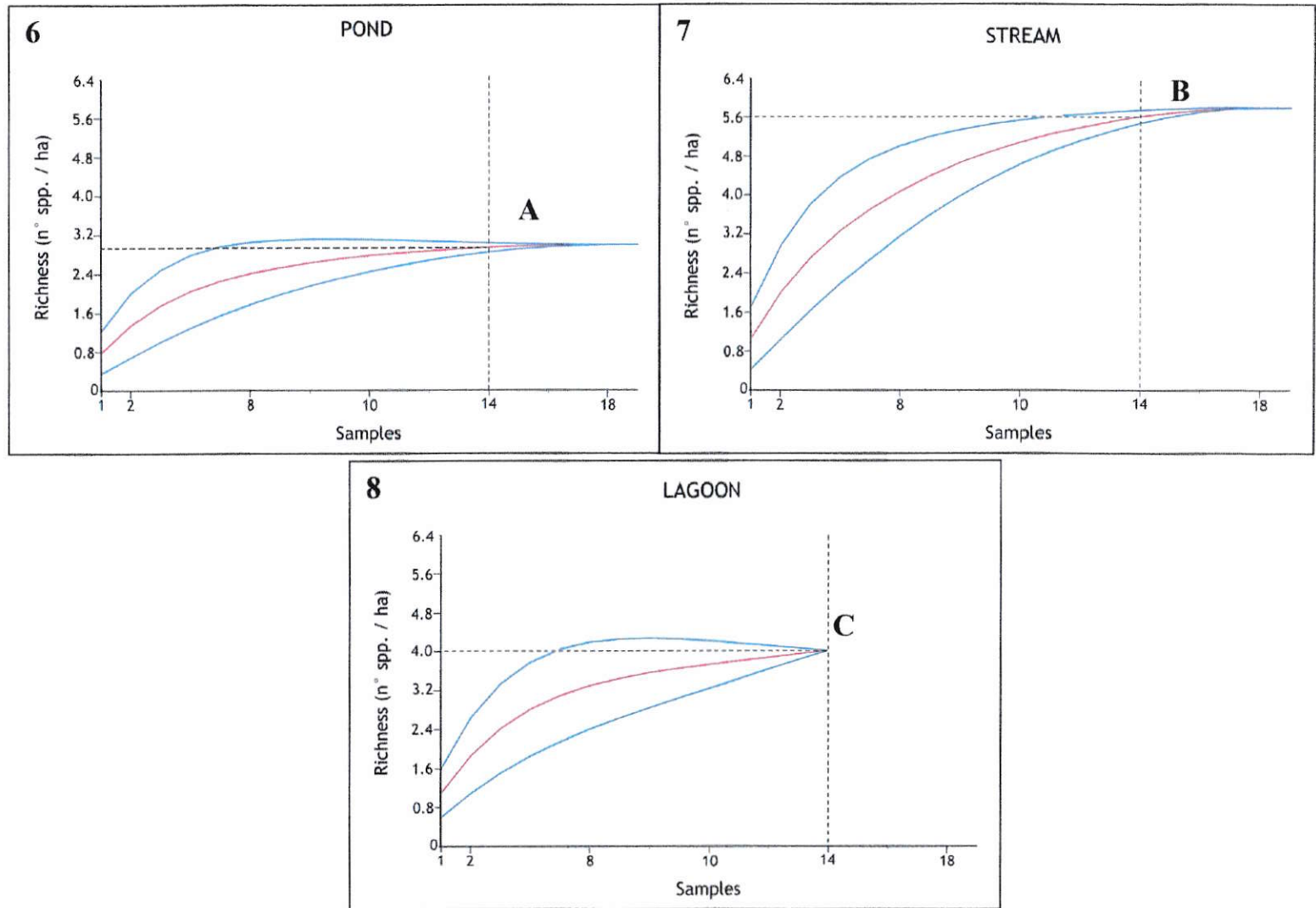
<b>Herbivores</b>	<b>Piscivores</b>
<i>Aythya collaris</i> <sup>2,3,†</sup> Donovan, 1809	<i>Gavia immer</i> <sup>3,†</sup> Brunnich, 1764
<i>Anas discors</i> <sup>2,†</sup> Linnaeus, 1766	<i>Mergus merganser</i> <sup>3,†</sup> Linnaeus, 1758
<i>Aix sponsa</i> <sup>1,2,3,†</sup> Linnaeus, 1758	<i>Megaceryle alcyon</i> <sup>1,3,§</sup> Linnaeus, 1758
<i>Anas americana</i> <sup>2,†</sup> Gmelin, 1789	<b>Shoreline omnivores</b>
<i>Branta canadensis</i> <sup>1,2,†</sup> Linnaeus, 1758	<i>Porzana carolina</i> <sup>1,3,†</sup> Linnaeus, 1758
<b>Omnivores</b>	<b>Shoreline carnivores</b>
<i>Anas platyrhynchos</i> <sup>1,2,*</sup> Linnaeus, 1758	<i>Botaurus lentiginosus</i> <sup>1,3,†</sup> Rackett, 1813
<i>Anas rubripes</i> <sup>2,*</sup> Brewster, 1902	<i>Ardea herodias</i> <sup>1,3,†</sup> Linnaeus, 1758
<i>Anas crecca</i> <sup>2,*</sup> Linnaeus, 1758	<i>Gallinago gallinago</i> <sup>1,3,†</sup> Linnaeus, 1758
<b>Carnivores</b>	<i>Actitis macularius</i> <sup>1,3,†</sup> Linnaeus, 1766
<i>Lophodytes cucullatus</i> <sup>1,2,3,†</sup> Linnaeus, 1758	<i>Tringa solitaria</i> <sup>1,†</sup> Wilson, 1813
<i>Podylymbus podiceps</i> <sup>3,†</sup> Linnaeus, 1758	
<i>Bucephala clangula</i> <sup>2,†</sup> Linnaeus, 1758	

References: <sup>1</sup>Grover and Baldassarre (1995), <sup>2</sup>Rempel *et al.* (1997), <sup>3</sup>Longcore *et al.* (2006).

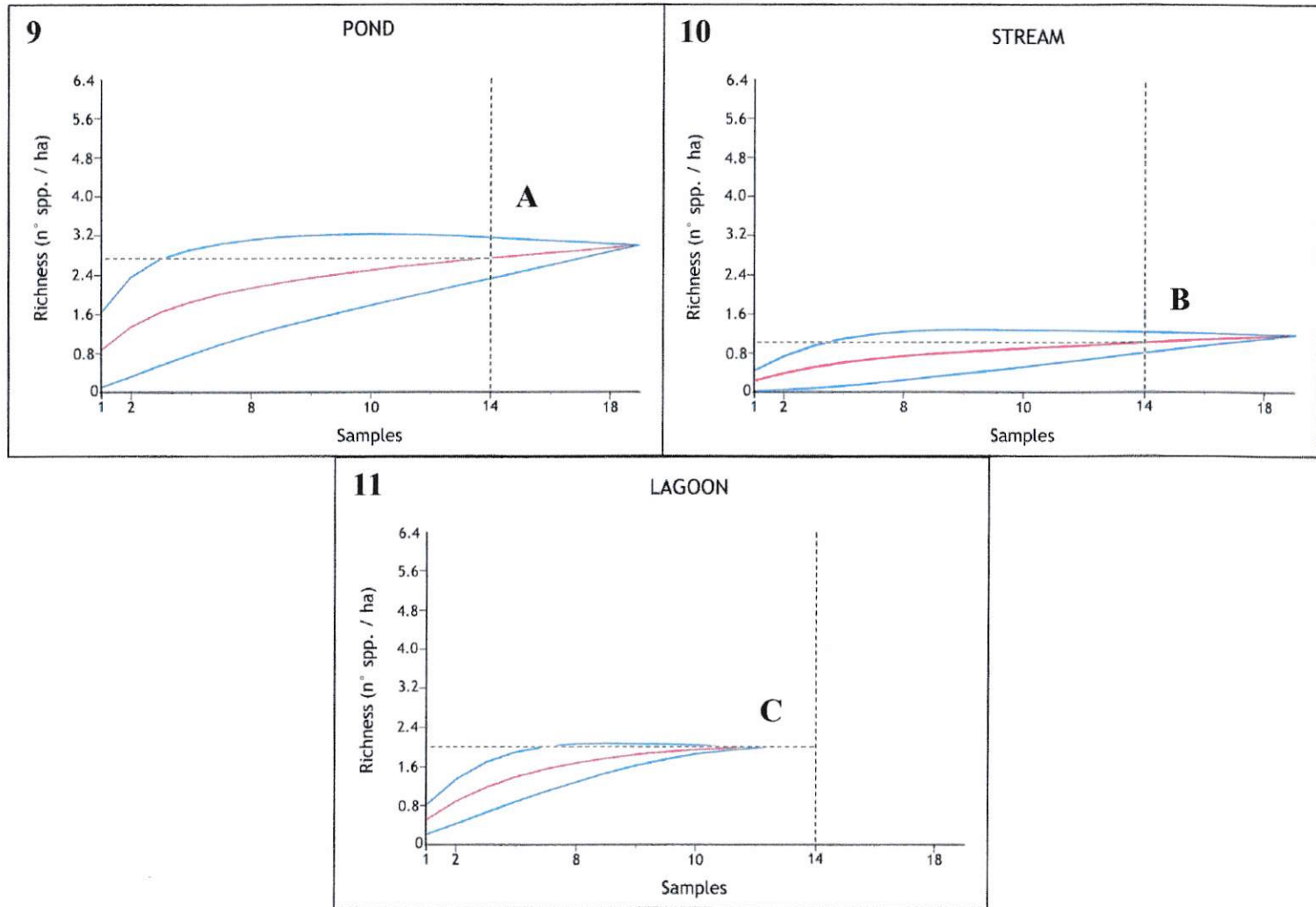
Foraging groups: \*Todd (1996), †Del Hoyo *et al.* (1992), §Fry & Fry (1992).



Figures 3-5. Rarefaction curves for carnivorous birds at the different habitat types. Red lines indicate the estimated species richness at each sample size, blue lines indicate 95% confidence intervals. There were no significant differences between habitat types at sample size =14.



Figures 6-8. Rarefaction curves for shoreline carnivorous birds at the different habitat types. Red lines indicate the estimated species richness at each sample size, blue lines indicate 95% confidence intervals. Different capital letters indicate significant differences between habitat types at sample size = 14.



Figures 9-11. Rarefaction curves for omnivorous birds at the different habitat types. Red lines indicate the estimated species richness at each sample size, blue lines indicate 95% confidence intervals. Different capital letters indicate significant differences between habitat types at sample size = 14.



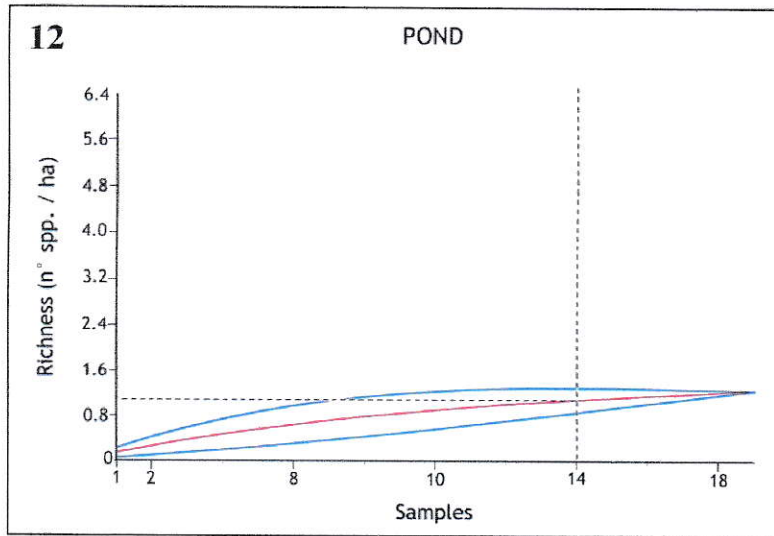


Figure 12. Rarefaction curve for herbivorous birds in beaver ponds. Red lines indicate the estimated species richness at each sample size, blue lines indicate 95% confidence intervals. No species were observed at streams or lagoons.

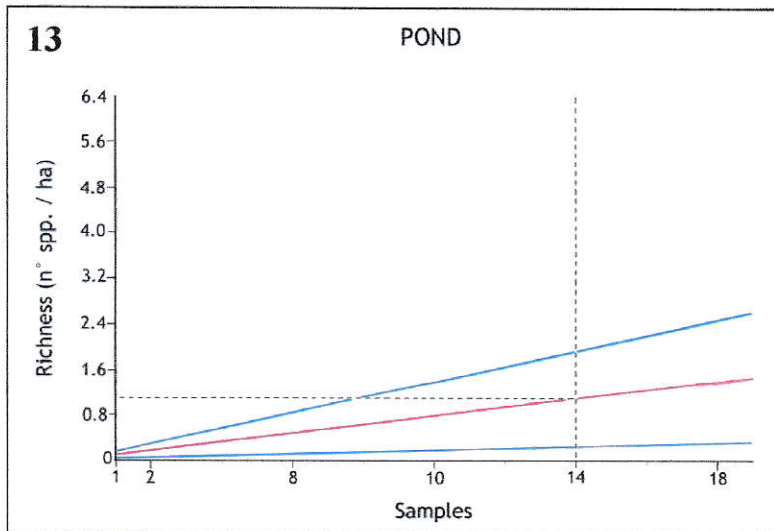


Figure 13. Rarefaction curve for piscivorous birds in beaver ponds. Red lines indicate the estimated species richness at each sample size, blue lines indicate 95% confidence intervals. No species were observed at streams or lagoons.

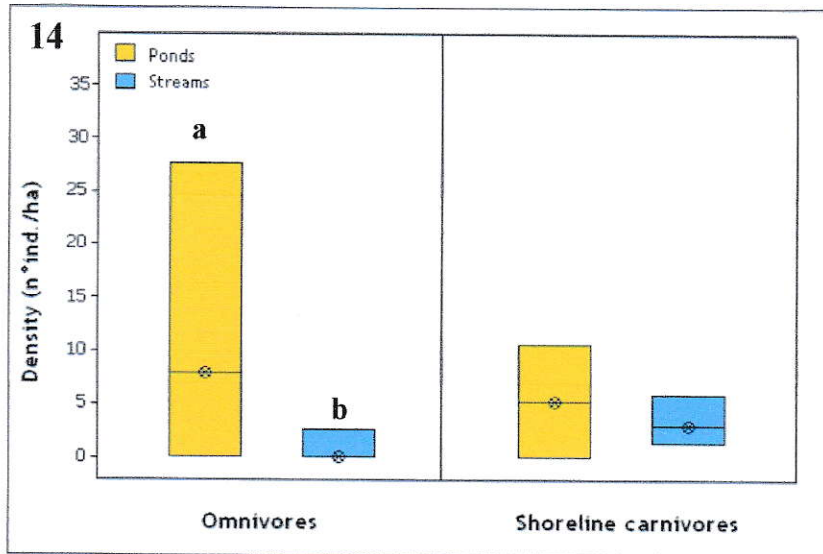
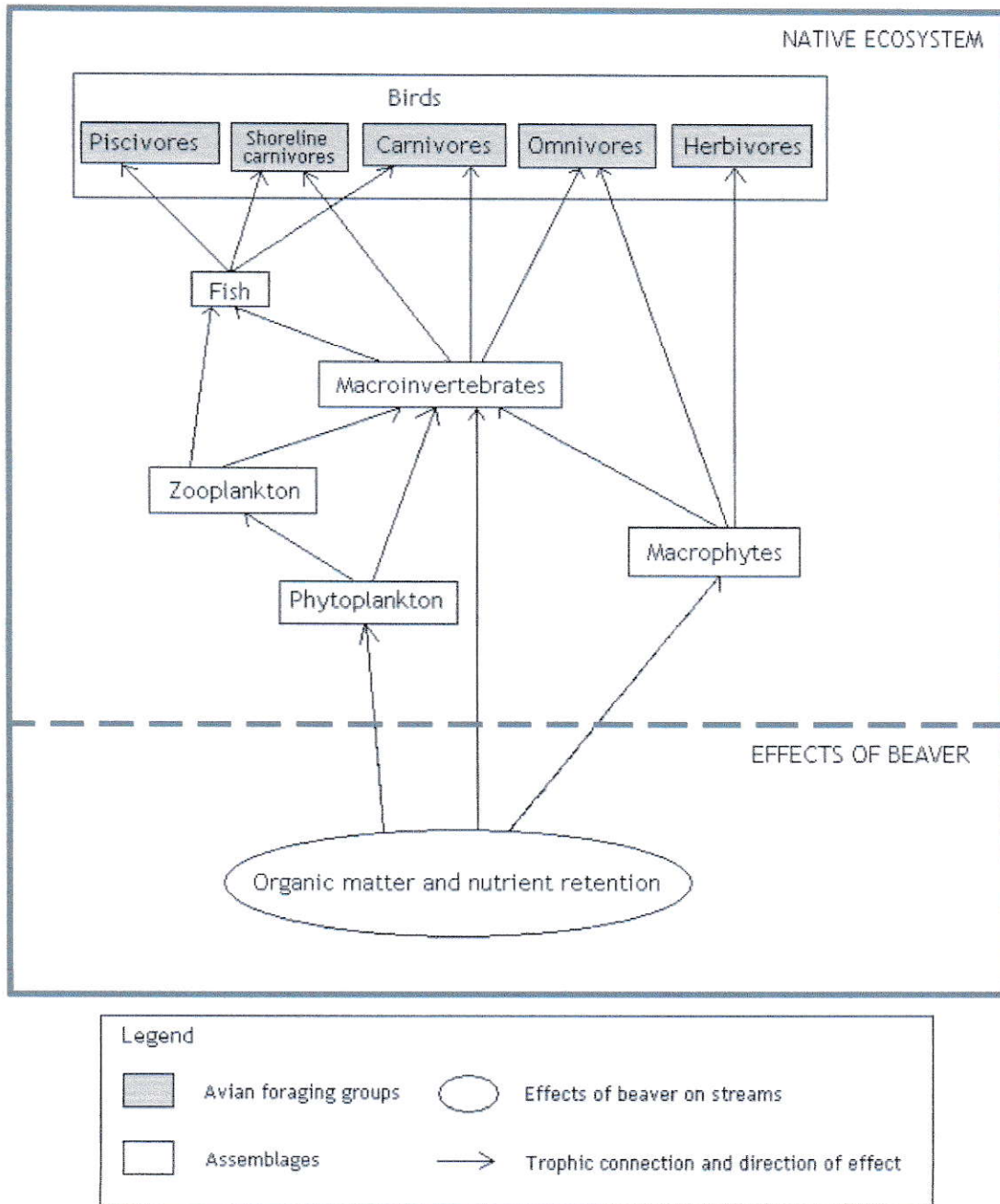


Figure 14. Density of omnivore and shoreline carnivore birds according to habitat type. Bars indicate first and third quartiles and circles indicate medians. Different letters indicate significant differences between habitat types.

Figure 15. Conceptual model of the effect of beavers on aquatic birds through trophic bottom-up processes.



## Discussion

The TdF archipelago is home to eleven native and twelve introduced mammal species with well-established populations (Anderson *et al.* 2006). Of those species introduced, the beaver is the most widespread and the one showing the highest number of potential ecological effects in the native ecosystem, even though only a fraction of them have been verified for the Archipelago (Anderson *et al.* 2006, Silva & Saavedra 2008). The exotic species present in the TdF provide an opportunity to increase our understanding on the ecological mechanisms of biological invasions as well as on those that shaped the Fuegian ecosystem prior to these introductions.

Rapidly accumulating evidence indicates that the effects of beavers on TdF are similar in direction and, to a lesser degree, in magnitude to those on their native range, and can therefore be readily predicted combining knowledge of their natural history with that of the recipient ecosystem (Vila *et al.* 1999, Anderson *et al.* 2006, Anderson & Rosemond 2007, Anderson *et al.* 2009, Arismendi 2009). The present study aimed to investigate if beaver ponds had a significant effect on the aquatic bird community and on other birds closely associated to water bodies, as it occurs in their range of origin where beaver ponds have a higher species richness and density of waterbirds (e.g. Merendino *et al.* 1995, Longcore *et al.* 2006).

In this study, species richness was higher in ponds than in native limnic habitats for three of the five avian foraging groups defined *a-priori*: herbivores, omnivores and piscivores. Birds in the herbivore group are exclusively primary consumers and are therefore expected to exhibit a higher difference between ponds and other habitats than



the other avian foraging groups, as the magnitude of the bottom-up effect is expected to decrease with increasing number of links separating a certain trophic level from the basal resources where the effect began (Lampert & Sommer 1997). Consistent with this idea, herbivorous birds are the group with the highest species richness of strict waterbirds in the North American bird community found in beaver ponds however, we cannot say the same from this study, where herbivores were limited to one species (of two potentially present, Table 1). The low relative species richness of this group is probably not an artifact of low sample size in this study but actually a characteristic of southern TdF, as it can be seen in Table 1. There are at least two other herbivorous waterbirds that reach the northern part of the Island (*Fulica rufifrons* and *Fulica leucoptera*, Couve & Vidal 2003) but do not reach the southern part. This could be an indicator of lower productivity of macrophytes in the southern part, perhaps influenced by the lower temperatures (Iturraspe & Urciolo 2000), which remains as a hypothesis to be tested. The herbivorous *A. sibilatrix* found in beaver ponds migrates north in the winter, avoiding any of eventual effects caused by the drop in temperature (Venegas 1994, Couve & Vidal 2003). The same strategy is shared by two of the three observed omnivore species, *A. flavirostris* and *A. georgica* (*op.cit.*). These and the other dabbling ducks sieve mud and retain invertebrates in their lamellae (Todd 1996), being able to efficiently forage on macroinvertebrates living both upon and inside the benthos. Their higher richness and density in ponds as compared to native water bodies could nonetheless not be related to any changes in the macroinvertebrate community, this in spite of a significant increase in standing stock of organic matter in ponds and a positive correlation between the latter variable and macroinvertebrate density. Given that Anderson & Rosemond (2007) found a significant increase in macroinvertebrate biomass as a result of beaver activity in Navarino Island notwithstanding a lack of

differences in macroinvertebrate density, it would still be adequate to check for the response of this latter variable in the present study area.

Carnivores and piscivores were also very scarce, something that could at least partially be related to their position in the trophic chain. Higher order consumers are expected to be scarcer than lower trophic levels (Elton 1927). In fact, these two foraging groups are among those having the lowest species richness in ponds both in North America and TdF. On the other hand, four of the carnivore and piscivore species that occur in the study area also forage in marine habitats (*L. specularioides*, *T. patachonicus*, *P. major* and *P. brasilianus*; Johnson & Goodall 1965, Venegas 1994), negatively influencing the probability of detection. In the case of the only sighting of a piscivore species in this study, and its presence in beaver ponds was probably more related to habitat provisioning, or to a combination of the later and trophic effects, as it corresponded to a breeding colony of *P. brasilianus* nesting in the trees killed by the flooding caused by the beaver. This observation highlights the importance of factors other than food availability in determining the selection of a certain habitat type. Provision of adequate breeding sites is another important factor influencing habitat selection by waterbirds (Todd 1996). In North America, vegetation interspersed has been found to be positively related to the presence of breeding pairs in beaver ponds, which would provide territorial isolation and cover for breeding pairs and nests (e.g. Edward & Otis 1999; Found *et al.* 2008).

In contrast to predictions, shoreline omnivores showed the lowest species richness in beaver ponds, and the highest in streams, although in terms of density no difference was observed between habitats. One possible explanation for this result is that one dominant method of foraging in this group is pecking on invertebrates that live hidden among the rocky substrate (Johnson & Goodall 1965, Todd 1996, Couve & Vidal 2003).



In beaver ponds, the rocky substrate is completely covered by soft sediment (Anderson & Rosemond 2007) and, although other invertebrates live inside the sediment, their visual localization will be limited (Lampers & Sommers 1997). Member species of this foraging group that are not particularly affected by this change can still forage in beaver ponds, and the individuals lost from the gone species could be compensated by an increase in the number of individuals of the remaining species as a result of the higher availability of food in ponds, so that density of the group remains similar between the two habitats. Macroinvertebrates living within the sediments will be nonetheless preyed upon most efficiently by dabbling ducks, as mentioned above.

In general terms, this study provides evidence that the beaver has significant effects on Fuegian birds living in close association with freshwater bodies, effects that in most, but not all cases are those expected from the changes the species causes in its native range. It must be noted though that there are several factors hampering the ability to draw strong conclusions from this study. First, no stabilization in the species accumulation curves for each habitat was reached, meaning that a larger sampling effort would have been necessary to fully account for the differences in the bird communities, especially for the scarcer groups. A good way of improving sampling efficiency other than increasing the number of sites is also increasing the number of skilled observers. A second observer can decrease in 15-25% the number of missed birds in a habitat with relatively good visibility such as water bodies (Preston 1970). Another limitation of this study is that the analysis is limited to trophic interactions, and more specifically only to bottom-up effects. Even if these were the dominant forces in this ecosystem, such an approach is a simplified version of real-world interactions and the influence of top-down effects and competition, among other factors, have been ignored. It is certainly possible that bottom-up and top-down effects are operating

simultaneously in determining species richness and abundance in a certain trophic levels (Hairston *et al.* 1960, Herenden 1995, Lampert & Sommer 1997).

### *Implications for management*

Currently, there is an ongoing binational (Chilean-Argentinean) initiative to eradicate beavers from the entire TdF Archipelago, being pushed forward by private and public stakeholders (Parkes *et al.* 2009). The magnitude of economic and labor resources required to carry out such endeavor urges that the largest possible amount of scientific understanding on the various aspects of beaver biology, ecology and effects is made available in order for stakeholders to make informed decisions in all the stages of the process. Below I summarize the implications of this study for this and other beaver management initiatives in TdF.

The effects of introduced species are not static but vary significantly with time. In fact, the impacts of introduced species can be thought of as having an acute phase (immediate impacts) and a chronic phase (impacts that arise after a lag time and that last in the long-term) (Strayer *et al.* 2006).

Beaver ponds reach an eutrophic state quickly, after which productivity gradually decreases until the ponds reaches a dystrophic state after approx. 10 years (Collen & Gibson). Thus, at the local scale, the bottom-up trophic effect of beaver ponds is temporary. For example, Renouf (1972) observed that active beaver ponds housed significantly more waterbird broods than older ponds that had been abandoned by beavers. Beavers move out of the colonized patch when the riparian vegetation has been out-consumed, between 5-15 years after colonization (Müller-Schwarze & Sun 2003). In their native range, abandonment of the site allows vegetation to recover, so



that the same patch can be recolonized after a few years (Müller-Scharze & Sun 2003, Rosell *et al.* 2005). In TdF however, the native tree species lack the capacity to recover from beaver flooding and cutting, so that there is little or no recovery of the original vegetation up to twenty years after beaver abandonment (Anderson *et al.* 2006, Martinez-Pastur *et al.* 2006) and therefore, at least theoretically, beavers would not recolonize the patch and the pond would be lost when the dam breaches from lack of repair. In reality, as the density of beavers increases and the non-colonized stream reaches become scarcer, beavers do recolonize old sites or settle in sub-optimal habitat such as streams in the steppe zone (Skewes *et al.* 2006; Claudio Moraga, WCS, *personal comm.*). Recolonized ponds will remain dystrophic (chronic effects) and thus their trophic value will be permanently lower than in the initial years.

The precise time that it has taken beavers to reach carrying capacity in TdF and start colonizing sub-optimal habitat and recolonize old sites is unknown, but it is likely that we are still in a period in which a number of old ponds co-exist in the landscape with others that are relatively new. Thus, the results of this study probably do not correspond entirely either to acute nor chronic effects, but to a transitional state. Studies that take into account pond age and their differential effects are encouraged, but until those are available I predict, based on the available literature, that values in aquatic bird richness and density in ponds will be higher in the initial years, to gradually decrease and reach values similar to natural lagoons, to finally decrease even further when ponds reach a dystrophic state.

Management plans need to deal with effects according to their time-frames. Acute effects of species are of importance for short-term management actions. For definitive, long-term initiatives such as eradication, chronic effects are more appropriate to use in cost-benefit analysis. Beaver eradication in TdF will imply the elimination of ponds in a

been out-consumed, between 5-15 years after colonization (Müller-Schwarze & Sun 2003). In their native range, abandonment of the site allows vegetation to recover, so that the same patch can be recolonized after a few years (Müller-Scharze & Sun 2003, Rosell *et al.* 2005). In TdF however, the native tree species lack the capacity to recover from beaver flooding and cutting, so that there is little or no recovery of the original vegetation up to twenty years after beaver abandonment (Anderson *et al.* 2006, Martinez-Pastur *et al.* 2006) and therefore, at least theoretically, beavers would not recolonize the patch and the pond would be lost when the dam breaches from lack of repair. In reality, as the density of beavers increases and the non-colonized stream reaches become scarcer, beavers do recolonize old sites or settle in sub-optimal habitat such as streams in the steppe zone (Skewes *et al.* 2006; Claudio Moraga, WCS, *personal comm.*). Recolonized ponds will remain dystrophic (chronic effects) and thus their trophic value will be permanently lower than in the initial years.

The precise time that it has taken beavers to reach carrying capacity in TdF and start colonizing sub-optimal habitat and recolonize old sites is unknown, but it is likely that we are still in a period in which a number of old ponds co-exist in the landscape with others that are relatively new. Thus, the results of this study probably do not correspond entirely either to acute nor chronic effects, but to a transitional state. Studies that take into account pond age and their differential effects are encouraged, but until those are available I predict, based on the available literature, that values in aquatic bird richness and density in ponds will be higher in the initial years, to gradually decrease and reach values similar to natural lagoons, to finally decrease even further when ponds reach a dystrophic state.

Management plans need to deal with effects according to their time-frames. Acute effects of species are of importance for short-term management actions. For definitive,

long-term initiatives such as eradication, chronic effects are more appropriate to use in cost-benefit analysis. Beaver eradication in TdF will imply the elimination of ponds in a chronic dystrophic state with little trophic value for aquatic birds, and will also allow the gradual reestablishment of streams, which are used by a several bird species. Thus, the present study does not find any evidence suggesting that beaver eradication could result in the elimination of the habitat of birds associated to waterbodies in TdF.

## Conclusion

This study provides evidence that beaver introduction into the Tierra del Fuego Archipelago has had significant effects on the birds that have a close trophic association with limnic habitats. In general terms, the results support the observations of other studies in the area that indicate that the impacts of beaver in TdF are similar to those on its range of origin, although unexpected responses in certain avian foraging groups were also found, which could be related to the temporal context of the effects of this rodent. Bottom-up trophic effects of beaver establishment in streams resulting in increased abundance of food resources for aquatic birds are expected to be relatively short-lasting. In the context of a project of beaver eradication in TdF, the elimination of ponds in a chronic dystrophic state is unlikely to reduce habitat availability for aquatic birds, on the contrary, eradication could render increased aquatic bird habitat availability by allowing the reestablishment of streams.



## References

- Anderson CB (2004). Clave para la identificación de macroinvertebrados dulceacuícolas en la región del Cabo de Hornos. Pp. 95-98 in: R Rozzi and CB Anderson (eds) Explorando la micro-biodiversidad del Cabo de Hornos: guías y actividades. Prensa Austral, Punta Arenas.
- Anderson CB & AD 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 CB, Griffith CR, Rosemond AD, Rozzi R & O Dollenz (2006). 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 CB, Pastur GM, Lencinas MV, Wallem PK, Moorman MC & AD 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.
- Arismendi I (2009). The success of non-native salmon and trout in Southern Chile: human, environmental and invader dimensions in a conceptual model of biological invasion processes. Doctoral Dissertation. Universidad Austral de Chile, Valdivia.
- Bulluck JF & MP Rowe (2006). The use of southern Appalachian wetlands by breeding birds, with a focus on neotropical migratory species. *Wilson Journal of Ornithology* 118:399-410.
- Collen P & RJ Gibson (2000). 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.
- Collier KJ (2007). Temporal patterns in the stability, persistence and condition of stream macroinvertebrate communities: relationships with catchment land-use and regional climate. *Freshwater Biology* 53: 603-616.

- Couve E & C Vidal (2003). Aves de Patagonia, Tierra del Fuego y Península Antártica. Fantástico Sur Birding, Punta Arenas.
- Crooks JA (2002). Characterizing ecosystem-level consequences of biological invasion: the role of ecosystem engineers. *Oikos* 97:153-166.
- Del Hoyo J, Elliot A & J Sargatal (1992). Handbook of the birds of the world. V.1. Ostrich to Ducks, First edn. Lynx Editions, Barcelona.
- Devito KJ & PJ Dillon (1993) Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. *Canadian Journal of Fisheries and Aquatic Science* 50: 2222–2234.
- Edwards NT & DL Otis (1999). Avian communities and habitat relationships in South Carolina piedmont beaver ponds. *American Midland Naturalist* 141:158-171.
- Elton C (1927). *Animal Ecology*. McMillan, New York.
- Fernández HR & E Domínguez (2001). Guía para la determinación de los artrópodos bentónicos sudamericanos. Universidad Nacional de Tucumán, Tucumán.
- Fjeldså J & N Krabbe (1990) *Birds of the high Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America*. Apollo Books, Svendborg.
- Found C, Webb SM & MS Boyce (2008). Selection of lake habitats by waterbirds in the boreal transition zone of northeastern Alberta. *Canadian Journal of Zoology* 86:277-285.
- Francis MM, Naiman RJ & JM Melillo (1985). Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). *Hydrobiologia* 121:193-202.
- Fretwell SD (1987) Food chain dynamics: the central theory of ecology?. *Oikos* 50: 291-301.
- Fry CH & K Fry (1992) *Kingfishers, bee-eaters and rollers: a handbook*. Princeton University Press, New Jersey.
- Gregory RD, Gibbons DW, PF Donald (2004). Bird census and survey techniques. Pp. 17-52 in: WJ Sutherland, I Newton and RE Green (eds) *Bird Ecology and Conservation. A handbook of techniques*. Oxford University Press, Oxford.
- Grover AM & GA Baldassarre (1995). Bird species richness within beaver ponds in south central New York. *Wetlands* 15:108-128.
- Hairston NG, Smith FE & LB Slobodkin (1960) Community structure, population control and competition. *The American Naturalist* 94: 421-425.
- Hammer Ø, Harper DAT & PD Ryan (2001). PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 1-9.



- Hanson WD & RS Campbell (1963). The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a North Missouri stream. *American Midland Naturalist* 69: 136-149.
- Herenden RA (1995). A unified quantitative approach to trophic cascade and bottom-up:top-down hypotheses. *Journal of Theoretical Biology* 176: 13-26.
- Iturraspe R & A Urciolo (2000). Clasificación y caracterización de las cuencas hídricas de Tierra del Fuego. CADIC, Ushuaia.
- Johnson AW & JD Goodall (1965). The birds of Chile and adjacent regions from Argentina, Bolivia and Peru. vols I & II. Platt Establecimientos Gráficos, Buenos Aires.
- Krylov AV, Chalova IV & OL Tsel'movich (2007). Cladocerans under conditions of small river damming by man and beavers. *Russian Journal of Ecology* 38: 34-38.
- Lampert W & U Sommer (1997). *Limnoecology. The ecology of lakes and streams*. Oxford University Press, New York. .
- Lizarralde M (1993). Current status of the introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. *AMBIO* 22:351-358.
- Longcore JR, McAuley DG, Pendelton GW, Bennatti CR, Mingo TM & KL Stromborg (2006). Macroinvertebrate abundance, water chemistry, and wetland characteristics affect use of wetlands by avian species in Maine. *Hydrobiologia* 567:143-167.
- Mahoney M & R Magel (1996). Estimation of the power of the Kruskal-Wallis test. *Biometrical Journal* 38: 613-630.
- Margolis BE, Raesly RL & DL Shumway (2001). The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands* 21:554-563.
- Martínez Pastur G, Lencinas V, Escobar J, Quiroga P, Malmierca L & M Lizarralde (2006). Understory succession in areas of *Nothofagus* forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. *Journal of Applied Vegetation Science* 9:143-154.
- McCall TC, Hodgman TP, Diefenbach DR & RB Owen (1996). Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. *Wetlands* 16:163-177.
- McDowell DM & RJ Naiman (1986). Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* 68:481-489.
- McKinstry MC, Caffrey P & SH Anderson (2001). The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association* 37:1571-1577.

- Merendino MT, McCullough GB & NR North (1995). Wetland availability and use by breeding waterfowl in southern Ontario. *Journal of Wildlife Management* 59:527-532.
- Moore DM (1983). *Flora of Tierra del Fuego*. Anthony Nelson & Missouri Botanical Garden, St. Louis.
- Müller-Schwarze D & L Sun (2003). *The beaver: natural history of a wetlands engineer*. Cornell University Press, New York.
- Naiman RJ & JM Melillo (1984). Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia* 62:150-155.
- Naiman RJ, Melillo JM JE Hobbie (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254-1269.
- Nummi P & A Hahtola (2008). The beaver as an ecosystem engineer facilitates teal breeding. *Cerography* 31:519-524.
- Parkes JP, Paulson J, Dolan CJ & K Campbell (2009). Informe final estudio de factibilidad de erradicar al castor americano (*Castor canadensis*) en la Patagonia. Fundación InnovaT, Santiago.
- Peterson SR & JB Low (1977). Waterfowl use of Uinta Mountain wetlands in Utah. *Journal of Wildlife Management* 41:112-117.
- Preston FW (1979). The invisible birds. *Ecology* 60: 451-454.
- Ray AM, Rebertus AJ & HL Ray (2001). Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany* 79:487-499.
- Rempel RS, Abraham KF, Gadawski TR, Gabor S & RK Ross (1997). A simple wetland habitat classification for boreal forest waterfowl. *Journal of Wildlife Management* 61:746-757.
- Renouf RN (1972). Waterfowl utilization of beaver ponds in New Brunswick. *Journal of Wildlife Management* 36: 740-744.
- Rosell F, Bozsér O, Collen P & H Parker (2005). Ecological impact of beavers castor fiber and castor canadensis and their ability to modify ecosystems. *Mammal Review* 35:248-276.
- Scarsbrook M (2002). Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology* 47: 417-431.
- Silva CA & Saavedra B (2008). Knowing for controlling: ecological effects of vertebrate invaders in Tierra del Fuego. *Revista Chilena de Historia Natural* 81:123-136.
- Skewes O, González F, Olave R, Ávila A, Vargas V, Paulsen P & HE 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.



- Smith RIL (1985). Nutrient cycling in relation to biological productivity in Antarctic and Sub-Antarctic terrestrial and freshwater ecosystems. Pp- 138-153 in: WR Siegfried, PR Candy and RM Laws (eds) Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.
- Strayer DL, Eviner VT, Jeschke JM & ML Pace (2006). Understanding the long-term effects of species invasions. *TRENDS in Ecology and Evolution* 21: 645-651.
- Todd FS (1996) Natural history of the waterfowl. Ibis Publishing Co., California.
- Venegas C (1994). Aves de Magallanes. Universidad de Magallanes, Punta Arenas
- Victoriano PF, González AL & R Schlatter (2006). Estado de conocimiento de las aves de aguas continentales de Chile. *Gayana* 70:140-162.
- Vila I, Fuentes LS & M Saavedra (1999). Ictiofauna en los sistemas límnicos de la Isla Grande, Tierra del Fuego, Chile. *Revista Chilena de Historia Natural* 72:273-184.
- Vilina YA, Cofré H & C Pizarro (2006). Reporte final aves acuáticas en Chile. *Waterbird Conservation for the Americas*.

Table 3. Spatial correlation test for species density values in Vicuña area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	11	4.4	8	-0.46	-1.28	0.08
	Streams	11	6.2	6	-0.06	0.12	0.12
	All sites	31	2.8	26	-0.13	-0.48	0.03
Shoreline Carnivores	Ponds	11	4.4	8	-0.22	-0.40	0.08
	Streams	11	5.8	6	0.35	1.32	0.12
	All sites	31	2.8	26	0.14	1.02	0.04

\*Lag value was set at 3rd quartile distance values.

Table 4. Spatial correlation test for species density values in Lago Escondido area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	8	2.5	5	-0.30	-0.56	0.08
	Streams	8	2.2	6	-0.55	-1.23	0.11
	All sites	21	1.6	3	-0.20	-0.67	0.04
Shoreline Carnivores	Ponds	8	2.5	5	0.08	0.63	0.12
	Streams	8	2.2	6	0.18	1.40	0.05
	All sites	21	1.6	3	0.51	1.93	0.09

\*Lag value was set at 3rd quartile distance values.

## References

Sawada M (1999). ROOKCASE: An Excel 97/2000 Visual Basic (VB) Add-in for exploring global and local spatial autocorrelation. Bulletin of the Ecological Society of America 80:231-234.

## Appendix 1. Spatial autocorrelation analysis

Values for omnivore and shoreline carnivores species richness and abundance\* from all sampled sites (by habitat type and altogether) in Vicuña area and Lago Escondido area were tested to check whether values were influenced by the distance from a site to other sites, thereby differing from a random distribution. The Microsoft Excel Add-in RookCase© (Sawada 1999) was used to perform spatial correlation analysis by calculating Moran's I. Results indicate no spatial autocorrelation in the values (Null hypothesis = values are randomly spatially distributed).

Table 1. Spatial correlation test for species richness values in Vicuña area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	11	4.4	8	-0.48	-1.28	0.09
	Streams	11	6.2	6	-0.01	0.25	0.12
	Lagoons	9	5.2	9	0.26	1.73	0.05
	All sites	31	2.8	26	-0.07	-0.23	0.03
Shoreline Carnivores	Ponds	11	4.4	8	-0.14	-0.17	0.07
	Streams	11	5.8	6	-0.03	0.21	0.12
	Lagoons	9	5.2	9	0.07	1.03	0.04
	All sites	31	2.8	26	0.01	0.29	0.02

\*Lag value was set at 3rd quartile distance values.

Table 2. Spatial correlation test for species richness values in Lago Escondido area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	8	2.5	5	-0.54	-1.02	0.15
	Streams	8	2.2	6	-0.52	-1.23	0.09
	Lagoons	5	2.2	2	-0.38	-0.50	0.06
	All sites	21	1.6	3	-0.07	-0.04	0.28
Shoreline Carnivores	Ponds	8	2.5	5	0.22	1.14	0.10
	Streams	8	2.2	6	0.07	0.78	0.07
	Lagoons	5	2.2	2	0.56	1.21	0.44
	All sites	21	1.6	3	0.23	0.52	0.28

\*Lag value was set at 3rd quartile distance values.



Table 3. Spatial correlation test for species density values in Vicuña area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	11	4.4	8	-0.46	-1.28	0.08
	Streams	11	6.2	6	-0.06	0.12	0.12
	All sites	31	2.8	26	-0.13	-0.48	0.03
Shoreline Carnivores	Ponds	11	4.4	8	-0.22	-0.40	0.08
	Streams	11	5.8	6	0.35	1.32	0.12
	All sites	31	2.8	26	0.14	1.02	0.04

\*Lag value was set at 3rd quartile distance values.

Table 4. Spatial correlation test for species density values in Lago Escondido area.  $Z > |1.96|$  is considered significant at  $p \leq 0.05$ .

		n	Mean distance	# neighbors*	Moran's I	Z	Variance
Omnivores	Ponds	8	2.5	5	-0.30	-0.56	0.08
	Streams	8	2.2	6	-0.55	-1.23	0.11
	All sites	21	1.6	3	-0.20	-0.67	0.04
Shoreline Carnivores	Ponds	8	2.5	5	0.08	0.63	0.12
	Streams	8	2.2	6	0.18	1.40	0.05
	All sites	21	1.6	3	0.51	1.93	0.09

\*Lag value was set at 3rd quartile distance values.

## References

Sawada M (1999). ROOKCASE: An Excel 97/2000 Visual Basic (VB) Add-in for exploring global and local spatial autocorrelation. Bulletin of the Ecological Society of America 80:231-234.