PONTIFICIA UNIVERSIDAD CATÓLICA DE CHILE
Facultad de Ciencias Biológicas
Programa de Doctorado en Ciencias Biológicas
Mención Ecología

TESIS DOCTORAL

DISTRIBUCIÓN POTENCIAL Y POSIBLES RUTAS DE MIGRACIÓN DEL CASTOR NORTEAMERICANO (*CASTOR CANADENSIS*) EN SU RANGO INVASIVO UTILIZANDO EL CONCEPTO DE NICHO HUTCHINSONIANO.

Por

DEREK ANDREW CORCORAN BARRIOS

Septiembre, 2014

PONTIFICIA UNIVERSIDAD CATÓLICA DE CHILE
Facultad de Ciencias Biológicas
Programa de Doctorado en Ciencias Biológicas
Mención Ecología

DISTRIBUCIÓN POTENCIAL Y POSIBLES RUTAS DE MIGRACIÓN DEL CASTOR NORTEAMERICANO (*CASTOR CANADENSIS*) EN SU RANGO INVASIVO UTILIZANDO EL CONCEPTO DE NICHO HUTCHINSONIANO.

Tesis presentada a la Pontificia Universidad Católica de Chile como parte de los requisitos para optar al grado académico de Doctor en Ciencias Biológicas mención Ecología

Por

DEREK ANDREW CORCORAN BARRIOS

Director de Tesis: Dr. Fabián Jaksic

Comisión de Tesis: Dr. Pablo A. Marquet.
Dr. Francisco Bozinovic K.
Dr. Fabio Labra.
Dr. Mauricio Lima

Septiembre, 2014

PONTIFICIA UNIVERSIDAD CATÓLICA DE CHILE
Facultad de Ciencias Biológicas

LA DEFENSA FINAL DE LA TESIS DOCTORAL TITULADA

DISTRIBUCIÓN POTENCIAL Y POSIBLES RUTAS DE MIGRACIÓN DEL CASTOR NORTEAMERICANO (*CASTOR CANADENSIS*) EN SU RANGO INVASIVO UTILIZANDO EL CONCEPTO DE NICHO HUTCHINSONIANO.

Presentada por el Candidato a Doctor en Ciencias Biológicas Mención Ecología

DEREK ANDREW CORCORAN BARRIOS

Ha sido aprobada por el Tribunal Examinador, constituido por los profesores abajo firmantes, calificándose el trabajo realizado, el manuscrito sometido y la defensa oral con nota _________ (_______________________________).

Dr. Pablo A. Marquet
Jefe Mención Ecología
Facultad de Ciencias Biológicas

Dr. Juan A. Correa M.
Decano
Facultad de Ciencias Biológicas

Dr. Fabio Labra
Profesor invitado
Universidad Santo Tomás

Dr. Francisco Bozinovic.
Miembro comisión evaluadora
Facultad de Ciencias Biológicas

Dr. Fabián Jaksic A.
Director de Tesis
Facultad de Ciencias Biológicas

Dr. Mauricio Lima
Miembro comisión evaluadora
Facultad de Ciencias Biológicas

Septiembre de 2014

Índice de Contenidos

RESUMEN

Una de las preguntas más interesantes en ecología, es qué determina el rango de una especie. En este sentido, uno de los conceptos teóricos más útiles para estudiar tanto los límites como la estructura interna del rango de una especie es el Nicho Ecológico. Su concepto se ha visto redefinido en varias oportunidades, sin embargo un punto en común para estas definiciones es la búsqueda de cómo podemos predecir el hábitat de una especie.

Recientemente, surge una metodología capaz de predecir el rango de una especie: la modelación de distribución de especies basado en el concepto de nicho Grinelliano. Esta herramienta ha permitido mejorar la forma en que entendemos la distribución de las especies al generar distribuciones potenciales frente a distintos escenarios. Un siguiente paso en el estudio de la estructura interna de la distribución de una especie es la utilización de su adecuación biológica, a través de la generación de modelos a partir de nicho Hutchinsonianos espacialmente explícitos (biótopos).

El objetivo general de esta tesis es el modelar el nicho Hutchinsoniano del castor en la isla de Tierra del fuego, caracterizar la estructura de su rango, proyectarlo al continente y utilizar esta información para modelar el rango y rutas de dispersión de la especie para Sudamérica.

Se tomaron tres medidas de desempeño del castor norteamericano en tres ambientes de Tierra del fuego para probar entre tres hipótesis de mecanismos de invasión. Se evaluaron distintos algoritmos de modelación de nicho a través de presencias para predecir la adecuación biológica del castor desde el índice de idoneidad de hábitat. Se caracterizó la distribución de frecuencia del desempeño del castor en Tierra del Fuego a través de los datos tomados en terreno y de los modelos proyectados por la modelación del nicho Hutchinsoniano y se buscó el mejor ajuste

para compararlo con patrones descritos para la abundancia. Por último, se proyectó el modelo de nicho del castor a toda Sudamérica para determinar en qué lugares del sur del continente el castor podría generar colonias fuente y cuál sería la ruta de menor costo desde el lugar de llegada del castor al continente hacia el norte de Sudamérica.

Lo resultados indican que ninguna de las tres medidas de desempeño del castor tiene diferencias entre los ambientes identificados, lo cual sugiere como mecanismo de invasión la hipótesis de escape a enemigos naturales. Dado que el peso del castor norteamericano es mayor en el hábitat invasivo de Tierra del Fuego que en su hábitat nativo, probablemente la mejor hipótesis correspondería al escape a enemigos naturales compensatorios. Ninguno de los algoritmos de presencia logró predecir el desempeño del castor, sin embargo el Modelo Lineal Generalizado generado a partir del desempeño medido en terreno fue exitoso para predecir la fertilidad femenina del castor, es decir se logró modelar el nicho Hutchinsoniano espacialmente explícito o biotopo para la especie en Tierra del Fuego.

Las dos medidas de desempeño medidas en terreno y proyectadas por el modelo para el castor en el área de estudio mostraron distribuciones de frecuencia simétricas unimodales. En cuanto a la distribución potencial del castor en Sudamérica, se presenta como límite distribucional los 43° S. La migración ocurriría principalmente por territorio chileno hasta los campos de hielo sur, para después migrar por argentina hasta dicha latitud.

ABSTRACT

One of the most interesting questions in ecology is what determines the range of a species. In this sense, one of the most useful theoretical concepts for studying both the limits and the internal structure of the range of a species is the Ecological Niche. This concept has been redefined several times, however a shared goal to these definitions is finding how we can predict the habitat of a species.

A methodology capable of predicting the range of a species has recently emerged: The species distribution modeling based on the concept of the Grinellian niche. This tool has improved the way we understand the distribution of species by generting potential distributions in different scenarios. A next step in the study of the internal structure of the distribution of species is the use of fitness, through the generation of models based on spatially explicit Hutchinsonian niches (biotopes).

The main objective of this thesis is to model the Hutchinsonian niche of the beaver on the island of Tierra del Fuego, characterize the structure of its range, and project this model to the continent, in order to use this information to predict the range and dispersal routes of the specie in South America.

Three measurements of performance of the North American beaver were taken in three environments of Tierra del Fuego to test three hypotheses of invasion mechanisms. Different niche modeling algorithms were evaluated to predict fitness using presences to generate an habitat suitability index. The frequency distribution of the performance of the beaver in

Tierra del Fuego measured in the field and the projected Hutchinsonian niche models. The best fit was sought for comparison with patterns described for abundance. Finally, the niche model was projected to all of South America to determine which areas of the continent could generate source colonies of beavers and which would be the leas cost route from the point of arrival of the Beaver to the mainland to northern South America.

There are no significant differences in none of the three performance measurements for the beavers between environments, suggesting a mechanism of enemy release hypothesis. Since the weight of the North American beaver is higher in the invasive habitat of Tierra del Fuego than in their native habitat, probably the best hypothesis would correspond to a compensatory enemy release. None of the algorithms predicted the performance beavers, nevertheless the Generalized liner model generated from the performance measured in the field was successful at predicting female fitness, that is to say, it was possible to model the spatially explicit Hutchinsonian niche or biotope for the species in Tierra del Fuego.

The two measurements of fitness measured in the field and projected by the model for the beaver in the study area showed unimodal and symmetrical distributions. As for the potential distribution in South America, the model predicts a distributional limit of 43 ° S. The migration would occur primarily through the Chilean territory up to the southern ice fields, and then migrate to Argentina until reaching that latitude.

AGRADECIMIENTOS

Agradezco a la Beca para Estudios de Doctorado en Chile, año académico 2008 de CONICYT, al Centro de Estudios Avanzados de Ecología y Biodiversidad (CASEB), al Centro de Ecología Aplicada y Sustentabilidad (CAPES) por el apoyo económico al desarrollo de esta tesis, el financiamiento de los terrenos y mi mantención durante cuatro años.

También agradezco por su colaboración al Servicio Agrícola y Ganadero (SAG), TERAIKE, la Asociación de Ganaderos de Magallanes (ASOGAMA) y a Wildlife Conservation Society.

Por todo el apoyo al Departamento de Ecología de la Universidad Católica, en particular a mi tutor Fabian Jaksic, quien tuvo una paciencia eterna.

Agradezco a toda mi familia, a mi hermana, mi madre por su apoyo incondicional, y a mi padre, con quien me reencontré en Tierra del Fuego. A mi tío Chritian que me abrió muchas puertas y me apoyo siempre que pudo.

Finalmente agradezco a Giorgia, mi compañera de vida y de aventuras en esta tesis, la que nos llevó por los lugares más recónditos de Tierra del Fuego, Magallanes, y nuestras almas. Este ha sido un viaje que nos ha transformado a ambos y el recorrido fue más importante que el resultado. Se vienen más viajes y aventuras.

I. INTRODUCCIÓN GENERAL

1.1 El concepto de nicho y la distribución de especies

El nicho desde su proposición, ha sido uno de los conceptos centrales en ecología (Grinnell 1917, 1924; MacArthur 1968). Sin embargo, su definición ha sido reevaluada en varias oportunidades y podemos identificar al menos tres definiciones fundamentales, la propuesta por Grinnell en 1917 y 1924, Elton en 1927 y Hutchinson en 1918 y 1958.

El nicho grinnelliano se define como la relación que existe entre una especie y su ambiente, y resume las condiciones en las cuales una especie puede subsistir (Jackson & Overpeck 2000; Soberón 2007). Se describe como una propiedad del ambiente, en el cual el nicho puede estar ocupado o vacío (Grinnell 1917; Soberón 2007; Peterson *et al.* 2011) y por tanto presenta énfasis en variables estáticas y factores abióticos (Araujo & Guisan 2006; Soberón 2007; Hirzel & Le Lay 2008; Soberón & Nakamura 2009).

El nicho eltoniano está basado en relaciones recurso-consumidor (Elton 1927; Soberón 2007; Peterson *et al.* 2011) y fue originalmente pensado por Elton como el lugar que ocupaba un organismo dentro de las redes tróficas de un ecosistema. Esto posteriormente fue retomado y formalizando matemáticamente (Leibold 1995; Chase & Leibold 2003; Godsoe & Harmon

2012), utilizando isóclinas de crecimiento cero en planos de abundancia de recursos y con vectores que representan el efecto de especies coexistentes, pudiendo de esta manera predecirse si pueden coexistir en un ambiente dado. Este concepto se utiliza a una escala bastante local y no es adecuado para estudiar patrones geográficos (Peterson *et al.* 2011).

Hutchinson define nicho como un hipervolumen que resume el conjunto de factores abióticos y bióticos que definen dónde una especie presenta una adecuación biológica mayor a cero, por lo que su población puede persistir sin inmigración. Una de las distinciones más útiles de la definición de Hutchinson es la diferenciación entre el nicho fundamental y el nicho realizado, donde el primero es el conjunto de condiciones abióticas necesarias para su subsistencia y reproducción, y el segundo incluye las interacciones bióticas. Conceptualmente, la definición de nicho de Hutchinson ha sido la más utilizada en estudios de teoría ecológica por ser una formalización matemática. Esta acepción, a través de la cual se han generado numerosas hipótesis, es la utilizada en trabajos asociados a diferenciación o segregación de nicho (Schoener 1974; Fuentes & Jaksić 1979; Ross 1986), amplitud del nicho (Colwell & Futuyma 1971; Macpherson 1981) y exclusión competitiva (Hardin 1960; Hutchinson 1961; MacArthur 1968; Levin 1970).

Una de las principales búsquedas de una definición acertada de nicho ha sido la constante pregunta de cómo podemos predecir el hábitat de una especie y entender qué hace posible la coexistencia de varias especies similares (Hutchinson 1918, 1961; Holt 2009). De esta interrogante nace la modelación de distribución de especies, que corresponde a la determinación de la distribución actual o potencial de una especie mediante la utilización de algoritmos de inteligencia artificial, al relacionar datos de presencia de especies con variables ambientales (Araujo & Guisan 2006; Soberón 2007; Peterson *et al.* 2011). Estos modelos se basan en el concepto grinnelliano de nicho (Soberón 2007; Peterson *et al.* 2011), los métodos empleados utilizan ejes múltiples y valores de presencia o presencia- ausencia para predecir la distribución de una especie, entregando como resultado un índice de idoneidad de hábitat. Algunos autores proponen que este índice se encuentra correlacionado positivamente con el desempeño de la especie modelada (Nogués-Bravo 2009; VanDerWal *et al.* 2009; Peterson *et al.* 2011), sin embargo los pocos estudios que han intentado encontrar esta relación han encontrado muy bajo apoyo para esto (VanDerWal *et al.* 2009; Tôrres *et al.* 2012).

Si bien los modelos de distribución de especies se basan en nicho grinnelliano, existe una perspectiva hipervolumetrica similar al concepto de nicho de Hutchinson. A pesar de esto, el no considerar la adecuación biológica hace que no se trate de un trabajo basado en nicho hutchinsoniano. Dado que existe el supuesto de que el índice de idoneidad de hábitat representaría la adecuación biológica de una especie, de esta forma se tendría la ventaja de trabajar con esta última definición de nicho que presenta una dualidad que no presentan la demás definiciones. Por un lado se mostraría como una propiedad de la especie y por otro representaría un espacio físico en donde vive la especie o biotopo.

Es por esto que el objetivo central de esta tesis es evaluar la relación entre adecuación biológica y el índice de idoneidad de hábitat que entregan los modelos de distribución de especies y estudiar la estructura interna del rango de una especie.

El sujeto de estudio de esta investigación es el castor norteamericano (*Castor canadensis*) en su rango exótico en Sudamérica. Esta especie presenta características adecuadas para este estudio, en donde su rango invasivo presenta ventajas por sobre su rango nativo. Dentro de las ventajas de esta especie, se posee vasto conocimiento sobre su ecología e historia de vida (Aleksiuk 1968; Payne 1979, 1984a; b; Baker & Hill 2003; Muller-Schwarze & Sun 2003; Wallem *et al.* 2007; Fasanella 2012), es una especie conspicua, pudiéndose incluso detectar al volar sobre el terreno que ocupa (Payne 1981) y a través de imágenes satelitales, facilitando la determinación de su espacio habitado. Además, se ha estudiado bastante el proceso de invasión de esta especie en Sudamérica, contando con antecedentes ecológicos tempranos desde las primeras fases de su introducción en Tierra del Fuego (Wallem *et al.* 2007; Anderson *et al.* 2009; Fasanella 2012).

Por otro lado, existen varios factores que influencian la adecuación biológica de un individuo: el ambiente, su genotipo, la competencia intraespecífica y las interacciones interespecíficas entre otras. Para determinar el efecto del ambiente en la adecuación biológica de una especie es conveniente que el resto de los factores no sean variables entre los ambientes. En este sentido el castor norteamericano invasor en la isla de Tierra del Fuego presenta estas ventajas: 1) posee baja variabilidad genética (Fasanella 2012) debido al bajo número de castores introducidos provenientes del mismo lugar (Lamb 1969); 2) la competencia intraespecífica es preemtiva (competencia por explotación de espacio habitable), lo cual previene efectos de densodependencia una vez que un castor está asentado en un sitio (Bergerud & Miller 1977; Houlihan 1989; Welsh & Muller-Schwarze 1989); y 3) en cuanto a las interacciones interespecíficas, aparentemente los castores no presentan depredadores, patógenos importantes y competidores directos (Wallem *et al.* 2007; Anderson *et al.* 2009). A su vez, los castores pasan la mayor parte de su vida en el mismo sitio, ya que después de dispersar desde la castorera parental, en promedio entre 5-17 km dependiendo de la localidad (Beer 1955; Leege 1968; Sun, Müller-Schwarze & Schulte 2000), pasan el resto de su vida en una sola madriguera

(Muller-Schwarze & Sun 2003). Por lo tanto, la adecuación biológica observada en castores en Tierra del Fuego dependería casi exclusivamente del efecto ambiental del sitio en que fue muestreado.

La hipótesis general de esta tesis doctoral es que el índice de idoneidad de hábitat de las modelaciones de distribución basadas en puntos de presencias de los castores en región de Magallanes está correlacionado positivamente con la adecuación biológica medida en terreno. Para esto se evaluará si los modelos de distribución de especies basados en presencias logran predecir la adecuación biológica del castor norteamericano en la isla Tierra del Fuego y las consecuencias en la estructura de la distribución de esta especie basándose en el concepto de Nicho Hutchinsoniano.

Objetivos:

1. Comparar la adecuación biológica de los castores en tres ambientes de Tierra del Fuego e identificar a partir de esta el mecanismo de invasión más factible para esta especie en la isla.
2. Evaluar la relación entre el índice de idoneidad de hábitat y la adecuación biológica de los castores en la isla de Terra del Fuego.
3. Generar un modelo de distribución de especies basado en el nicho Hutchinsoniano y estudiar la estructura de su rango, al determinar la distribución de frecuencia y patrones espaciales de la adecuación biológica dentro del área muestreada.
4. Utilizar el modelo generado para extrapolar a toda Sudamérica y determinar el alcance de invasión del castor y las rutas posibles y el alcance de la invasión del castor en el continente.

1.2 Referencias

Aleksiuk, M. (1968) Scent-Mound Communication, Territoriality, and Population Regulation in Beaver (*Castor canadensis* Kuhl). *Journal of Mammalogy*, **49**, 759.

Anderson, C.B., Pastur, G., Lencinas, M.V., Wallem, P.K., Moorman, M.C. & Rosemond, A.D. (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.

Araujo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.

Baker, B.W. & Hill, E.P. (2003) Beaver (*Castor canadensis*). *Wild mammals of North America: biology, management, and conservation*, Second (eds G.A. Feldhamer, B. Thompson & J.A. Chapman), pp. 288–310. John Hopkins University Press, Baltimore.

Beer, J.R. (1955) Movements of tagged beaver. *J. Wildl. Manage*, **19**, 492–493.

Bergerud, A.T. & Miller, D.R. (1977) Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, **55**, 1480–1492.

Chase, J.M. & Leibold, M. (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*, Second. University Of Chicago Press, Chicago.

Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, 567–576.

Elton, C.S. (1927) *Animal Ecology*. University Of Chicago Press, Chicago.

Fasanella, M. (2012) *Variabilidad Genética Espacial Y Ecología Molecular En Dos Especies de Roedores Del Archipiélago de Tierra Del Fuego: Ctenomys Magellanicus, Especie Nativa Y Castor Canadensis, Especie Invasora*. Doctoral thesis. Universidad de Buenos Aires, Argentina.

Fuentes, E.R. & Jaksić, F.M. (1979) Latitudinal size variation of Chilean foxes: tests of alternative hypotheses. *Ecology*, 43–47.

Godsoe, W. & Harmon, L.J. (2012) How do species interactions affect species distribution models? *Ecography*, **35**, 811–820.

Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk,* 427–433.

Grinnell, J. (1924) Geography and evolution. *Ecology*, **5**, 225–229.

Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292–1297.

Hirzel, A.H. & Le Lay, G. (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372–1381.

Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, **106**, 19659–19665.

Houlihan, P.W. (1989) *Scent Mounding by Beaver (Castor Canadensis): Functional and Semiochemical Aspects*. State University of New York. College of Environmental Science and Forestry, Syracuse.

Hutchinson, A.H. (1918) Limiting factors in relation to specific ranges of tolerance of forest trees. *Botanical Gazette*, 465–493.

Hutchinson, A.H. (1958) Concluding remarks. Populations studies: Animal ecology and demography. Cold Spring Harbourd. *Symposia on Quantitative Biology* pp. 415–427.

Hutchinson, G.E. (1961) The paradox of the plankton. *American Naturalist*, 137–145.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

Lamb, T. (1969) Carta a Harold Wells describiendo la introducción y transporte de castores desde Prince Albert a Ushuaia.

Leege, T.A. (1968) Natural movements of beavers in southeastern Idaho. *The Journal of Wildlife Management*, 973–976.

Leibold, M.A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology*, **76**, 1371–1382.

Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, 413–423.

MacArthur, R.H. (1968) The theory of the niche. *Population biology and evolution*, **159**, 176.

Macpherson, E. (1981) Resource partitioning in a Mediterranean fish community. *Marine Ecology Progress Series*, **4**, 183–193.

Muller-Schwarze, D. & Sun, L. (2003) *The Beaver: Natural History of a Wetlands Engineer*, 1 edition. Comstock Publishing Associates, Ithaca, N.Y.

Nogués-Bravo, D. (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, **18**, 521–531.

Payne, N.F. (1979) Relationship of pelt size, weight, and age for beaver. *The Journal of Wildlife Management*, 804–806.

Payne, N.F. (1981) Accuracy of aerial censusing for beaver colonies in Newfoundland. *The Journal of Wildlife Management*, 1014–1016.

Payne, N.F. (1984a) Mortality rates of beaver in Newfoundland. *The Journal of wildlife management*, 117–126.

Payne, N.F. (1984b) Reproductive rates of beaver in Newfoundland. *The Journal of wildlife management*, 912–917.

Peterson, A.T., Soberón, J., Pearson, R.G. & Anderson, R.P. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, N.J.

Ross, S.T. (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia*, 352–388.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters*, **10**, 1115–1123.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, **106**, 19644–19650.

Sun, L., Müller-Schwarze, D. & Schulte, B.A. (2000) Dispersal pattern and effective population size of the beaver. *Canadian Journal of Zoology*, **78**, 393–398.

Tôrres, N.M., De Marco, P., Santos, T., Silveira, L., de Almeida Jácomo, A.T. & Diniz-Filho, J.A. (2012) Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Diversity and Distributions*, **18**, 615–627.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009) Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance. *American Naturalist*, **174**, 282–291.

Wallem, P.K., Jones, C.G., Marquet, P.A. & Jaksic, F. (2007) Identificación de los mecanismos subyacentes a la invasión de C*astor canadensis* (Rodentia) en el archipiélago de Tierra del Fuego, Chile. *Revista chilena de historia natural*, **80**, 309–325.

Welsh, R.G. & Muller-Schwarze, D. (1989) Experimental habitat scenting inhibits colonization by beaver, *Castor canadensis*. *Journal of Chemical Ecology*, **15**, 887–893.

II. EL DESEMPEÑO DEL CASTOR, CASTOR CANADENSIS (RODENTIA), EN TRES AMBIENTES DIFERENTES DE TIERRA DEL FUEGO, CHILE: UNA PRUEBA DE HIPÓTESIS DE INVASIÓN.

THE PERFORMANCE OF BEAVERS, CASTOR CANADENSIS (RODENTIA), IN THREE DIFFERENT ENVIRONMENTS OF TIERRA DEL FUEGO, CHILE: A TEST OF INVASION HYPOTESES

Derek Corcoran[1], Giorgia Graells[2], Petra K. Wallem[3] & Fabián M. Jaksic[1]

1. Center of Applied Ecology & Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
2. Universidad de Magallanes. Instituto de la Patagonia, Punta Arenas, Chile
3. Flora y Fauna Chile, Ltda

Corresponding author e-mail: derek.corcoran.barrios@gmail.com

Short title: Performance of beavers in Tierra del Fuego

2.1 Abstract

Background: Twenty-five North American beaver pairs were introduced to Tierra del Fuego in 1946; today, there are more than 100,000 specimens on the island. Most studies in North America have found that beavers (*Castor canadensis*) are more successful in forests than in any other habitat in their native range. We measured their performance as uterine scars, body size, and fat reserves of 66 beavers, sampled at three different environments of Tierra del Fuego (forest, scrub, and steppe). Comparisons in performance were carried out with and without age as a covariate. We also compared the performance of invasive beaver with data from their native range in Canada, and contrasted our results with predictions made for three different invasion mechanisms (climatic match, resource limitation and enemy release hypothesis).

Results: Our results show that all three habitat types are suitable for the exotic beaver, not finding any evidence for differences in beaver performance among them. Furthermore, our data shows that invasive beavers have a better performance in terms of weight than their Canadian native counterparts.

Conclusions: Given the absence of predators for beavers in Tierra del Fuego, we argue that our results are consistent with the enemy-release hypothesis proposed as an underlying mechanism for successful invasions. Moreover, the fact that beavers in their introduced range out weighted beavers in their native range is consistent with predictions of the compensatory enemy release hypothesis.

Keywords: climatic match, enemy release hypothesis, fitness, resource limitation.

2.2 Introduction

Castor canadensis (Kuhl 1820) is a rodent native to most of North America and invasive in Europe, South America, and Asia (Lahti & Helminen 1974, Danilov & Kan'shiev 1982, Lizarralde 1993, Danilov 1995, Nummi 1996, Saveljev & Safonov 1999, Anderson et al. 2009). In South America beavers were introduced to the Argentinean side of Tierra del Fuego Island in 1946 by the Argentinean Navy, which released 25 pairs into the Claro River near Fagnano Lake (Lizarralde 1993, Jaksic 1998, Anderson et al. 2009). Since then, beavers have occupied the entire Fuegian Archipelago, including Tierra del Fuego, Navarino, Hoste, Dawson, Picton, Nueva, Lenox, and Gordon Islands, encompassing at least 56,858 km^2 (Skewes et al. 2006, Menvielle et al. 2010). Estimated population size achieved, approximately 65,000 to 100,000 individuals on the entire Island, and around 41,000 individuals only considering the Chilean side of the Island (Skewes et al. 1999, Choi 2008, Parkes et al. 2008). Due to the rapid expansion of this invasion, we consider this estimated population size as the lower expected value assuming it has increased in the past 14 years. In North America, beavers prefer and perform better in forests (Retzer et al. 1956, Howard & Larson 1985, Beier & Barret 1987, Dieter & McCabe 1989, McComb et al. 1990, Robel et al. 1993, Busher 1996, Curtis & Jensen 2004), even though they can inhabit a vast array of environments (Hill 1982, Novak 1987, Robel et al. 1993, Baker & Hill 2003, Müller-Schwarze & Sun 2003). In South America, most of the studies focusing on beaver ecology have been conducted in forest environments (Lizarralde 1993, Lizarralde et al. 2004, Martinez Pastur et al. 2006, Lizarralde et al. 2008, Anderson et al. 2009, Wallem et al. 2009). Lenga forests dominated by *Nothofagus pumilio* are recognized as the "best" environment for beavers, supported by the fact that their densities area higher in these forested areas of Tierra del Fuego (Lizarralde 1993, Skewes et al.1999, Briones et al. 2001). It has been suggested that this pattern could be explained by a diffusion invasion model (Wallem et al. 2007); however, none of the aforementioned studies estimated beaver performance simultaneously at the three different habitat types present at the Tierra del Fuego Island. In this study, we compare the performance of invading *C. canadensis*, estimated through uterine scars, body size, and fat reserves, in three contrasting environments of Tierra del Fuego (forest, scrub, and steppe) using age as a covariate.

2.3 Methods

Study area

This study was conducted on the Chilean side of Tierra del Fuego Island, located at the southernmost tip of South America between parallels 52 and 55 ºS. Tierra del Fuego Island extends approximately 48,598 km^2, of which 22,592.7 km^2 corresponds to the Chilean province of Tierra del Fuego. Forested areas comprise around 18.3 % of the province's area (4,056.3 km^2) (Dollenz 1995, CONAF et al. 1999). The island presents a strong pluviometric gradient going from 200 mm rainfall in the northeast side up to 2,000 mm in the southwest, as well as a the influence of strong west winds which reach over 100 km h-1 (Enlicher & Santana 1988, Santana et al. 2006). These climatic influences result in three contrasting environments: a) forest, b) scrub and c) steppe (Pisano 1977, Dollenz 1995).

(a) Forest: Most of the fuegian forest is dominated by lenga (*Nothofagus pumilio*). Precipitation ranges from 400 to 620 mm yr-1, placing the forest into a Dfc climate type following Köppen's classification. In the southwestern coast, the forest changes to an evergreen forest dominated by coigüe trees (*Nothofagus betuloides*), and to a lesser extent by canelo trees (*Drimys winterii*). Precipitation ranges from 800 to 2,000 mm yr-1, matching a Cfc climate type (Gerding & Thiers 2002).

(b) Scrub: It corresponds to the transition between the steppe and the forest, in the center of the island. This environment is characterized by a Bsk climate type, with precipitation ranging from 200 to 400 mm, the dominant shrub species being mata negra (*Chilliotrichum diffusum)* followed by calafate (*Berberis microphylla).*

(c) Steppe: The northern part of the island has a Bsk climate type with precipitation ranging from 200 to 300 mm yr-1. Vegetation is dominated by graminoids, such as *Festuca gracillima*.

Hypotheses to be tested

Among the several hypotheses proposed to explain the success of invasive species (Catford et al. 2008), only four have been considered to be applicable to the beaver phenomenon in Tierra del Fuego: climatic match; resource opportunity; enemy release; and plasticity to novel conditions (Wallem et al. 2007). In this paper our goal is to test the first three hypotheses, comparing beaver performance in the three habitat types described above.

Climatic match hypothesis

Climatic match predicts that a species' distribution is at least partially determined by climatic conditions (Woodward 1987, Baker et al. 2000, Duncan et al. 2001, Kriticos & Randall 2001, Forsyth et al. 2004, Bomford 2009). Beavers are generalists, with a broad distribution across North America encompassing several different climates (Baker & Hill 2003). However, litter sizes vary between different geographic areas of that continent (Benson 1936, Grinell et al. 1937, Hammond 1943, Hodgdon 1949, Osborn 1953, Bond 1956, Provost 1958, Wilkinson 1962, Brenner 1964, Novakowski 1965, Leege & Williams 1967, Henry & Bookhout 1969, Gunson 1970, Woodward 1977, Wigley 1983, Payne 1984), with a mean of 3.4 uterine scars per female and a range of 2.2 to 5.5 scars. Not all of these studies were conducted in the same manner, and not all of them clearly specified the exact location of the study site. Thus, comparison among them is rather difficult, though they provide a baseline data set to compare with our data. The highest mean (± SD) for uterine scar counts (4.14 ± 1.23) is in Köppen's Dfa category of climate, a type not found in Tierra del Fuego (Table 1). Among the climates actually found on the Island, Bsk has the highest mean (± SD) for uterine scar counts (3.50 ± 0.66) (Hammond 1943, Osborn 1953, Leege & Williams 1967, Gunson 1970), and corresponds to the climate present in the scrubland and steppe. Furthermore, niche models considering data on beaver native distribution range, also predict a better fit for scrub and steppe among beavers in Tierra del Fuego (D Corcoran, unpublished data). Following this reasoning, if climatic match explains beaver success in Tierra del Fuego, they should perform better, as measured through uterine scars, in steppe and scrub than in forest.

Resource opportunity hypothesis

Beavers are generalist herbivores (Aleksuik 1970a, Svendsen 1980, Jenkins 1980, Olson & Hubert 1994, Wallem 2009), but plant quality and availability limits their presence, as well as their performance (McNaughton et al. 1989, Oesterheld et al. 1998). Their body length and weight are good measures to appraise environment quality, in terms of food availability (Stephenson 1956, Pearson 1960). In the beaver's native environment plant productivity varies between 200 and 1400 g m2 yr-1 (Reichle et al. 1975), values higher than those measured in Patagonia. In Tierra del Fuego, steppe and scrub environments have a productivity of 56 to 149 g m2 yr-1 (Fernández-A et al. 1991, Defossé & Bertiller 1991, Jobbagy & Sala 2000). The productivity of lenga forests has been estimated at 90 to 790 g m2 yr-1 (Barrera et al. 2000, Frangi et al. 2005). Moreover, there is evidence indicating a positive correlation between productivity measured as Normalized Difference Vegetation Index (NDVI) and secondary productivity in Tierra del Fuego (Oesterheld et al. 1998, Posse & Cignolani 2000). Thus, if food availability is the primary limiting factor for beavers, they should perform better in lenga forests.

Enemy release hypothesis

Enemy release occurs when an invasive species is not controlled by predators, parasites and/or pathogens in the new habitat (Torchin et al. 2001, Keane & Crawley 2002, Torchin et al. 2002, Mitchell & Power 2003, Torchin et al. 2003, Colautti et al. 2004, Catford et al. 2008, Shwartz et al. 2009). In the case of beavers, several reports demonstrate that predators are an important factor determining habitat selection in North America (Aleksiuk 1970a, Dieter & McCabe 1989, Zurowski 1992, Macdonald et al. 1995, Fustec et al. 2003). In Tierra del Fuego, there are four potential predators for beavers: mink (*Neovison vison*), dogs (*Canis familiaris*), Culpeo fox (*Lycalopex culpaeus*), and humans (*Homo sapiens*). Swank (1949) described the mink as a predator of beaver cubs in North America. However, studies of mink diet in the Fuegian archipelago have found beaver traces in less than 2 % of the feces analyzed (Ibarra et al. 2009). Only qualitative evidence of dog and culpeo fox attacks on fuegian beavers exists (Andrade 2005). These two carnivores are more abundant in the south; thus, beaver performance should be better in the northern part of the Island. Finally, some human pressure exists on the three environments of Tierra del Fuego, where people go after beavers since a governmental program taught them how to hunt them. Thus, predator pressure is expected to be low and similar among the three environments of the Island.

If beavers are relatively free of natural enemies and that is the primary reason for their being so successful in Tierra del Fuego, they should perform similarly in all three environments of Tierra del Fuego. Furthermore, two different responses are predicted by the enemy release hypothesis: regulatory and compensatory enemy release. In the first case, no increase in growth and reproductive outcome is expected as compared to the species' native habitat. In the second case, an improvement in growth and or reproductive outcome is expected due to increased energy allocation performance, as compared to their native habitat (Catford et al. 2008).

Measurements

Flied work was carried out on Tierra del Fuego Island, from February 24th of 2010 until March 3rd of 2011. Four different sampling periods were considered, comprising a total of 159 trapping days, distributed equally between the three different environments described above. Beaver were hunted using Connibear traps, snares, and rifles. Beaver performance was estimated taking the following measurements:

1. Female reproductive performance: Number of offspring bred during the last season was determined by counting uterine scars (Hodgdon 1949) and, depending on the season, fetuses.
2. Fat storage: Weight and volume of the tail was measured to estimate the amount of fat stored in that appendage (Smith & Jenkins 1997, Aleksiuk 1970b).

3. Body size: Beaver were weighed and their total length measured, because a positive relationship between total weight and litter size has been reported (Rutherford 1955). Additionally, both measurements are a proxy for the quality and variety of food availability for beaver in North America (Pearson 1960, Stephenson 1956).
4. Previous studies have reported that age has an important effect on size, weight, and female reproductive performance in North American beaver (Payne 1984, Müller-Schwarze & Sun 2003). Thus, age was determined by assessing tooth development (Van Nostrand & Stephenson 1964, Larson & Van Nostrand 1968) and considered as a covariant for the preceding beaver performance estimates (Aleksiuk 1970b, Payne 1979, Payne 1984)

Statistical analysis

To determine if age differed among the tree environments a Kruskal-Wallis test was performed, because data distribution was not normal. Once assured that there was no significant difference of age distribution among environments, an ANOVA or Kruskal-Wallis (depending on presence or absence of a normal distribution of data) analysis was performed to test for differences in weight (all beavers), tail volume (all beavers) and uterine scars (females only) between environments.

To compare performance measures of tail volume and weight among the three environments, an ANCOVA analysis was carried out, considering age as a covariate. For female reproductive performance this analysis could not be performed because data did not fulfill assumptions of this test.

In order to determine if beavers had better, worse or the same performance in Tierra del Fuego compared to their natural range, mean values for weight and litter size at each age category were taken from studies in Newfoundland, by far the best studies in terms of number of beaver sampled, (Payne 1979, Payne 1984). Data obtained in Newfoundland were considered as expected values, thus the following formula was applied to obtain a standardized performance index.

$$Standardized\ performance\ = \frac{(Observed\ value - Expected\ value)}{Expected\ value}$$

If the average of the standardized performance is zero, then the beavers in Tierra del Fuego have the same performance as their Canadian counterparts. If, on the other hand, the average of the standardized performance is above or below zero, then beavers in Tierra del Fuego perform better or worse than their Canadian counterparts respectively. To test this a one sample t-test was performed to see if the mean of either measure of performance was different from zero.

2.4 Results

A total of 66 beavers were captured: 19 in steppe, 23 in scrub, and 24 in forest (Fig. 1). Of the total, 27 were female: seven in steppe, 10 in shrubland, and 10 in forested areas. The mean (± 95% confidence interval) weight for all beavers was 15.2 ± 1.08 kg: 15.7 ± 1.85 kg for steppe, 14.4 ± 1.76 kg for scrub, and 15.5 ± 1.93 in forest. Tail volume averaged (± 95% confidence interval) 1054.7 ± 97.29 cm^3 for all beavers: 1109.5 ± 167.72 cm^3 in steppe, 1047.9 ± 174.48 cm^3 in shrubland, and 1017.7 ± 166.49 cm^3 in forest.

The mean number (± 95% confidence interval) of uterine scars for all female beaver was 2.74 ± 0.36, but this varied depending on the environment: 2.50 ± 1.10 in steppe, 3.25 ± 1.27 in shrub land, and 2.44 ± 0.81 in forest. Five of the females sampled were in non-reproductive stage: one in steppe, two in scrub, and two in forest. Differences in age among the three environments were not detected, neither considering only females, Kruskal-Wallis (Chi-sq2 = 0.381; P = 0.8272), nor the total individuals trapped, Kruskal-Wallis (Chi-sq2 = 0.241; P = 0.8872). Thus, comparisons of performance measures among the three environments did not need to be corrected by age. There was no evidence of differences in weight, Kruskal-Wallis (Chi-sq2 = 1.369; P = 0.5044), litter size, Kruskal-Wallis (Chi-sq2 = 0.258; P = 0.2584) or tail volume, ANOVA (F2 = 0.277; P = 0.7594) between the environments. Only weight (R^2 = 0.349; P = 2.225 10-8) and tail volume (R^2 = 0.4675; P = 3.443 10-8) showed significant linear relationships with age, with R square values of 0.394 and 0.468, respectively. When comparing the slopes with ANCOVA, neither weight ANCOVA (F2 = 0.005; P=0.995) nor tail volume ANCOVA (F2 = 0.028; P=0.973) had significant differences between environments (Fig. 2). Thus no differences in age, weight, tail volume, litter size, or slopes of age against weight, or age against tail volume were detected between environments.

Standardized values for weight and litter size for all beavers and for every environment had a normal distribution, hence a t-test was carried out to detect if the mean was statistically different from zero. The weight standardized by age, for all beavers and for each environment was statistically higher than zero (Table 2). This would mean that beavers in Tierra del Fuego weighed more than their counterparts in Newfoundland. However, the increased weight in Tierra del Fuego was not translated into an increase of litter size (Table 2).

2.5 Discussion

Our results show that invasive beaver have a similar performance in three different environments of Tierra del Fuego. However, long-term studies developed in North America, suggest that there could be variations in temporal stability in different environments. In North America, beavers have less stable populations in the boreal areas of their distribution (Hall 1960, Aleksiuk 1970a). The interpretation of these results has been that beaver in northernmost regions deplete their woody resources, and eventually cannot gather enough bark and branches for their food cache. Similarly, in Tierra del Fuego it has been shown that forests do not regenerate after being disturbed by beavers (Martínez-Pastur et al. 2006). Furthermore, the rate of consumption of lenga is higher in South America than that of woody species in North America (Baldini et al. 2008), which would indicate that lenga is a low-quality food item for beavers. On the other hand, *Chilliotrichum diffusum*, the most abundant woody species and the most used by beavers in the Fuegian scrub (D Corcoran, unpublished data), regrows rapidly after being cut (O Dollenz, pers. com. 2010). This would render this woody species a more stable resource for beavers.

In terms of the hypotheses tested, our results indicate that enemy-release (absence of predators) is the most plausible explanation for the beaver success in Tierra del Fuego and accounts for their equal success in all environments. One of the predictions of the enemy release hypothesis is that the performance of invasive populations is better than the performance of the native counterpart (Catford et al. 2008). The performance of beavers in Newfoundland seems to be a perfectly good comparison to beavers in Tierra del Fuego, because most of that Canadian province has a climate type Dfb, and beavers brought to Tierra del Fuego came from territories close to Prince Albert, which shares the same type of climate (Peel et al 2007).

Because beavers in Tierra del Fuego are heavier than their Canadian counterparts, we may say that our results support a Compensatory Enemy Release (Colautti et al. 2004). According to theory, this increase in performance occurs when a species loses enemies that they have defended against, and that resources previously used for defense are reallocated to growth and reproduction, thereby facilitating invasion. In our case it has been documented that beavers venture farther from their pond to browse on lenga (Wallem et al. 2007). This behavioral novelty could explain the better performance, and it could be considered an allocation of energy in terms of missed opportunity.

Several studies show the energy cost of avoiding predators in terms of finding mates and/or foraging behavior (Milinski & Heller 1978, Sih 1980, Grubb & Greenwald 1982, Werner et al. 1983, Lima et al. 1985). In beavers, predator avoidance can cause missed opportunities for foraging behavior but not for mating, because pairs live in the same beaver lodge, and they do not have to search for a mate in order to reproduce. This might explain why the increase of weight doesn't translate in an increase in litter size. The recent colonization on the South American continent from Tierra del Fuego Island affords an opportunity to test this hypothesis, because there is a higher diversity of predators in the former, and there have been observations of cougar cats or mountain lions (*Puma concolor*, absent from Tierra del Fuego) with beaver remains (Anthoni Muñoz, pers. com. 2010). Further studies will need to be conducted on the continent to determine if predation significantly affects the abundance and/or performance of beaver in comparison to those across the Straits of Magellan.

2.6 Acknowledgments

We thank programs 2 and 8 From Centro de Estudios Avanzados en Ecología & Biodiversidad, FONDAP 1501-0001, Servicio Agrícola y Ganadero for the traps and support, especially to Jose Luis Cabello. We thank all ranchers and friends who live and work in Tierra del Fuego, who kindly let us stay and work in their properties, taught us to learn how to identify beaver signs and helped us in any way they could; particularly we give our special thanks to Pedro Mancilla, his wife Eliana, Juan Carlos Cavada, Derek Morrison and Magallanes Rovira. Thanks to WCS for letting us stay and work in Karukinka Park, and the support of Miguel Millán and Claudio Moraga in the field, moral support and further discussions. DC thanks to CONICYT PhD scholarship.

2.7 Bibliography

Aleksiuk M (1970a) The seasonal food regime of arctic beavers. Ecology 51:264–270

Aleksiuk M (1970b) The function of the tail as a fat storage depot in the beaver (*Castor canadensis*). J Mammal 51:145–148

Anderson CB, Martinez-Pastur G, Lencinas MV, Wallem PK, Moorman MC, Rosemond AD (2009) Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. Mammal Rev 39: 33–52.

Andrade BS (2005) Gestión para la caza y aprovechamiento de fauna dañina en XII Región (Informe Técnico). Servicio Agrícola y Ganadero, Punta Arenas.

Baker BW, Hill EP (2003) Beaver (*Castor canadensis*). In: Feldhamer GA, Thompson BC, Chapman JA (eds) Wild mammals of North America: biology, management, and conservation, second edition. John Hopkins University Press, Baltimore.

Baker RHA, Sansford CE, Jarvis CH, Cannon RJC, Macleod A, Walters KFA (2000) The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. Agr Ecosyst Environ 82: 57–71.

Baldini AB, JO Oltremari, M Ramírez (2008) Impacto del castor (*Castor canadensis*, Rodentia) en bosques de lenga (*Nothofagus pumilio*) de Tierra del Fuego, Chile. Bosque 29: 162–169.

Barrera MD, Frangi JL, Richter LL, Perdomo MH, Pinedo LB (2000) Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. J Veg Sci 11: 179–188.

Beier P, Barrett RH (1987) Beaver habitat use and impact in Truckee River basin, California. J Wildlife Manage 51: 794–799.

Benson SB (1936) Notes on the sex ratio and breeding of the beaver in Michigan. Occas.Pap Mus Zool Univ Mich 335: 1-6.

Bomford M, Kraus F, Barry SC, Lawrence E (2009) Predicting establishment success for alien reptiles and amphibians: a role for climate matching. Biol Invasions 11: 713–724.

Bond CF (1956) Correlations between reproductive condition and skull characteristics of beaver. J Mammal 37: 506–512.

Brenner FJ (1964) Reproduction of the beaver in Crawford County, Pennsylvania. J Wildlife Manage 28: 743–747.

Briones M, Schlatter R, Wolodarsky A, Venegas C (2001) Clasificación ambiental para hábitat de *Castor canadensis* (KUHL 1820, Rodentia), de acuerdo a características de cuencas en un sector de Tierra del Fuego. Anales del Instituto de la Patagonia 29:75–93.

Busher PE (1996) Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. Am Midl Nat 135: 343–348.

Catford JA, Jansson R, Nilsson C (2008) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distribution 15: 22–40.

Colautti RI, Ricciardi A, Grigorovich IA, Macisaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7: 721–733.

CONAF, CONAMA, BIRF (1999) Catastro y evaluación de recursos vegetacionales nativos de Chile, Informe regional Duodécima Región, primera edición. Gobierno de Chile, Santiago.

Curtis PD, Jensen PG (2004) Habitat features affecting beaver occupancy along roadsides in New York state. J Wildlife Manage 68: 278–287.

Choi C (2008) Tierra del Fuego: the beavers must die. Nature 453: 968.

Danilov P (1995) Canadian and European beavers in Russian northwest (distribution, number, comparative ecology) In: Ermala A, Lahti S (eds). Proceedings of the Third Nordic Beaver Symposium. Finnish Game and Fisheries Research Institute, Helsinki.

Danilov P, Kan'shiev V (1982) Some morphological and ecological features of the Eurasian and North American beaver in the USSR north west. Fauna: ecologiya ptic (mlekopitajvscic): 109–123.

Defossé GE, Bertiller MB (1991) Comparison of four methods of grassland productivity assessment based on *Festuca pallescens* phytomass data. J Range Manage 44: 199–203.

Dieter CD, Mccabe TR (1989) Factors influencing beaver lodge-site selection on a prairie river. Am Midl Nat 122: 408–411.

Dollenz O (1995) Los árboles y bosques de Magallanes, segunda edición. Ediciones Universidad de Magallanes, Punta Arenas.

Duncan RP, Bomford M, Forsyth DM, Conibear L (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. J Anim Ecol 70: 621–632.

Endlicher W, Aguila AS (1988) El clima del sur de la Patagonia y sus aspectos ecológicos: Un siglo de mediciones climatológicas en Punta Arenas. Anales del Instituto de la Patagonia 18: 57-86.

Fernández-A RJ, Sala OE, Golluscio RA (1991) Woody and herbaceous aboveground production of a Patagonian steppe. J Range Manage44: 434–437.

Forsyth DM, Duncan RP, Bomford M, Moore G (2004) Climatic Suitability, Life-History Traits, Introduction Effort, and the Establishment and Spread of Introduced Mammals in Australia. Conserv Biol 18: 557–569.

Frangi JL, Barrera MD, Richter LL, Lugo AE (2005) Nutrient cycling in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. Forest Ecol Manag 217: 80–94.

Fustec J, Cormier JP, Lodé T (2003) Beaver lodge location on the upstream Loire River. CR Acad Sci II Vie 326: 192–199.

Gerding V, Thiers O (2002) Caracterización de suelos bajo bosques de *Nothofagus betuloides* (Mirb) Blume, en Tierra del Fuego, Chile. Rev Chil Hist Nat75: 819–833.

Grinnell J, Dixon JS, Linsdale JM (1937) Fur-bearing mammals of California: their natural history, systematic status, and relations to man. University of California press, Berkeley.

Grubb TC, Greenwald L (1982) Sparrows and a brushpile foraging responses to different combinations of predation risk and energy cost. Anim Beha 30: 637-640.

Gunson JR (1970) Dynamics of the beaver of Saskatchewan’s northern forest. University of Alberta, Edmonton.

Hall JG (1960) Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41: 484–494.

Hammond MC (1943) Beaver on the Lower Souris Refuge. J Wildlife Manag 7:316-321

Henry DB, Bookhout TA (1969) Productivity of beavers in northeastern Ohio. J Wildlife Manage 33: 927–932.

Hill E (1982) Beaver (*Castor canadensis*). In: Chapman JA, Feldhamer GA (eds) Wild mammals of North America: biology, management, and economics, first edition. John Hopkins University Press, Michigan.

Hodgdon KW (1949) Productivity data from placental scars in beavers. J Wildlife Manage 13: 412–414.

Howard RJ, Larson JS (1985) A stream habitat classification system for beaver. J Wildlife Manage 49: 19–25.

Ibarra JT, Fasola L, Macdonald DW, Rozzi R, Bonacic C (2009) Invasive American mink *Mustela vison* in wetlands of the Cape Horn Biosphere Reserve, southern Chile: what are they eating? Oryx 43: 87–90.

Jaksic FM (1998) Vertebrate invaders and their ecological impacts in Chile. Biodivers Conserv 7: 1427–1445.

Jenkins S (1981) Problems, progress and prospects in studies of food selection by beavers. In: Chapman JA, Pursley D (eds) Worldwide Furbearer Conference Proceedings, vol 1. University of Maryland, Frostburg, pp 559–579.

Jobbágy EG, Sala OE (2000) Controls of grass and shrub aboveground production in the Patagonian steppe. Ecol Appl 10: 541–549.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecol Evol 17: 164–170.

Kriticos D, Randall R (2001) A comparison of systems to analyze potential weed distributions. In: Groves R, Panetta F and Virtue J (eds) Weed risk assessment. CSIRO Publishing, Melbourne.

Pérez J (1982) Lizards as laboratory animals. In: Veronese BG (ed) Laboratory animals, second edition. Moulin Editors, Paris.

Lahti S, Helminen M (1974) The beaver *Castor fiber* (L.) and *Castor canadensis* (Kuhl) in Finland. Acta Theriol 19: 177–189.

Larson JS, Van Nostrand F (1968) An evaluation of beaver aging techniques. J Wildlife Manage 32: 99–103.

Leege TA, Williams RM (1967) Beaver productivity in Idaho. J Wildlife Manage 31: 326–332.

Lizarralde MS (1993) Current status of the introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. AMBIO 22: 351–358.

Lizarralde MS, Bailliet G, Poljak S, Fasanella M, Giulivi C (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 MS, Escobar J, Deferrari G (2004) Invader species in Argentina: a review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. Interciencia 29: 352-355.

MacDonald DW, Tattersall F, Brown E, Balharry D (1995) Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity? Mammal Rev 25: 161–200.

Martínez-Pastur G, Lencinas MV, Escobar J, Quiroga P, Malmierca L, Lizarralde MS, Townsend P (2006) Understorey succession in Nothofagus forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. Applied Vegetation Science 9: 143–154.

McComb WC, Sedell JR, Buchholz TD (1990) Dam-site selection by beavers in an eastern Oregon basin. West N Am Naturalist 50: 273–281.

McNaughton S, Oesterheld M, Frank D, Williams K (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341: 142-144.

Menvielle MF, Funes M, Malmierca L, Ramadori D, Saavedra B, Schiavini A, Soto N (2010) American beaver eradication in the southern tip of South America: main challenges of an ambitious project. Aliens: Invasive Species Bulletin 29: 9–16.

Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.) Nature 275: 642-644.

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421: 625–627.

Müller-Schwarze D, Sun L (2003) The Beaver: Natural History of a Wetlands Engineer, first edition. Cornell University Press, New York.

Novak M (1987) Beaver. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in North America. Ashton-Potter Limited, North Bay.

Novakowski NS (2010) Population dynamics of a beaver population in northern latitudes. PHD Thesis, Department of Biology, University of Saskatchewan, Saskatoon.

Nummi P (1996) Wildlife introductions to mammal-deficient areas: the Nordic countries. Wildlife Biol 2: 221–226.

Oesterheld M, Dibella C, Kerdiles H (1998) Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. Ecol Appl 8: 207–212.

Olson RA, Hubert WA (1994) Beaver: water resources and riparian habitat manager, first edition. University of Wyoming, Laramie.

Osborn DJ (1953) Age classes, reproduction, and sex ratios of Wyoming beaver. J Mammal 34: 27–44.

Parkes J, Paulson J, Donlan CJ, Campbell K (2008) Control of North American beavers in Tierra del Fuego: feasibility of eradication and alternative management options. In: Contract Report, Landcare Research. http://advancedconservation.squarespace.com/storage/library/parkes_etal_2008.pdf Accesed september 27, 2012.

Payne NF (1979) Relationship of pelt size, weight, and age for beaver. J Wildlife Manage 43: 804–806.

Payne NF (1984) Reproductive rates of beaver in Newfoundland. J Wildlife Manage48: 912–917.

Pearson AM (1960) A study of the growth and reproduction of the beaver (*Castor canadensis* Kuhl) correlated with the quality and quantity of some habitat factors. University of British Columbia, Vancouver.

Peel MC, Finlayson BL, Mcmahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Syst Sc11: 1633-1644 .

Pisano E (1977) Fitogeografía de Fuego-Patagonia Chilena. I. Comunidades vegetales entre las latitudes 51 y 56^{o} Sur. Anales del Instituto de la Patagonia 8: 121-250.

Posse G, Cingolani AM (2000) Environmental controls of NDVI and sheep production in the Tierra del Fuego steppe of Argentina. Applied Vegetal Science 3: 253–260.

Provost EE (1958) Studies on reproduction and population dynamics in beaver, first edition. State College of Washington, Pullam.

Reichle D, Franklin J, Goodall D (1975) Productivity of world ecosystems, first edition. National Academy of sciences, Washington DC.

Retzer JL, Swope HM, Remington JD, Rutherford WH (1956) Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. Technical Bulletin of the Colorado Department of Game and Fish 2: 1-32.

Robel RJ, Fox LB, Kemp KE (1993) Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. Wildlife Soc B 21: 415–421.

Rutherford WH (1955) Wildlife and environmental relationships of beavers in Colorado forests. J Forest 53: 803–806.

Santana A, Porter C, Butorovic N & Olave C (2006) Primeros antecedentes climatológicos de estaciones automáticas (AWS) en el Canal Beagle, Magallanes, Chile. Anales del Instituto de la Patagonia 34: 5-20.

Saveljev AP, Safonov VG (1999) The beaver in Russia and adjoining countries. In: Busher PE, Dzieciolowski RM (eds) Beaver protection, management, and utilization in Europe and North America, first edition. Kluwer publishers, New York

Shwartz A, Strubbe D, Butler CJ, Matthysen E, Kark S (2009) The effect of enemy-release and climate conditions on invasive birds: a regional test using the rose-ringed parakeet (*Psittacula krameri*) as a case study. Diversity and Distributions 15: 310–318.

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands ? Science 210: 1041-1043.

Skewes O, Gonzalez F, Olave R, Ávila A, Vargas V, Paulsen P, König HE (2006) Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. European Journal of Wildlife Reserch 52: 292–296.

Skewes RO, Gonzalez F, Rubilar L, Quezada OM, Olave RR, Vargas V, Avila AC (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.

Smith DW, Jenkins SH (1997) Seasonal change in body mass and size of tail of northern beavers. J Mammal 78: 869–876.

Stephenson AB (1956) Preliminary studies on growth, nutrition, and blood chemistry of beavers. M.A. Thesis, Department of Zoology. University of British Columbia, Vancouver.

Svendsen GE (1980) Seasonal change in feeding patterns of beaver in southeastern Ohio. J Wildlife Manage 44: 285–290.

Swank WG (1949) Beaver ecology and management in West Virginia. Conservation Commission of West Virginia Bulletin 1: 1-65.

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333–345.

Torchin ME, Lafferty KD, Dobson AP, Mckenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421: 628–630.

Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. Parasitology 124: 137–151.

Van Nostrand FC, Stephenson AB (1964) Age determination for beavers by tooth development. J Wildlife Manage 28: 430–434.

Wallem PK (2009) El invasor *Castor canadensis* en los bosques sub-antárticos del archipiélago de Tierra del Fuego, Chile: Historia, hábitos e impactos. Tesis Doctoral, Facultad de Ciencias Biológicas. Pontificia Universidad Católica de Chile, Santiago, Chile.

Wallem PK, Jones CG, Marquet PA, Jaksic FM (2007) Identificación de los mecanismos subyacentes a la invasión de *Castor canadensis* (Rodentia) en el archipiélago de Tierra del Fuego, Chile. Rev Chil Hist Nat 80: 309–325.

Werner EE, Gilliam JF, Hall DJ, Mittlebach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548

Wigley TB, Roberts TH, Arner DH (1983) Reproductive characteristics of beaver in Mississippi. J Wildlife Manage 47: 1172–1177.

Wilkinson PM (1962) A life history study of the beaver in east-central Alabama. MS Thesis. Auburn University, Auburn.

Woodward DK (1977) Status and ecology of the beaver (*Castor canadensis carolinensis*) in South Carolina with emphasis on the Piedmont region. MS Thesis. Clemson University, Clemson.

Woodward FI (1987) Climate and Plant Distribution, first Edition. Cambridge University Press, Cambridge.

Zurowski W (1992) Building activities of beavers. Acta Theriol 37: 403-411.

2.8 Figures

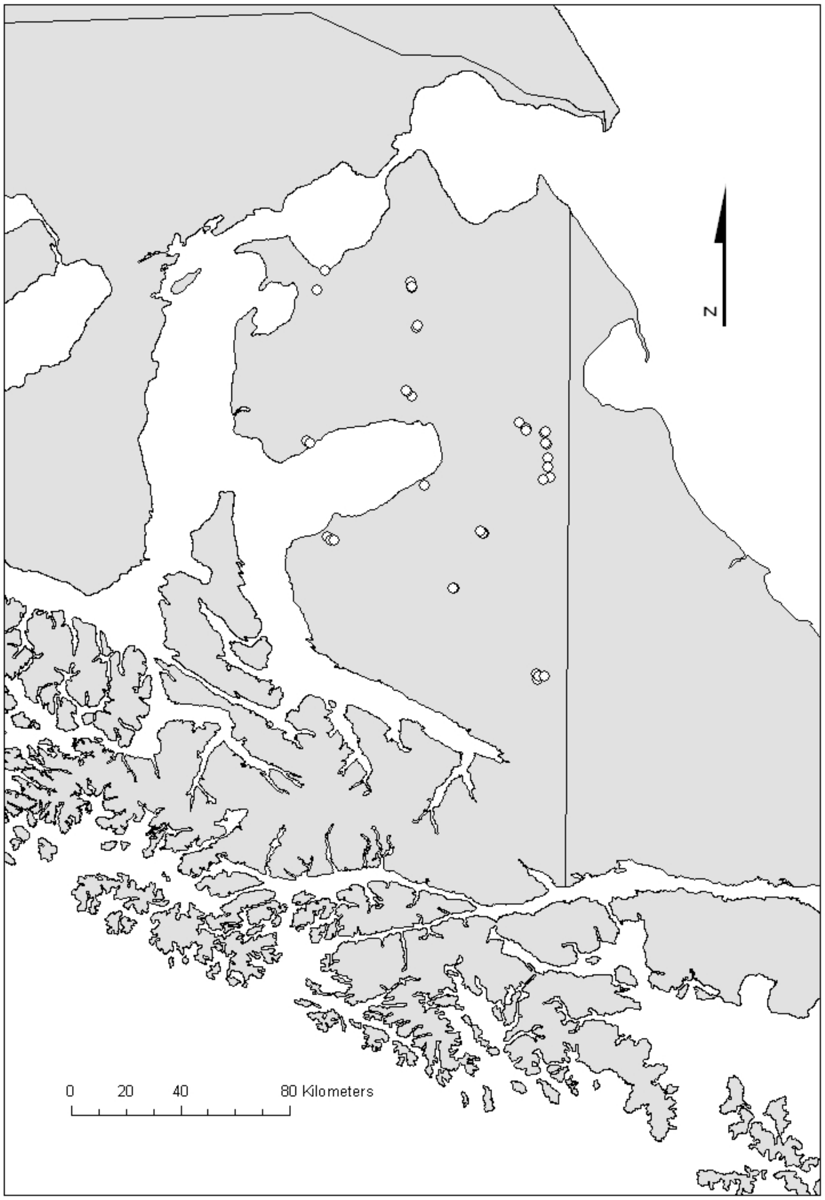

Fig. 1: Map showing the locations where beavers were sampled on Chilean Tierra del Fuego.

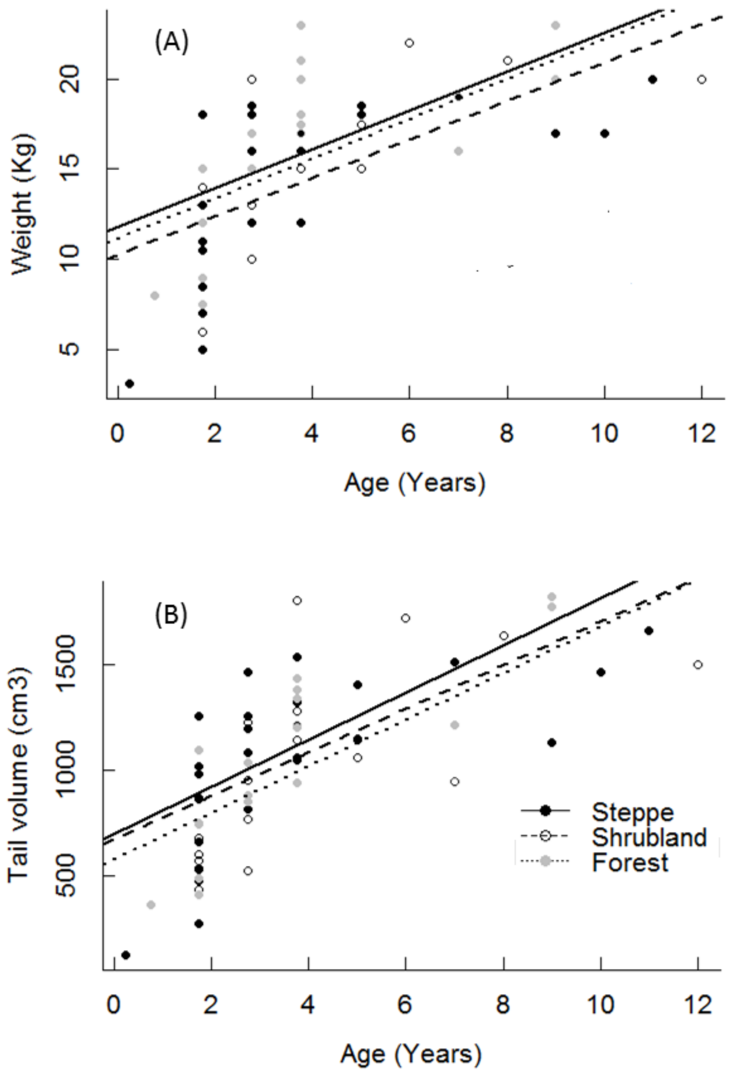

Fig. 2: A Ordinary Linear Regressions of age against weight for each environment. B Ordinary Linear Regressions of age against tail volume for each environment.

2.9 Tables

Table 1. Number of uterine scars recorded in studies in North America for Köppen type of climates.

Climate Type	Mean ± SD	n (number of studies)
Bsk	3.50±0.66	3
Cfa	2.50±0.26	3
Cfb	3.05±0.78	2
Dfa	4.13±1.23	3
Dfb	3.85±0.28	3
Dfc	2.85±0.07	2
Dfd	2.90	1

Table 2. Average weights and litter size standardized by age, t values and significance.

	Standardized weight (kg)				Standardized Litter size			
Environment	Mean	t value	p value	DF	Mean	T value	p value	DF
All	0.3095082	8.3613	7.45E-12	64	0.197019	1.6174	0.1232	18
Steppe	0.3719291	6.0993	9.20E-06	18	0.109674	0.7146	0.5144	4
Shrubland	0.2451472	3.6231	0.002	21	0.280326	1.1894	0.2732	7
Forest	0.3190892	5.1176	3.49E-05	23	0.15873	0.7372	0.4941	5

III. ¿PUEDE LA MODELACIÓN DE DISTRIBUCIÓN DE ESPECIES GENERAR UN NICHO HUTCHINSONIANO? UNA PRUEBA DE CAMPO UTILIZANDO A LA ESPECIE INVASORA *CASTOR CANADENSIS* EN EL SUR DE CHILE

CAN SPECIES DISTRIBUTION MODELS GENERATE HUTCHINSONIAN NICHES? A FIELD TEST USING INVADING *CASTOR CANADENSIS* IN SOUTHERN CHILE

Derek Corcoran[1], Giorgia Graells[2], Petra K. Wallem[3], Fabián M. Jaksic[1]

1. Pontificia Universidad Católica de Chile, Departamento de Ecología. Santiago, Chile.
2. Universidad de Magallanes. Punta Arenas, Chile
3. Flora y Fauna Chile Ltda. Santiago, Chile.

Short title: Can niche modeling generate Hutchinsonian niches?

3.1 Abstract

Aim: To test whether species distribution models (SDM) can predict performance for the North American beaver as an invasive species, and thus generate a Hutchinsonian niche, and to develop a predictive model for that species' performance

Location: Magallanes region, Chile

Methods: Surveys were carried away on rivers in Tierra del Fuego and the Chilean mainland, where 117 presence points were established. With these data, SDMs were developed, using six bioclimatic layers (Worldclim) and two Topographic layers (Hydro 1k) as predictors, and seven different algorithms. The performance of 65 beavers in Tierra del Fuego was measured by litter size in females and by weight in males and females; the age of each beaver was determined via tooth development.

Linear and quantile regressions were performed using the age-standardized performance as dependent variable and presence probability as the independent variable. Also, generalized linear models (GLMs) were performed using the same layers used for SDMs as predictors, and performance was standardized by age as a response variable.

Results: All seven models performed well according to their area under the curve (AUC), but failed to predict performance; that is, there were no significant positive relationships. On the other hand, the predictive model (GLM) for species performance worked well for litter size ($R^2=0.6434$, $p= 3.61 \times 10^{-05}$).

Main conclusions: For invasive beavers a SDM model cannot predict the performance of the species using any of the seven algorithms applied. Thus, we could not model a Hutchinsonian niche. If this is true for other species it will be harder to use it as a tool to predict performance or develop management practices for invasive species or to establish protected areas. GLM, on the other hand, can predict the performance of beavers, and thus it is proposed as a tool for modeling spatially-explicit Hutchinsonian niches.

Keywords: Beaver, *Castor canadensis*, Grinnellian Niche, Hutchinsonian Niche, Invasive Species, Niche Modeling.

3.2 Introduction

Niche is a central concept in ecology, currently there being three different definitions (Leibold 1995, Chase & Leibold 2003, Odling-Smee et al. 2003). The most widely used is that by Hutchinson's (1957), in which he states that a species' niche is the set of points in a hypervolume of environmental variables were the species has a positive value of fitness. On the other hand, Grinnel's definition does not deal with fitness and it only defines the environmental characteristics of a species' geographical distribution (Grinnell 1917, Jackson & Overpeck 2000). Finally Elton's definition of niche is related to the consumption of resources and a given species' impact in its habitat (Leibold 1995).

Niche modeling (Based on the Grinnellian concept) has been successfully used to predict species' potential distributions for over a decade (Guisan & Zimmerman 2000, Peterson 2001, Peterson & Nakazawa 2008). Its success is partly due to the development of biodiversity databases and the development of the Geographic Information System (Coppock & Rhind 1991, Soberón & Peterson 2004).

There are several algorithms for species distribution models, and even when there are some reports that evaluate their performance, it has been proposed that several algorithms should be used and compared, or analyzed by consensus models (Segurado & Araújo 2004, Elith et al. 2006, Prasad et al. 2006).

It has been suggested that there should be a positive relationship between fitness and suitability index (Nogués-Bravo 2009), which is defined as an index that can predict the likelihood of occurrence of species on the base of environmental variables (Franklin, 1995; Guisan & Zimmermann, 2000). Niche models are algorithms that relate presence data with environmental layers and thus do not include population parameters such as fitness or migration (Mustin *et al.* 2009, Peterson *et al.* 2011). Further, the relationship between presence probability and fitness has seldom been studied (Torres et al. 2012).

This paper studies the relationship between beaver performance and habitat suitability to create a spatially explicit performance model for *Castor canadensis* (Kuhl 1820) in southern South America.

3.3 Methods

Study site

This study was conducted on the Chilean side of Tierra del Fuego Island (TDF), and the Magallanes Province on the Chilean Mainland (Figure 1). (TDF) is located in the southernmost tip of South America between parallels 52 and 55ºS. Its surface is 48,598 km^2, of which 22,592.7 km^2 correspond to the Chilean province of Tierra del Fuego. The Magallanes Province has an area of 36,400.8 km^2 and is bordered by the Tierra del Fuego Province to the East and South. The whole region has a strong pluviometric gradient going from 200 mm of rainfall in the northeast to 2,000 mm in the southwest, as well as strong winds from the west that may reach 160 km/hour (Enlicher & Santana 1988; Santana et al. 2006).

At least three different environments can be distinguished in these two provinces: forest, shrubland, and steppe (Pisano 1977; Dollenz 1995).

(a) Forest: Most of the Magellanic forest is dominated by Lenga (*Nothofagus pumilio*((Poepp. & Endl.) Krasser 1896)), with precipitation ranging 400 to 620 mm per year, and a Dfc climate type following Köppen’s classification. In the southwestern coast, the forest becomes evergreen and is dominated by Coigüe (*Nothofagus betuloides* ((Mirb.) Oerst 1871)) and to a lesser extent by Canelo (*Drimis winteri* (Forst 1776)). Yearly precipitation ranges 800 to 2000 mm, matching a Cfc type of climate (Gerding & Thiers 2002). It has been shown that the forests of Tierra del Fuego do not regenerate after being disturbed by beavers (Martínez-Pastur et al. 2006).

(b) Shrubland: A Bsk climate with annual precipitations between 200 and 400 mm, the dominant shrub is *Chilliotrichum diffusum* (G.Forst.) Kuntze) followed by *Berberis microphylla* (G. Forst). The former regrows after its branches have been cut down by beavers (Corcoran, personal observation).

(c) Steppe: A Bsk climate with an environment dominated by graminoids such as *Festuca gracillima* (Hook.F), and precipitations ranging from 200 to 300 mm per year.

Sampling for presence

Sampling took place in Tierra del Fuego from February 24th of 2010 to March 3rd 2011 with four different sampling periods, totaling 159 sampling days and 23 different rivers. On the other hand, on the continent, ground surveys were conducted in 19 different rivers covering 208 linear km of rivers (Graells & Corcoran 2011).

All surveys were done on foot, walking along rivers, or at times on mountain bikes or snowshoes depending on the surface. While we trekked, we used an *e-trex H* GPS, and marked a waypoint every time a beaver sign was found, including gnawed trees, lodges or dams.

Performance and age measurements

Beavers were hunted using Connibear traps, and rifles according to Chilean law regulations; this latter sampling technique took place only in Tierra del Fuego. To estimate the performance of beavers, several measurements were taken:

1. Female reproductive performance. The number of offspring bred during the last season was determined by counting uterine scars (Hodgdon 1949) and --depending on the season-- fetuses.
2. Body size. Beavers were weighted and their total length measured. There is a documented positive relationship between total weight and litter size (Rutherford 1955). Further, both measurements represent the quality and variety of food available for beavers in North America (Pearson 1960; Stephenson 1956).

Age was determined by tooth development (Van Nostrand & Stephenson 1964; Larson & Van Nostrand 1968). Because beavers can live up to 20 years, all performance measures have to be standardized by age. In order to do that we took averages for weight and litter size for each determined age (Payne 1979; Payne 1984) and considered them as expected values and applied formula 1 (we did not square the parenthesis because the sign needs to be revealed).

$$(1)\ Standardized\ performance\ = \frac{(Observed\ value - Expected\ value)}{Expected\ value}$$

If the standardized performance of a beaver is zero, then that beaver in Tierra del Fuego has the same performance as its Canadian counterparts. If, on the other hand, the standardized performance is above or below zero, then beavers in Tierra del Fuego perform better or worse than their Canadian counterparts respectively.

Niche modeling

The potential distribution of beavers in South America was modeled using R version 2.15.1 and the dismo package (Hijman et al. 2011, Hijman & Elith 2013) with seven algorithms: Bioclim, Domain, GLM (Gaussian), GLM (Logistic), GAM, Maxent and SVM. 117

occurrence records from Tierra del Fuego and chilean mainland were used with six of the 18 bioclimatic layers from Worldclim (Isothermality, Temperature Seasonality, Mean Temperature of Wettest Quarter, Mean Temperature of Coldest Quarter, Precipitation Seasonality, Precipitation of Driest Quarter, the other layers were eliminated due to high collinearity, |r|>0.7) (Hijman et al. 2005) and two predictors from Hydro1k (Flow accumulation and Slope), which are good characteristics of river sites (United States Geological Survey) as predictors.

Analysis

Linear regressions were performed using suitability indexes as predictors of performance. These tests were applied using R version 2.15.1

A triangular envelope explains the relationship between presence probability and fitness better than a linear relationship (Austin, 2007). That is, in poor environmental conditions species should always perform poorly, and in better environmental conditions it should vary from optimum to poor due to other factors such as species interactions (i.e. prey or predator´s abundance, competitors, etc.). Because of that a quantile regression was performed (Cade et al. 2005, Koenker & Machado 1999) using R and the quantreg package (Koenker & Koenker 2007). To evaluate the effect of presence probability on their corresponding maximum weights, we applied quantile regression for the 80, 85, 90 and 95th percentiles.

The same layers previously applied for SDMs were used to develop a predictive model for the performance standardized by age using GLM (Generalized Lineal Models). The glmulti package 1.0.7. version (Calcagno & de Mazancourt 2010), was used to run an exhaustive analysis using all possible first order models for the eight predictors and keeping the ones with the lower AICc (Corrected Akaike Information Criterion; Hurvich & Tsai 1989). From the models with the same AICc, only those with all of their parameters significant were used for further analysis and projected spatially. A consensus model was developed for all the selected models using the raster package (Hijman & van Etten 2010). To evaluate the consensus models, an ordinary linear regression was performed using the predictions of the model as an explanatory variable for the data obtained in the field.

3.4 Results

One hundred and sixteen presence points were determined; of these, eight points were from the continent, one hundred and seven from Tierra del Fuego, and there was one sample from Navarino Island obtained from an opportunistic field trip (Figure 2).

Of the 116 presence points, 66 beavers were sampled, all of them in Tierra del Fuego; twenty seven of the 66 beavers were females. The mean number of uterine scars was 2.46. The mean weight for beavers was 15.2 kg.

The seven algorithms had very high AUC (Area Under the Curve), which means that they performed very well. When we check the results of the Linear regressionsonly three of the 14 linear regressions showed a significant relationship between presence probability and Standardized weight or litter size (Table 1), but showed a very low R^2 (0.08643,0.09781 and 0.08579, respectively). When we examined the Quantile regression (Table 1), only three of the models show a significant slope. But in all cases they are negative, which is opposite to what we expected, and only at the 80th quantile, reinforcing the fact that there is no positive relationship between presence probability and performance for beavers in Tierra del Fuego.

Seven GLMs were selected by their AICc to be the best models to predict the weight standardized by age (Table 2). Two of these models were significant for all of their parameters (Models 4 and 5). Model 4 considers three layers to predict the beaver's standardized weight: BIO15 (Precipitation Seasonality), BIO17 (Precipitation of Driest Quarter) and the Topographic slope. Similarly Model 5 considers two layers to predict the beaver's standardized weight: BIO4 (Temperature Seasonality) and BIO 15 (Precipitation Seasonality). The consensus of both models is presented in Figure 3 and its evaluation through Ordinary Linear Regression shows significant values for R^2 ($y=1.22-0.06$, $R^2=0.1572$, $p=0.001$).

Four GLM models were selected by their AICc to predict litter size standardized by age (Table 3). Two were significant for all of their parameters (Models 1 and 4). Model one considers five layers to predict litter size standardized by age: BIO 4 (Temperature Seasonality), BIO 8 (Mean Temperature of Wettest Quarter), BIO 11 (Mean Temperature of Coldest Quarter), BIO 15 (Precipitation Seasonality), and BIO 17 (Precipitation of Driest Quarter). Model four considers three layers to predict the litter size of beavers: BIO 8 (Mean Temperature of Wettest Quarter), BIO 11 (Mean Temperature of Coldest Quarter), and BIO 15 (Precipitation Seasonality). The consensus of both models is presented in Figure 4 and its evaluation through Ordinary Linear Regression presents significant values for R2 ($y=1.11x-0.02$, $R^2=0.6434$, $p<0.001$).

3.5 Discussion

This work shows that seven niche modeling algorithms cannot predict performance in invasive beavers in Tierra del Fuego, i.e., there is no significant correlation between presence probability and performance. This suggests that niche modeling does not generate Hutchinsonian niches under these conditions. These results are consistent with another study (Torres et al. 2012), in which presence probability was weakly correlated with fitness (R^2=0.33).

Nevertheless, the GLM approach to model a spatially explicit Hutchinsonian niche was very successful, predicting the performance of this species, particularly in litter size. The low R^2 value for weight could be explained by having sampled in different seasons. Weight variability in beavers among seasons has been thoroughly studied (Payne 1979, Mèuller-Schwarze & Sun 2003). We recommend to use performance variables that will not change seasonally, such as litter size.

The use of presence databases is very useful for modeling distributions, but it seems that the same data will not allow the generation of spatially explicit Hutchinsonian niche through GLM. This methodology is proposed to solve problems and answer question were performance is important, which would require a more complex sampling methodology to determine performance.

Our work and the work of Torres et al. (2012) show that we cannot trust in SDM though presence-only algorithms to predict performance. This does not mean that SDMs are not useful. They have proved to be useful for many theoretical and practical applications (Peterson et al. 2011), and can also be used in complement with our proposed methodology to answer more complex theoretical and practical questions.

There are several proposed or applied uses for Grinnellian niche modeling which could be improved through the use of Hutchinsonian niche modeling. Among these we find the selection of where to establish protected areas, because we could select not only the intersection of distribution of species, but also ensure high performance for the species involved in the analysis. Probably it is not feasible to model a Hutchinsonian niche for many species at the same time, but at least this could be done on the most endangered species and be complemented with Grinnellian niche modeling for the less vulnerable species.

Another potential use for spatially explicit Hutchinsonian niche modeling is the management of invasive species, were we could elaborate selective control strategies in areas were high performance is predicted, thus eliminating potential source populations. Using this approach limited resources could be focused on a more efficient control with better results.

3.6 Acknowledgments

Thanks to Fabio Labra, Patricio Pliscoff and Ramiro Bustamante for the discussions we had about this article, we also thank FONDAP 1501-0001 Centro de estudios avanzados de Ecología y Biodiversidad programs 2 and 8 for funding most of the research, as well as fund Nº1162-136-SE11 of SAG for complementary funding. Special thanks to all ranchers that allowed us to use their properties for our research. DC thanks to CONICYT PhD scholarship.

3.7 References

Austin M. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological modelling*, **200**, 1–19.

Cade B.S. & Noon B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.

Calcagno V. & de Mazancourt C. (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 29.

Chase J.M. & Leibold M.A. (2003) *Ecological niches: linking classical and contemporary approaches.* University of Chicago Press, Chicago.

Coppock J.T. & Rhind D.W. (1991) The history of GIS. *Geographical information systems: Principles and applications*, **1**, 21–43.

Dollenz O. (1995) *Los árboles y bosques de Magallanes.* Ediciones de la Universidad de Magallanes,

Elith J., P Anderson R., Dudík M., Ferrier S., Guisan A., J Hijmans R., Huettmann F., R Leathwick J., Lehmann A., Li J., & G Lohmann L. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Endlicher W. & Santana A. (1988) El clima del sur de la Patagonia y sus aspectos ecológicos. Un siglo de mediciones climatológicas en Punta Arenas. *Anales del Instituto de la Patagonia*, **18**, 57–86.

Franklin J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.

Gerding V. & Thiers O. (2002) Caracterización de suelos bajo bosques de Nothofagus betuloides (Mirb) Blume, en Tierra del Fuego, Chile. *Revista chilena de historia natural*, **75**, 819–833.

Graells G. & Corcoran D. (2011) *Informe Final Proyecto prospección y control de foco de castores Provincia de Magallanes*. Servicio Agrícola y Ganadero, Punta Arenas.

Grinnell J. (1917) The niche-relationships of the California Thrasher. *The Auk*, **34**, 427–433.

Guisan A. & Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. *Ecological modelling*, **135**, 147–186.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**, 1965–1978.

Hijmans R.J. & Elith J. (2013) Species distribution modeling with R.

Hijmans R.J. & van Etten J. (2010) raster: Geographic analysis and modeling with raster data. *R package version*, **1**, r948.

Hijmans R.J., Phillips S.J., Leathwick J.R., & Elith J. (2011) *Species distribution modeling (dismo).* Package version *0.7–8.*

Hodgdon K.W. (1949) Productivity data from placental scars in beavers. *The Journal of Wildlife Management*, **13**, 412–414.

Hurvich C.M. & Tsai C.-L. (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Hutchinson G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Jackson S.T. & Overpeck J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

Koenker R. & Koenker M.R. (2008) *The quantreg package.* http://CRAN.R-project.org/package=quantreg.

Koenker R. & Machado J.A. (1999) Goodness of fit and related inference processes for quantile regression. *Journal of the american statistical association*, **94**, 1296–1310.

Larson J.S. & Van Nostrand F.C. (1968) An evaluation of beaver aging techniques. *The Journal of Wildlife Management*, 99–103.

Leibold M.A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology*, **76**, 1371–1382.

Martínez Pastur G., Lencinas M.V., Escobar J., Quiroga P., Malmierca L., Lizarralde M., & Townsend P. (2006) Understorey succession in Nothofagus forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. *Applied Vegetation Science*, **9**, 143–154.

Mèuller-Schwarze D. & Sun L. (2003) *The beaver: natural history of a wetlands engineer*. Cornell University Press,

Mustin K., Benton T.G., Dytham C., & Travis J.M. (2009) The dynamics of climate-induced range shifting; perspectives from simulation modelling. *Oikos*, **118**, 131–137.

Nogués-Bravo D. (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, **18**, 521–531.

Odling-Smee F.J., Laland K.N., & Feldman M.W. (2003) *Niche construction: the neglected process in evolution.* Princeton University Press,

Payne N.F. (1979) Relationship of pelt size, weight, and age for beaver. *The Journal of Wildlife Management*, **43**, 804–806.

Payne N.F. (1984) Reproductive rates of beaver in Newfoundland. *The Journal of wildlife management*, **48**, 912–917.

Pearson A.M. (1960) *A study of the growth and reproduction of the beaver (Castor canadensis Kuhl) correlated with the quality and quantity of some habitat factors.* University of British Columbia, Vancouver.

Peterson A.T. (2001) predicting species'geographic distributions based on ecological niche modeling. *The Condor*, **103**, 599–605.

Peterson A.T. & Nakazawa Y. (2008) Environmental data sets matter in ecological niche modelling: an example with Solenopsis invicta and Solenopsis richteri. *Global Ecology and Biogeography*, **17**, 135–144.

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M., & Araújo M.B. (2011) *Ecological niches and geographic distributions (MPB-49).* Princeton University Press,

Pisano E. (1977) Fitogeografía de Fuego-Patagonia chilena. *Anales del Instituto de la Patagonia*, **8**, 121-250.

Prasad A.M., Iverson L.R., & Liaw A. (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems*, **9**, 181–199.

Rutherford W.H. (1955) Wildlife and environmental relationships of beavers in Colorado forests. *Journal of Forestry*, **53**, 803–806.

Santana A., Porter C., Butorovic N., & Olave C. (2006) Primeros antecedentes climatológicos de estaciones automáticas (AWS) en el Canal Beagle, Magallanes, Chile. 34,

Segurado P. & Araujo M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555–1568.

Soberón J. & Peterson T. (2004) Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **359**, 689–698.

Tôrres N.M., De Marco P., Santos T., Silveira L., de Almeida Jácomo A.T., & Diniz-Filho J.A. (2012) Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Diversity and Distributions*, **18**, 615–627.

Van Nostrand F.C. & Stephenson A.B. (1964) Age determination for beavers by tooth development. *The Journal of Wildlife Management*, **28**, 430–434.

3.8 Figures

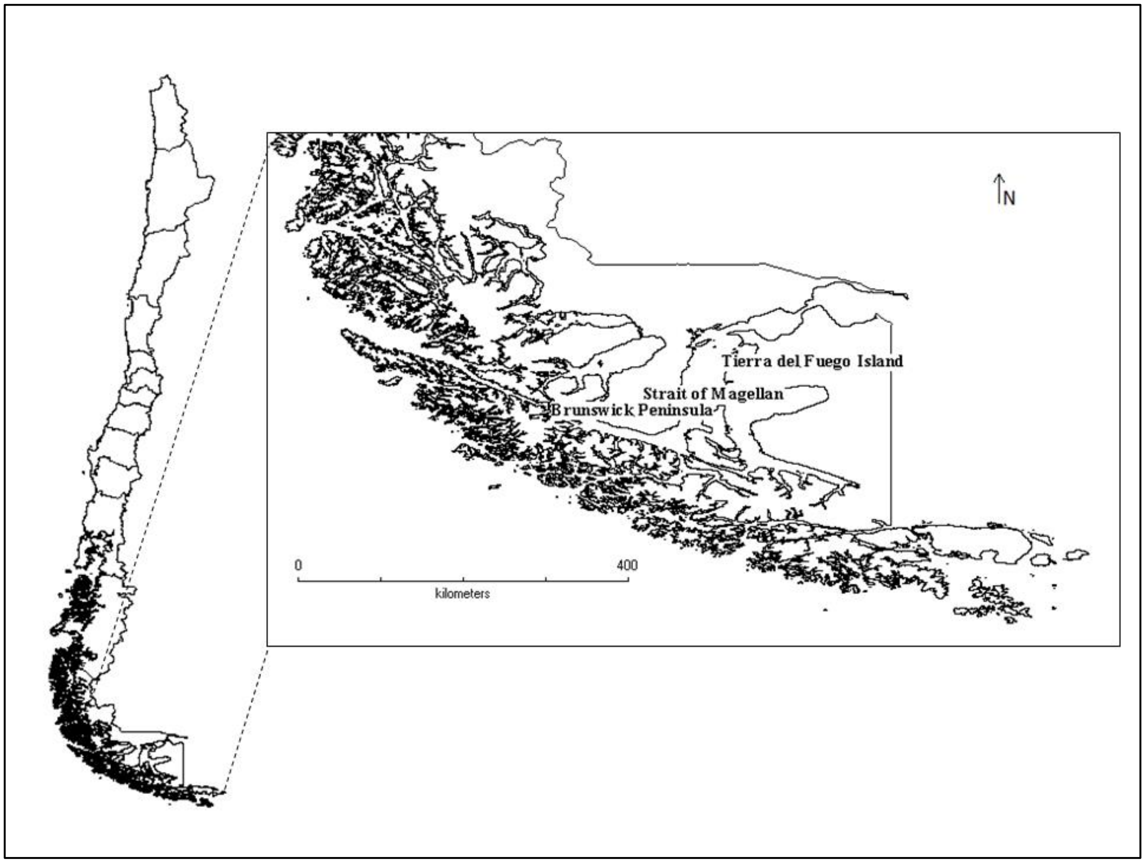

Fig. 1 Map showing the study site in relation to Chile.

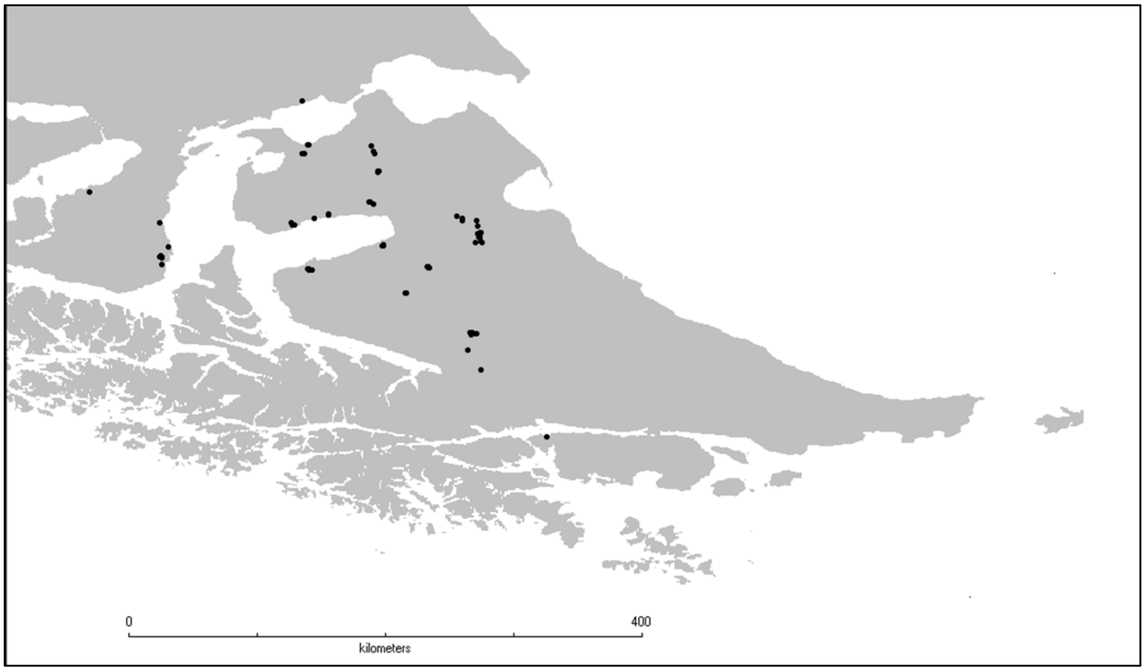

Fig. 2 Map showing records of beaver presences detected on the field

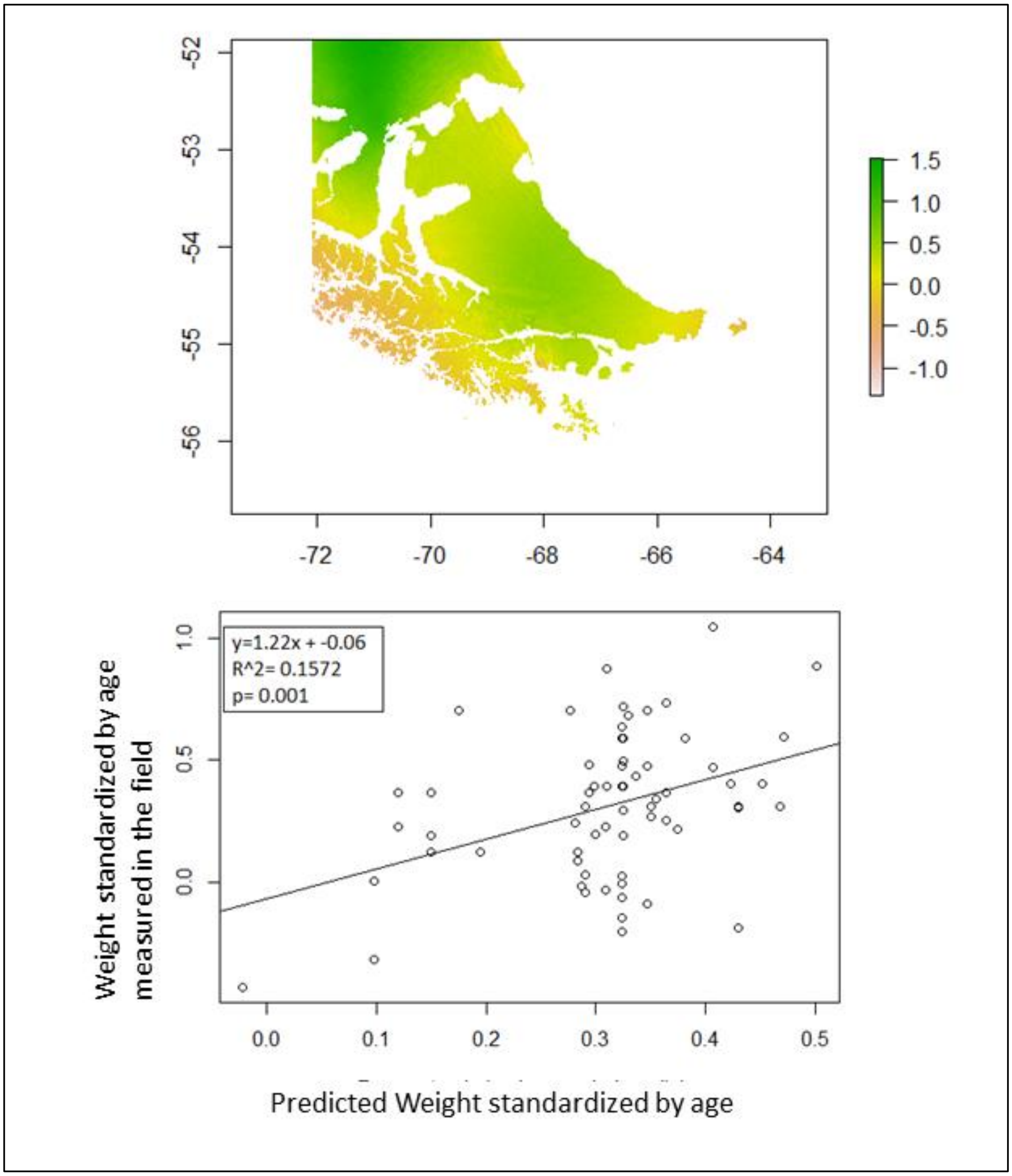

Fig. 3 Map showing the predicted weight standardized by age for beavers on Tierra del Fuego and Magallanes provinces and a graph showing the performance of the model at predicting the values encountered in the field.

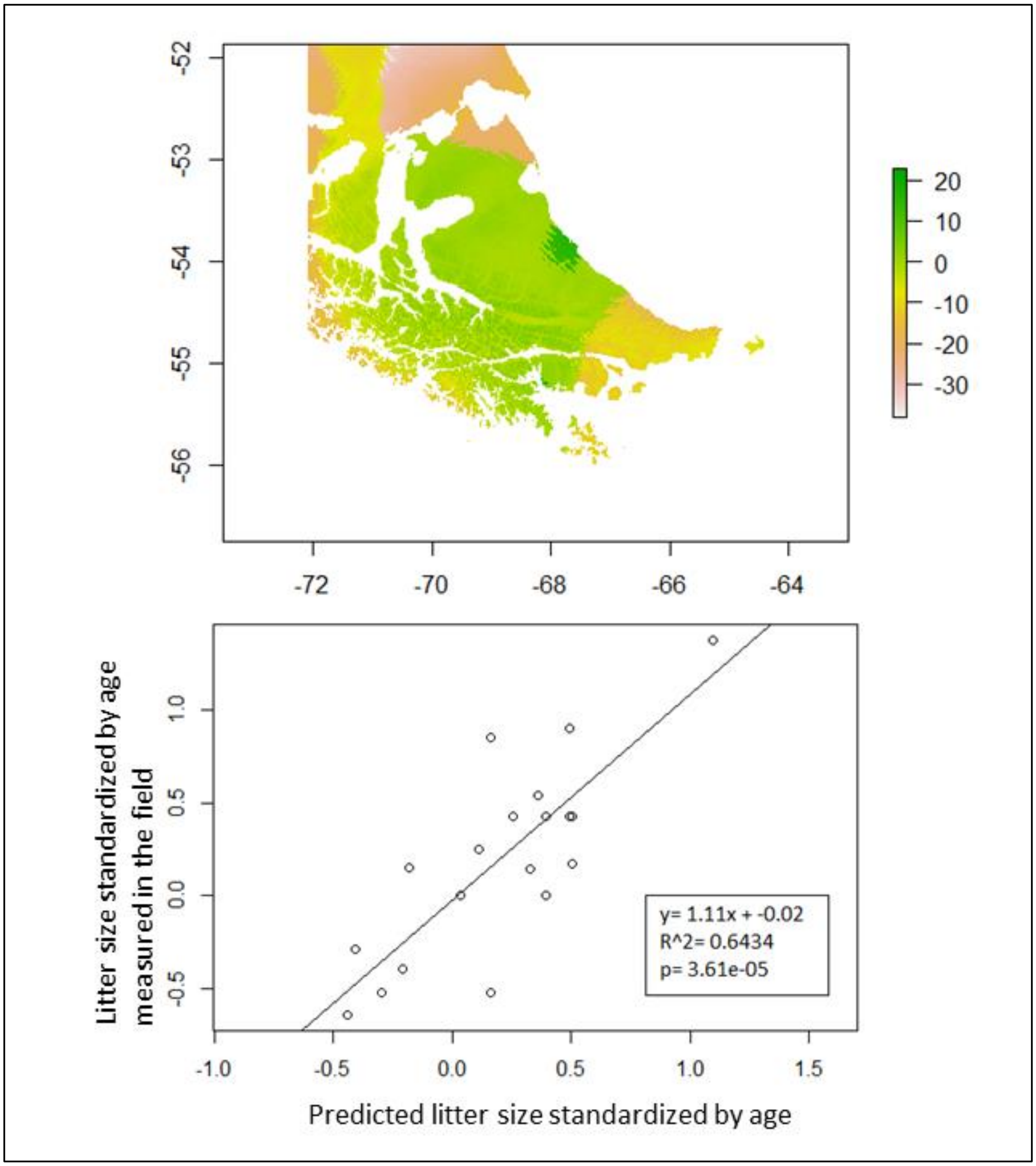

Fig. 4 Map showing the predicted litter size standardized by age for beavers on Tierra del Fuego and Magallanes provinces and a graph showing the performance of the model at predicting the values encountered in the field.

3.9 Tables

Table 1 Results of Linear regressions showing the R squared and p values; and Quantile Regressions showing the slope for the 80th, 85th, 90th and 95 quantile. All showing the relationship between presence probability and suitability index predicted by seven niche modeling algorithms and two measures of performance (Standardized weight and litter size).

		OLS		**Quantile Regression slope**			
SDM	**AUC**	**R squared**	**P**	**80th**	**85th**	**90th**	**95th**
Bioclim weight	0.939	-0.014	0.729	0	0.358	-0.102	-0.580
Bioclim litter size		-0.050	0.7	-0.495	-1.126	0.206	-2.321
Domain weight	0.931	0.008	0.223	-0.652	-0.413	-0.226	-0.710
Domain litter size		-0.046	0.657	0.790	-4.003	-4.717	-8.289
GLM2 weight	0.948	0.086*	0.018	-2.478*	-1.984	-2.368	-1.963
GLM2 Litter size		0.030	0.480	-4.064	-4.064	-5.638	10.515
GLM1 weight	0.949	0.098*	0.011	-0.171	-0.144	-0.164	-0.129
GLM1 Litter size		0.057	0.323	0.073	-0.188	0.060	0.371
GAM weight	0.948	0.086*	0.018	-2.479*	-1.972	-2.370	-1.966
GAM Litter size		0.0297	0.481	-4.046	-4.046	-5.603	10.540
Maxent weight	0.967217	0.0330	0.147	-0.236*	-0.119	-0.477	-0.539
Maxent Litter size		0.001	0.885	-1.485	-0.927	1.318	-2.581
SVM weight	0.941	0.016	0.312	-0.882	-0.404	0	0.676
SVM Litter size		0.0001	0.959	-2.638	-2.909	-3.068	-5.337

Table 2 GLM models selected by AICc to show the best performance in predicting weight (kg) standardized by age for invasive *Castor canadensis*. All factors are presented with their parameters, significance, AICc, Chi squared values, and significance for the whole model.

		Factors								**Model**			
	Intercept	**Bio3**	**Bio4**	**Bio8**	**Bio11**	**Bio15**	**Bio17**	**Fa**	**Slope**	**AICc**	**CHI**	**GL**	**p**
Model 1	-2.444*	NS	1.3e-03*	NS	NS	-5.4e-02	NS	NS	1.4e-04*	25.35	4.75	61	1
Model 2	-2.247	NS	1.3e-03*	NS	NS	-5.8e-02*	NS	4.8e+41	1.4e-04*	26.30	4.64	60	1
Model 3	-1.678	NS	6.9e-04	NS	NS	NS	NS	NS	1.5e-04*	26.98	5.04	62	1
Model 4	2.250*	NS	NS	NS	NS	-7.4e-02*	-6.9e-03*	NS	1.4e-04*	27.01	4.87	61	1
Model 5	-2.686*	NS	0.001**	NS	NS	-0.050*	NS	NS	NS	27.25	5.07	62	1
Model 6	-2.259	NS	NS	1.03e-01*	-9.4e-02*	-8.5e-02	NS	NS	1.2e-04	27.31	4.71	60	1
Model 7	-4.092	2.8e-02	1.4e-03**	NS	NS	-5.1e-02	NS	NS	1.3e-04	27.34	4.71	60	1

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’

NS: Not selected.

Table 3 GLM models selected by AICc to show the best performance in predicting litter size standardized by age for invading *Castor canadensis*. All factors are presented with their parameters, significance, AICc, Chi squared values, and significance for the whole model.

	Factors							Model			
	Intercept	**Bio3**	**Bio4**	**Bio8**	**Bio11**	**Bio15**	**Bio17**	**AICc**	**CHI**	**GL**	**P**
Model 1	38.54***	NS	-0.01 *	-0.64 **	0.45**	0.60 **	-0.04 **	30.47	1.55	13	0.99
Model 2	0.72	0.21	NS	-0.52**	0.37 **	0.68**	NS	30.95	2.09	14	0.99
Model 3	23.85**	NS	NS	-0.77**	0.61**	0.60**	0.07	31.55	2.15	14	0.99
Model 4	12.42**	NS	NS	-0.55**	0.40**	0.63**	NS	31.64	2.72	15	0.99

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’

NS: Not significant

IV. LA ESTRUCTURA DE LA ADECUACIÓN BIOLÓGICA DENTRO DEL RANGO DEL CASTOR NORTEAMERICANO (*CASTOR CANADENSIS*), UNA ESPECIE INVASORA EN LA ISLA DE TIERRA DEL FUEGO

THE STRUCTURE OF FITNESS WITHIN THE RANGE OF AMERICAN BEAVER (CASTOR CANADENSIS), AN INVASIVE SPECIES ON THE ISLAND OF TIERRA DEL FUEGO

Derek Corcoran[1], Giorgia Graells[2], Fabián M. Jaksic[1]

1. Center of Applied Ecology & Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
2. Universidad de Magallanes. Instituto de la Patagonia, Punta Arenas, Chile

*****Corresponding authors: e-mail: derek.corcoran.barrios@gmail.com

4.1 Summary

1. Within the study of the range of species, one of the least studied aspects is the internal structure of the distribution. The spatial structure of abundance within a species' range has been studied but the spatial structure of fitness has not.
2. The purpose of this work is to study the fitness of invasive species *Castor canadensis*, determining the frequency distribution of fitness and its spatial relationships within its range.
3. Beavers were sampled in Tierra del Fuego and its performance was measured from uterine scars and weight. The performance was standardized by age and GLM models were developed to predict their performance under different environmental conditions. A minimum convex polygon was generated using the sampled points, the GLM were projected within those polygons. Frequency distribution was measured for each performance measurement, using field data and data generated by the models. The generated distributions were fitted to theoretical models of distribution by nonlinear regression and the best models were selected based on AIC values.
4. The distributions of female fitness modelled and measured in the field, and the weight measured in the field correspond to generalized trapezoidal distributions with platykurtic and symmetrical features. The distribution for the modelled weight corresponds to a Johnson SU distribution with leptokurtic and symmetrical features. Both models exhibit high spatial autocorrelation, however the performance measured by female fertility is more variable than the model of weight since it has a higher coefficient of variation and multimodal features.

5. This is the first study in which the internal structure of the distribution of a species through fitness is described. The theoretical distributions that fit these patterns are different from those found previously for abundance. However, this could be explained by density dependence models which would show that the pattern detected for Beaver generate the abundance distribution reported for other species, with the concordant results.

4.2 Introduction

Most of the research on the range of species are focused on the study and determination of its limits and what generates these ecological frontiers (presented for the first time by Merriam 1895). These studies have shown that the limits of the range are complex, they have discontinuities, shifting depending on the time of year and evolving over time in ways that are difficult to predict (MacArthur 1984; Gorodkov 1986; Caughley *et al.* 1988; Grubb 1989). The range limits of a species may be due to climatic factors (Merriam 1895; Hutchinson 1918; Root 1988), other abiotic barriers such as pH, slope, heavy metals, presence of rivers or seas (MacArthur 1984; Gaston 2003), and biotic factors like the presence of competitors or predators, or absence of preys or mutualists (Darwin 1859; Davis *et al.* 1998; Quinn, Gaston & Roy 1998; Bullock *et al.* 2000).

The study of the geographic ranges of species is key to answer basic questions of ecology, as are explaining the abundance and biodiversity of organisms in the context of the environment (May 1999). Furthermore the understanding of the patterns that explain the distribution of species, has potential for the management of invasive or endangered species conservation as it would allow to predict and/or understand: the effect that global warming will have on the distribution of certain species (Walther *et al.* 2002; García-Valdés *et al.* 2013; Parmesan *et al.* 2013); which is the best way to generate protected areas (Graham & Hijmans 2006; Thomas *et al.* 2012); and even determine which species will be invasive and what will be its potential distribution(Peterson 2003; Jiménez-Valverde *et al.* 2011).

However, few studies have dealt with the internal structure of the distribution range of species, and when this has been done, it has been based on abundance data (MacArthur 1984; Brown, Mehlman & Stevens 1995; Brewer & Gaston 2002; Gaston 2003; Sagarin, Gaines & Gaylord 2006). As for the abundance patterns, it has been observed repeatedly that there are many places with few individuals, and few places with high abundance, that is the distribution of abundance is strongly and positively skewed. This pattern has been found in insects, birds, mammals and other groups and at scales ranging from a few square meters to the entire European continent (Anscombe 1949; Bliss & Fisher 1953; Taylor, Woiwod & Perry 1978; Perry, Taylor & Kemp 1988; Root 1988; Brown *et al.* 1995; Brewer & Gaston 2002; Gaston 2003).

The abundance of a species within its range depends on factors such as immigration, emigration, death and birth. While abundance is a function of fitness, they do not necessarily have the same behavior in terms of frequency, because in locations of high abundance, where conditions are ideal for the reproduction of a species, density dependence can generate low reproductive outputs (Watkinson & Sutherland 1995).

Some of the most important factors affecting biological fitness are the genotype of the individual, the environment in which the organism develops, intraspecific competition

(Watkinson & Sutherland 1995) and interspecific interactions. The *Castor canadensis* population in South America, after its introduction in 1946 has unique features to study this phenomenon. On the one hand, we know that the genetic diversity of the beavers in Tierra del Fuego is low (Fasanella 2012), also, intraspecific competition in beavers is preemptive which prevents density-dependent effects on female fertility (Bergerud & Miller 1977; Houlihan 1989; Welsh & Muller-Schwarze 1989b) and as for interspecific interactions it appears that in Tierra del Fuego beavers lack natural enemies and direct competitors (Wallem *et al.* 2007; Anderson *et al.* 2009), This coupled with the fact that individuals of this species spend most of their life in the same lodge (Muller-Schwarze & Sun 2003) makes the fitness that we observed in the field almost exclusively dependant on the environment in which they were sampled.

The range and fitness have not been thoroughly studied simultaneously and so far the question of how fitness is structured within the range of a species has not been answered. In this paper the structure of fitness within the range of the invader American beaver on the Chilean side of Tierra del Fuego is studied.

4.3 Methods

Study site

This study was conducted on the Chilean side of Tierra del Fuego Island (TDF), located in the southernmost tip of South America between parallels 52 and 55ºS (Figure 1). Its surface is 48,598 km^2, of which 22,592.7 km^2 correspond to the Chilean province of Tierra del Fuego.

This island has a strong pluviometric gradient ranging from 200 mm of rainfall in the northeast to 2,000 mm in the southwest, as well as strong winds from the west that may reach 160 km/hour (Endlicher & Santana 1988; Santana *et al.* 2006; Santana, Butorovic & Olave 2009).

Sampling for performance

Sampling took place in Tierra del Fuego from February 24th of 2010 to March 3rd 2011 with four different sampling periods, totaling 159 sampling days in 23 different rivers. Beavers were hunted using Connibear traps, and rifles according to Chilean law regulations. Every individual was weighted and sexed, if the beaver was female, the number of offspring bred during the last season was determined by counting uterine scars (Hodgdon 1949) and ,depending on the season, fetuses.

Age was determined by tooth development (Van Nostrand & Stephenson 1964; Larson & Van Nostrand 1968). Because beavers can live up to 20 years, performance measures have to be standardized by age. In order to do that we took averages for litter size for each determined age (Payne 1979, 1984) and considered them as expected values and applied formula 1 (we did not square the parenthesis because the sign needs to be revealed).

Formula 1:

$$Standardized\ performance\ = \frac{(Observed\ value - Expected\ value)}{Expected\ value}$$

If the standardized performance of a beaver is zero, then that beaver in Tierra del Fuego has the same performance as its Canadian counterparts. If, on the other hand, the standardized performance is above or below zero, then beavers in Tierra del Fuego perform better or worse than their Canadian counterparts respectively.

GLM

To predict the performance of beavers in South America 23 predictor layers were used. Four topographic layers were selected from the HYDRO 1K: Slope, Flow Accumulation, Digital elevation model and Compound topographic index (Data available from the U.S. Geological Survey). The remaining 19 bioclimatic layers were obtained from Pliscoff & Luebert 2013 and the nomenclature following Hijmans *et al.* 2005.

These layers were used to develop a predictive model for the performance standardized by age using GLM (Generalized Lineal Models). The glmulti package 1.0.7. (Calcagno & de Mazancourt 2010), was used to run an exhaustive analysis using all possible first order models for the 23 predictors and keeping the ones with the lower AICc (Corrected Akaike Information Criterion) (Hurvich & Tsai 1989). This method in addition to selecting the best models, deals with collinearity (Dormann *et al.* 2013).

In order to apply the model only to the sampled area, a minimum convex polygon analysis was performed using the R package *adehabitat* (Calenge 2006). Only the area inside these polygons was considered for further analysis.

Two independent polygons where constructed, one for the female fitness and another for weight, for females and total individuals, respectively.

Distribution fitting

Distribution fitting for female finess and weight were performed, for both field data as for the data obtained from modeling. The Propagate package was used (Spiess 2014) , this package fits 21 different continuous distributions by (weighted) NLS to the kernel density, the best fit is selected by AIC.

4.4 Results

A total of 65 beavers were captured, of the total, 27 were female. The mean number (±SD) of uterine scars for all female beaver was 2.46 ± 1.61. The mean (± SD) weight for beavers was 15.2 ± 4.1 kg. Five of the females sampled were in non-reproductive stage.

For litter size, the selected model (AICc = 23.80124) contains only bioclimatic layers (Table 1). The four selected layers were Annual Mean Temperature (Bio1), Mean Temperature of Wettest Quarter (Bio8), Precipitation of Driest Month (Bio14) and Precipitation Seasonality (Bio 15). The model was significant (P chisq= 0.99) and had a Nagelkerke R^2 of 0.65.

For weight, the selected model (AICc = 15.12469) contains both bioclimatic and topographic layers (Table 1). The bioclimatic layer is the Mean Temperature of Driest Quarter (Bio 9), while the topographic layers were Slope, Compound Topographic Index (CTI) and Digital Elevation Model (DEM). The model was significant (P chisq= 1) and had a Nagelkerke R^2 of 0.32.

The two polygons generated using the minimum convex polygon method have an area of 7407.75 km2 for litter size and 8908.11 km^2 for weight (Figures 1 and 2). The projection of the GLM model to the selected polygons shows contrasting results. In both models the mean of the performance is positive (0.52 for age-standardized litter size and 0.34 for the age-standardized weight). The projection of the number of offspring (Figure 3A) shows two areas of high fitness with values greater than 1.0, reaching a maximum of 2,421. Although most of the polygon presents values over 0, there are lower values with a minimum of -0.8885. For the weight model (Figure 3B), the resulting layer is a smooth surface with little relief, the maximum values for this model are of 0.857. The rest of the polygon has mostly values over 0, although its minimum value is -1.274.

The litter size model exhibits greater variability than the weight model, as seen by both the roughness of the relief (Figure 3A), as by their differing performance values (coefficients of variation of 125.02 and 54.15, respectively). Despite that, the Moran index of spatial autocorrelation was higher for the litter size (0.88) than it was for the weight model (0.84).

The best distributions fits for field and modelled data are presented for litter size and weight of beavers (Figure 4). All the distributions are symmetric, since they exhibit low values of skewness and similar values of means and medians (Table 2). For both the litter size measured in the field and for the modelled data within the polygon, the distribution that best fits the data is the generalized trapezoidal distribution (van Dorp & Kotz 2003). For the weight measured in the field the distribution that better fits the data is the generalized trapezoidal distribution, whereas the data modelled within the polygon fits the Johnson SU distribution (Johnson 1949). The three trapezoidal distributions are platykurtic and the Johnson SU distribution is leptokurtic (DeCarlo 1997). The values for each of the frequency distributions are presented in Table 2.

4.5 Discussion

This work is the first to our knowledge, in which the internal structure of the distribution of a species is shown through performance. The performance, measured by litter size and weight of a species, behaves very differently from the patterns found by various studies regarding the structure of abundance of a species within its range, where there was a large positive skewness (Anscombe 1949; Taylor *et al.* 1978; Perry *et al.* 1988; Mehlman 1994; Brown *et al.* 1995; Gregory & Blackburn 1998; Brewer & Gaston 2002; Gaston 2003). Despite this difference, the frequency distributions in both performance measures are consistent with models made from abundance distributions described above (Corcoran unpublished data), which suggests that the detected pattern of fitness are not different to the distributions described for the abundance of other species..

Although in our case study we found that the frequency distributions are unimodal (Figure 3) this does not translate directly to what happens spatially (Figure 2), where in particular for litter size we observe at least two performance peaks, which indicates that this area is at least bimodal, more similar to the spatial complexity of the structure of a species range proposed by Sagarin *et al.* 2006. This is in contrast to previous assumptions that propose unimodal structures with high performance in the center of the range and lower at the edges (MacArthur 1984; Gaston 2003).

The positive skewness described above for abundance, indicates that there are many sites where the species is absent or there are just a few individuals, and there are a few locations where there are many individuals. In contrast, for both measures of performance we found symmetric distributions indicating few places where performance is low, many places where performance is average and few places where performance is high. Therefore, there are important differences between the abundance data and performance data and it may have to do with not being able to measure performance in areas with zero abundance. While abundance is based on densities and considers points without individuals (inside and outside of the range, respectively), performance on the other hand can only be measured within the distribution range of the species.

Possibly, the distribution of fitness is distinct for different stages of a biological invasion. If we compare a species recently invading a new found habitat to another already established as the beaver, we believe that in the first case we would find that within the occupied range, it would have more individuals with high fitness than already established specie. If we consider that an exotic species has a better chance to become invasive if it reaches a favourable environment, it is expected then, that in the first stage of an invasion most of the individuals sampled would present high fitness and few would have low fitness. Thus, it would have a skewed distribution with a negative skewness. If this holds true, this tool is proposed to establish at what stage of an invasion is a species. Assuming an advanced stage of the invasion for the American beaver in South America.

4.6 Acknowledgments

Thanks to FONDAP 1501-0001 Centro de Estudios Avanzados de Ecología y Biodiversidad programs 2 and 8 for funding most of the research, as well as fund Nº1162-136-SE11 of SAG for complementary funding. Special thanks to all ranchers that allowed us to use their properties for our research. DC thanks CONICYT PhD Scholarship 2008.

4.7 References

Anderson, C.B., PASTUR, G., Lencinas, M.V., Wallem, P.K., Moorman, M.C. & Rosemond, A.D. (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.

Anscombe, F.J. (1949) The statistical analysis of insect counts based on the negative binomial distribution. *Biometrics*, **5**, 165–173.

Bergerud, A.T. & Miller, D.R. (1977) Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, **55**, 1480–1492.

Bliss, C.I. & Fisher, R.A. (1953) Fitting the negative binomial distribution to biological data. *Biometrics*, **9**, 176–200.

Brewer, A.M. & Gaston, K.J. (2002) The geographical range structure of the holly leaf-miner. I. Population density. *Journal of animal ecology*, **71**, 99–111.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Bullock, J.M., Edwards, R.J., Carey, P.D. & Rose, R.J. (2000) Geographical separation of two Ulex species at three spatial scales: does competition limit species' ranges? *Ecography*, **23**, 257–271.

Calcagno, V. & de Mazancourt, C. (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1–29.

Calenge, C. (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological modelling*, **197**, 516–519.

Caughley, G., Grice, D., Barker, R. & Brown, B. (1988) The edge of the range. *The Journal of Animal Ecology*, 771–785.

Darwin, C. (1859) *On the Origin of Species: By Means of Natural Selection*. Dover Publications.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600–612.

DeCarlo, L.T. (1997) On the meaning and use of kurtosis. *Psychological methods*, **2**, 292.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J. & undefined, others. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 027–046.

Van Dorp, S. & Kotz, S. (2003) Generalized trapezoidal distributions. *Metrika*, **58**, 85–97.

Endlicher, W. & Santana, A. (1988) El clima del sur de la Patagonia y sus aspectos ecologicos. Un siglo de mediciones climatologicas en Punta Arenas. *Anales del Instituto de la Patagonia*, **18**.

Fasanella, M. (2012) *Variabilidad Genética Espacial Y Ecología Molecular En Dos Especies de Roedores Del Archipiélago de Tierra Del Fuego: Ctenomys Magellanicus, Especie Nativa Y Castor Canadensis, Especie Invasora*. Doctoral thesis. Universidad de Buenos Aires, Argentina.

García-Valdés, R., Zavala, M.A., Araujo, M.B. & Purves, D.W. (2013) Chasing a moving target: projecting climate change-induced shifts in non-equilibrial tree species distributions. *Journal of Ecology*, **101**, 441–453.

Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Gorodkov, K.B. (1986) Three-dimensional climatic model of potential range and some of its characteristics. II. *Entomological Review*, **65**, 1–18.

Graham, C.H. & Hijmans, R.J. (2006) A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, **15**, 578–587.

Gregory, R.D. & Blackburn, T.M. (1998) Macroecological patterns in British breeding birds: covariation of species’ geographical range sizes at differing spatial scales. *Ecography*, **21**, 527–534.

Grubb, P.J. (1989) Toward a more exact ecology: a personal view of the issues. *Toward a More Exact Ecology, 30th Symposium of the British Ecological Society* pp. 3–29.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**, 1965–1978.

Hodgdon, K.W. (1949) Productivity data from placental scars in beavers. *The Journal of Wildlife Management*, 412–414.

Houlihan, P.W. (1989) *Scent Mounding by Beaver (Castor Canadensis): Functional and Semiochemical Aspects*. State University of New York. College of Environmental Science and Forestry, Syracuse.

Hurvich, C.M. & Tsai, C.-L. (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Hutchinson, A.H. (1918) Limiting factors in relation to specific ranges of tolerance of forest trees. *Botanical Gazette*, 465–493.

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P. & Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. *Biological Invasions*, **13**, 2785–2797.

Johnson, N.L. (1949) Systems of frequency curves generated by methods of translation. *Biometrika*, 149–176.

Larson, J.S. & Van Nostrand, F.C. (1968) An evaluation of beaver aging techniques. *The Journal of Wildlife Management*, 99–103.

MacArthur, R.H. (1984) *Geographical Ecology*. Princeton University Press, Princeton, N.J.

May, R. (1999) Unanswered questions in ecology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **354**, 1951–1959.

Mehlman, D.W. (1994) Rarity in North American passerine birds. *Conservation Biology*, 1141–1145.

Merriam, C.H. (1895) Laws of temperature control of the geographic distribution of terrestrial animals and plants.

Muller-Schwarze, D. & Sun, L. (2003) *The Beaver: Natural History of a Wetlands Engineer*, 1 edition. Comstock Publishing Associates, Ithaca, N.Y.

Van Nostrand, F.C. & Stephenson, A.B. (1964) Age determination for beavers by tooth development. *The Journal of Wildlife Management*, 430–434.

Parmesan, C., Burrows, M.T., Duarte, C.M., Poloczanska, E.S., Richardson, A.J., Schoeman, D.S. & Singer, M.C. (2013) Beyond climate change attribution in conservation and ecological research. *Ecology letters*, **16**, 58–71.

Payne, N.F. (1979) Relationship of pelt size, weight, and age for beaver. *The Journal of Wildlife Management*, 804–806.

Payne, N.F. (1984) Reproductive rates of beaver in Newfoundland. *The Journal of wildlife management*, 912–917.

Perry, J.N., Taylor, L.R. & Kemp, A.W. (1988) Families of distributions for repeated samples of animal counts. *Biometrics*, 881–890.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly review of biology*, **78**, 419–433.

Pliscoff, P. & Luebert, F. (2013) A new improved dataset of climatic surfaces for Southern South America. URL http://www.unil.ch/ecospat/page89413.html [accessed 8 June 2014]

Quinn, R.M., Gaston, K.J. & Roy, D.B. (1998) Coincidence in the Distributions of Butterflies and Their Foodplants. *Ecography*, 279–288.

Root, T. (1988) Environmental factors associated with avian distributional boundaries. *Journal of Biogeography*, 489–505.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, **21**, 524–530.

Santana, A., Butorovic, N. & Olave, C. (2009) Variación de la temperatura en Punta Arenas (Chile) en los últimos 120 años. *Anales del Instituto de la Patagonia* pp. 85–96. SciELO Chile.

Santana, A., Porter, C., Butorovic, N. & Olave, C. (2006) Primeros Antecedentes Climatológicos de Estaciones Automáticas (AWS) en el Canal Beagle, Magallanes, Chile.

First climatologic Antecedents of Automatic Weather Stations (AWS) in the Beagle Channel, Magallanes, Chile. *Anales del Instituto de la Patagonia* pp. 5–20.

Spiess, A.-N. (2014) *Propagate: Propagation of Uncertainty*.

Taylor, L.R., Woiwod, I.P. & Perry, J.N. (1978) The density-dependence of spatial behaviour and the rarity of randomness. *The Journal of Animal Ecology*, 383–406.

Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A., Crick, H.Q., Findon, R.A., Fox, R. & others. (2012) Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences*, **109**, 14063–14068.

Wallem, P.K., Jones, C.G., Marquet, P.A. & Jaksic, F. (2007) Identificación de los mecanismos subyacentes a la invasión de *Castor canadensis* (Rodentia) en el archipiélago de Tierra del Fuego, Chile. *Revista chilena de historia natural*, **80**, 309–325.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Watkinson, A.R. & Sutherland, W.J. (1995) Sources, Sinks and Pseudo-Sinks. *The Journal of Animal Ecology*, **64**, 126.

Welsh, R.G. & Muller-Schwarze, D. (1989a) Experimental habitat scenting inhibits colonization by beaver, *Castor canadensis*. *Journal of chemical ecology*, **15**, 887–893.

Welsh, R.G. & Muller-Schwarze, D. (1989b) Experimental habitat scenting inhibits colonization by beaver, *Castor canadensis*. *Journal of Chemical Ecology*, **15**, 887–893.

4.8 Tables

Table 1 Estimates for the parameters in the GLM models for litter size and weight standardized by age.

Measures of performance	Bio1	Bio8	Bio9	Bio14	Bio15	Slope	CTI	DEM
Litter size	-0.529	0.456	NA	0.072	0.198	NA	NA	NA
Weight	NA	NA	0.009	NA	NA	0.002	0.001	0.001

Table 2 Characteristics of the frequency distribution for the litter size measured in the field and modelled by GLM, and for the weight measured in the field and modelled by GLM.

	Litter size Field	Litter size model	Weight Field	Weight Model
Distribution	Generalized Trapezoidal	Generalized Trapezoidal	Generalized Trapezoidal	Johnson SU
AIC	-3752.102	-6581.304	-5674.461	-4344.963
Mean	0.175	0.517	0.310	0.343
Median	0.154	0.470	0.311	0.356
Skewness	0.408	0.384	-0.038	-1.337
Kurtosis	0.508	-0.444	-0.176	6.331
N	19	12148	65	15018

4.9 Figures

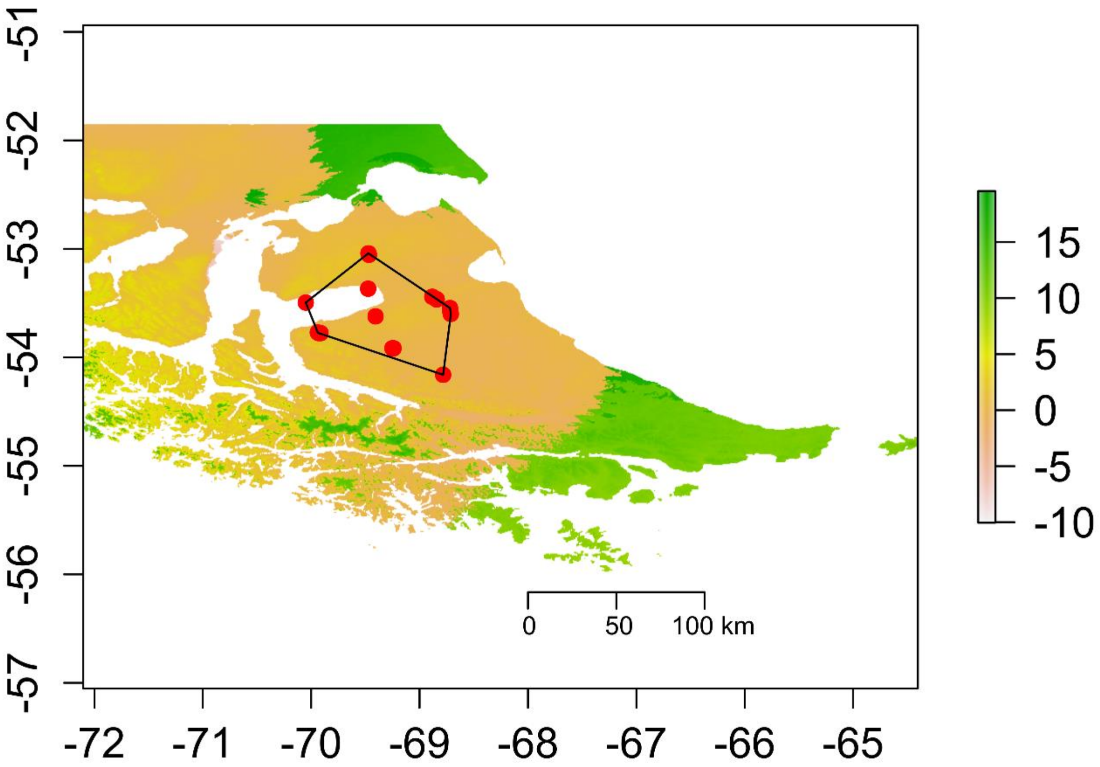

Figure 1 Study area located on the island of Tierra del Fuego. In red circles, the sampling points for litter size and represented by a solid line, the corresponding minimum convex polygon, in colours the litter size standardized by age predicted by the GLM.

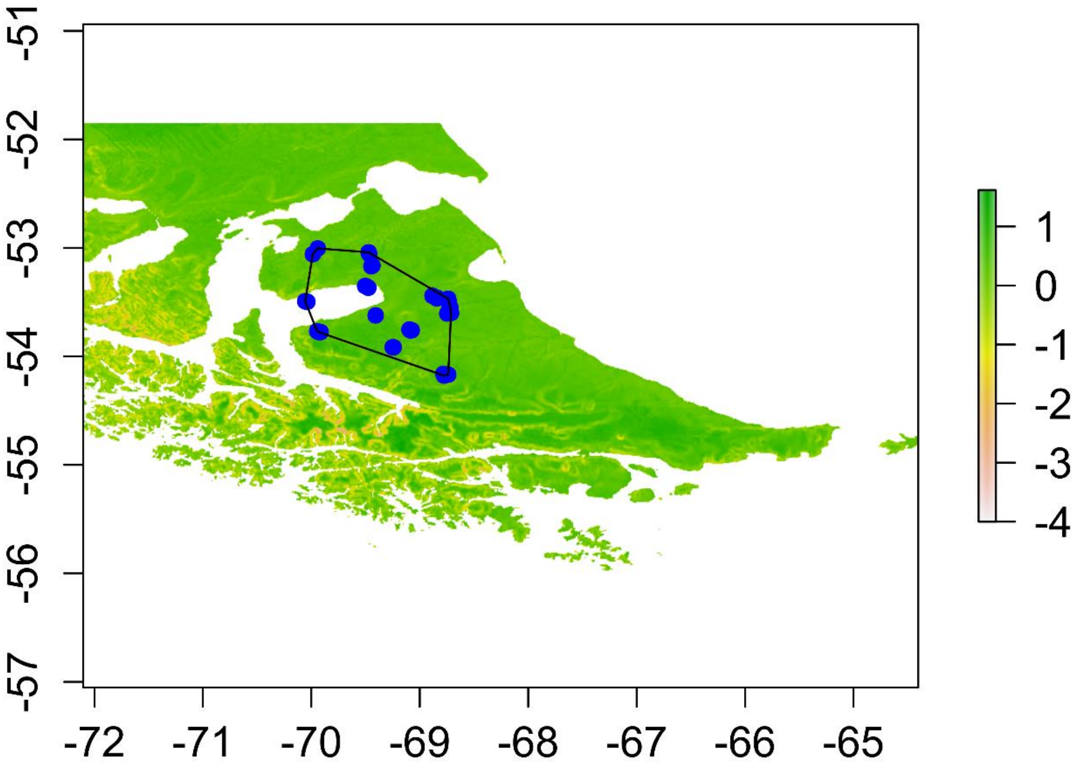

Figure 2 Study area located on the island of Tierra del Fuego. In blue circles, the sampling points for weight and the corresponding minimum convex polygon represented by a solid line, in colours the weight standardized by age predicted by the GLM model.

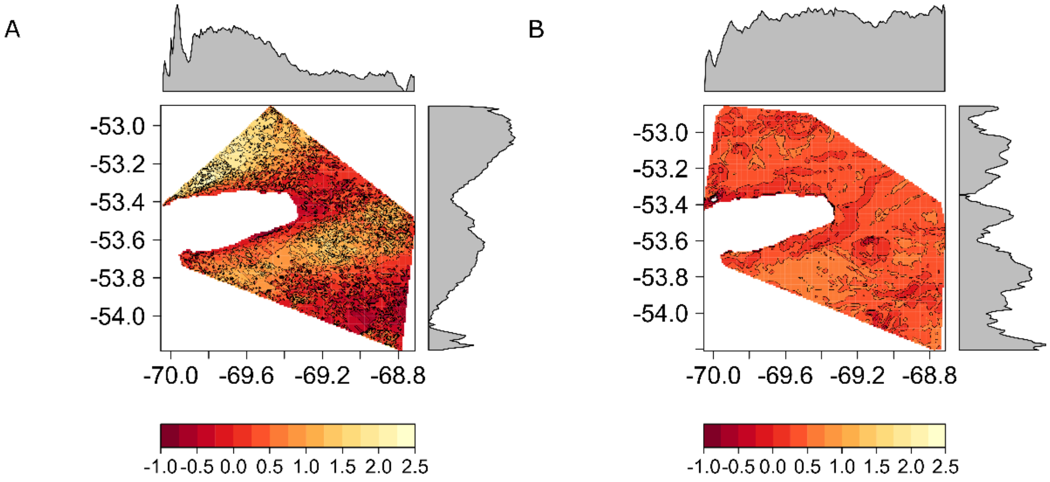

Figure 3 Layers generated by the projection of the GLM models within the selected polygon. A litter size standardized by age. B weight standardized for age.

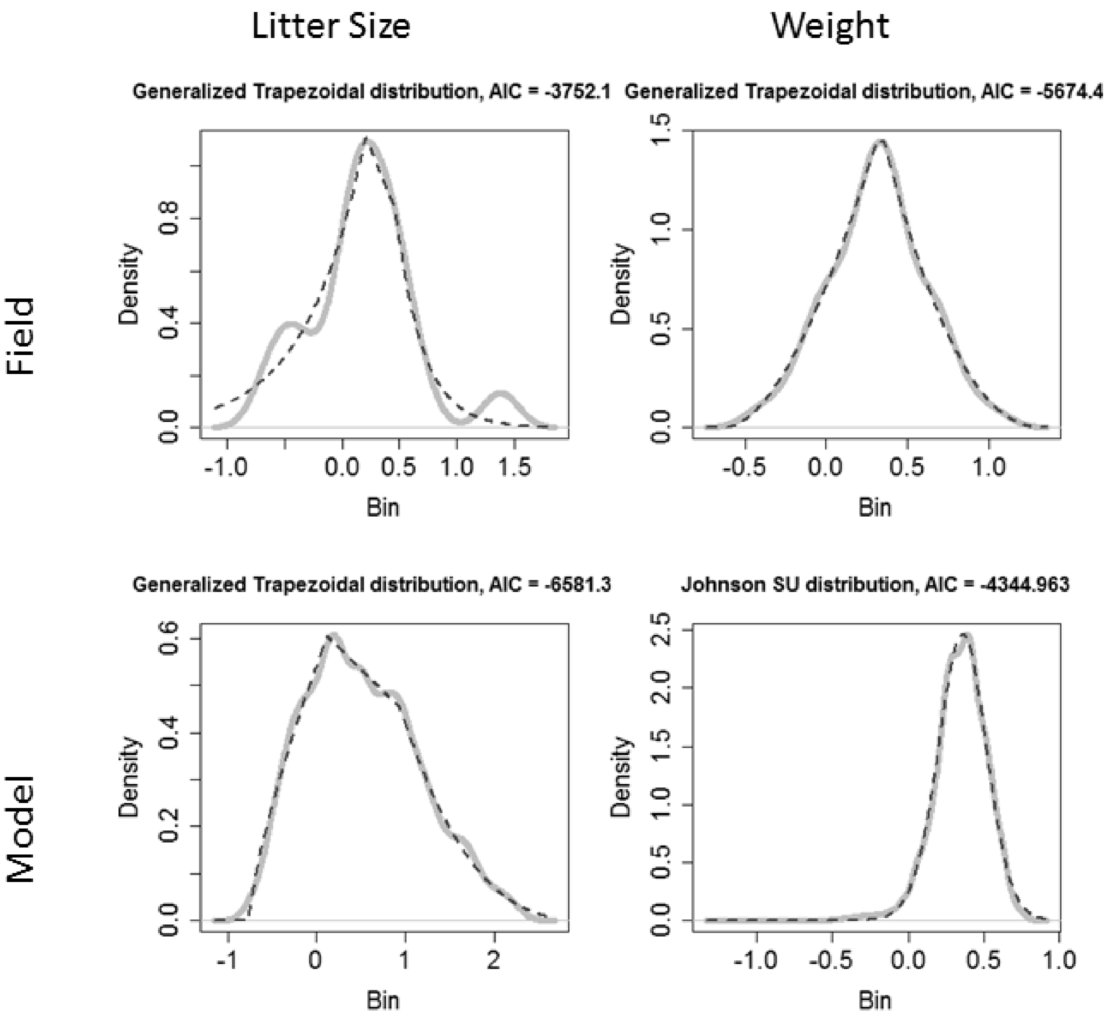

Figure 4 Graphics of the frequency distribution of the data observed in the field and generated by the model for litter size and weight standardized for age. The continuous grey line represents the Kernel density estimation for the data and the dashed black line represents the best theoretical fit to these data. Each graph shows the selected distribution and the corresponding AIC.

V. DISTRIBUCIÓN POTENCIAL Y DISPERSIÓN DE LA ESPECIE INVASIVA *CASTOR CANADENSIS* EN SUDAMÉRICA UTILIZANDO MODELOS DE CONECTIVIDAD ELÉCTRICA Y ADECUACIÓN BIOLÓGICA ESPACIALMENTE EXPLÍCITA

POTENTIAL DISTRIBUTION AND DISPERSAL OF INVASIVE CASTOR CANADENSIS IN SOTH AMERICA USING ELECTRICAL CONNECTIVITY AND SPATIALLY EXPLICIT FITNESS MODELS

Derek Corcoran[1], Giorgia Graells[2], Fabián M. Jaksic[1]

1. Center of Applied Ecology & Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
2. Universidad de Magallanes. Instituto de la Patagonia, Punta Arenas, Chile

Corresponding author: e-mail: derek.corcoran.barrios@gmail.com

Short title: Potential distribution and dispersal of invasive North American beaver in South America.

5.1 Abstract

Aim: To make a spatially explicit model of fitness for the North American beaver in South America, and to use it as a connectivity layer in order to model the dispersal routes of the species in its potentially invasive range.

Location: Southern South America

Methods: The uterine scars of 27 female beavers from Tierra del Fuego were counted; the age of each beaver was determined via tooth development. The number of offspring for each female was then standardized by age using data from North America.

A GLM model was developed with bioclimatic and topographic layers used as predictors for litter size, then it was determined where beavers would have one or more offspring or fewer than one (on average). The first condition was labeled as a potential source, and the latter as a potential sink. The layer developed by the GLM was used in combination with river and freshwater layers in order to model the most plausible dispersal routes for beavers in the South American continent.

Results: Most of the areas where beavers can reproduce are in Chile. This species should be able to colonize South America at least up to 43°S of latitude. Possible barriers include the southern Patagonian Ice Field and the decrease in precipitation during the dry season going north. The migration route passes through many of the known presence points of beavers in the continent showing the validity of the model.

Main conclusions: The model developed in this research is accurate and a good representation of this species' biology in its invasive range. There is a need to incorporate the permeability of saltwater for beavers in order to develop a full model of the dispersal of this species in South America. This model can be used to develop more focused surveys to find and control beavers in South America, and in turn, the results of management actions can serve as a feedback to further improve the model.

Keywords: Beaver, Connectivity models, invasion biology, niche modelling, Patagonia, Tierra del Fuego

5.2 Introduction

The introduction of alien species and their subsequent invasion potential are among the most discussed topics in ecology from its earliest descriptions (Darwin, 1859; Elton, 1958). From a scientific point of view, the arrival of a new species to an ecosystem is an opportunity for research, both in ecological and evolutionary terms (Darwin, 1859; Jaksic, 2000; Daleo et al., 2009). In addition, biological invasions represent an issue of great importance in conservation biology, as they have been blamed for the loss of biodiversity (Sala et al., 2000; Vázquez, 2002), and large economic losses (Pimentel et al., 2000; Curtis & Jensen, 2004).

The north American beaver (*Castor canadensis* (Kuhl 1820)) is a rodent native to most of North America and invasive in Europe, South America, and Asia (Lahti & Helminen, 1974; Danilov & Kan’shiev, 1983; Lizarralde et al., 1993; Danilov, 1995; Nummi, 1996; Saveljev & Safonov, 1999; Anderson et al., 2009). In South America beavers were introduced to the Argentinean side of Tierra del Fuego Island in 1946 by the Argentinean Navy, which released

25 pairs into the Claro River near Fagnano Lake (Lizarralde at al., 1993; Jaksic, 1998; Anderson et al., 2009). Since then, beavers have occupied the entire Fuegian Archipelago, including Chilean Tierra del Fuego, Navarino, Hoste, Dawson, Picton, Nueva, Lennox, and Gordon Islands, encompassing at least 56,858 km^2 (Skewes et al., 2006; Menvielle et al., 2010). The estimated population size for this species is of approximately 65,000 to 100,000 individuals on the entire Tierra del Fuego Island, and around 41,000 individuals just on the Chilean side of that island (Skewes et al., 1999; Choi, 2008; Parkes et al., 2008). Due to rapid expansion of this invasion, we consider this estimated population size as conservative, assuming that it has increased in the past 14 years. In North America, beavers prefer and perform better in forests (Retzer, 1956; Howard & Larson, 1985; Beier & Barrett, 1987; Dieter & McCabe, 1989; McComb et al., 1990; Robel et al., 1993; Busher, 1996; Curtis & Jensen, 2004), even though they can inhabit a vast array of environments (Hill, 1982; Novak, 1987; Robel et al., 1993; Baker & Hill, 2003; Muller-Schwarze & Sun, 2003).

Beavers have a profound effect on the sub-Antarctic ecosystems, including altering the dynamics of succession in riparian forests, mainly due to the flooding caused by this species (Anderson et al., 2006; Martínez Pastur et al., 2006). In riverine forest sites abandoned by beaver, there is a replacement of the forest by a meadow primarily composed of exotic species (Anderson et al., 2006; Martínez Pastur et al., 2006). Until 1999 it was estimated that 50,000 hectares of forest were affected by beaver, considering only the Chilean side of Tierra del Fuego (Skewes et al., 1999).

Despite there being a map of migration for beavers in the Fuegian archipelago and part of the continent, obtained thought interviews (Skewes et al., 2006; Anderson et al., 2009), a recent study focused on continental Brusnwick Peninsula using cross dating through dendrochronology, indicates that the human community perception is unrelated to the actual date of arrival of these animals. Indeed, that study changes the date of arrival of beavers to the continent from 1994 back to 1968 (Graells, 2014). In parallel, the northernmost presence point of beavers in the continent, is now set at the Hollemberg River, approximately 200 km north of the previously reported most proximate point in Brunswick Peninsula.

Given the problems caused by beaver in South America and recent results showing that detection has been suboptimal (Graells, 2014), it is now necessary to predict the maximum distribution that this species can achieve in South America and generate possible migration paths to perform more targeted survey efforts. In order to do this, we will use both spatially explicit fitness models and migration models based in electric theory (McRae et al., 2008; van Etten, 2012) to estimate the possible routes of Beaver towards the north of the South American continent.

5.3 Methods

Study site

This study was conducted on the Chilean side of Tierra del Fuego Island (TDF), and the Magallanes province on the Chilean mainland (Figure 1). TDF is located in the southernmost tip of South America between parallels 52 and 55ºS. Its surface is 48,598 km^2 of which 22,592.7 km^2 correspond to the Chilean province of Tierra del Fuego. The Magallanes province has an area of 36,400.8 km^2 and is bordered by the Tierra del Fuego province to the east and south. The whole region has a strong pluviometric gradient going from 200 mm of rainfall in the northeast to 2,000 mm in the southwest, as well as strong winds from the west that may reach 44.44 m• s^{-1} (Endlicher & Santana, 1988; Santana et al., 2006, 2009).

Sampling

Sampling took place on Chilean Tierra del Fuego from February 24th 2010 to March 3rd 2011 encompassing four different sampling periods, totaling 159 sampling days and 23 different rivers. Beavers were hunted using Connibear traps, and rifles according to Chilean law regulations, The number of offspring bred during the last season was determined by counting uterine scars (Hodgdon, 1949) and --depending on the season-- fetuses.

Age was determined by tooth development (Van Nostrand & Stephenson, 1964; Larson & Van Nostrand, 1968). Because beavers can live up to 20 years, performance measures have to be standardized by age. In order to do that we took averages for litter size for each determined age (Payne, 1984) and considered them as expected values and applied formula 1 (we did not square the parenthesis because the sign needs to be revealed).

Formula 1:

$$Standardized\ performance = \frac{(Observed\ value - Expected\ value)}{Expected\ value}$$

GLM

To determine the performance of beavers in South America, 23 predictor layers were used. Four topographic layers were selected from the HYDRO 1K: Slope, Flow accumulation, Digital elevation model, and Compound topographic index (Data available from the U.S. Geological Survey). The remaining 19 bioclimatic layers were obtained from Pliscoff & Luebert (2013) and the nomenclature followed Hijmans et al. (2005).

The above layers were used to develop a predictive model for the performance standardized by age using GLM (Generalized Linear Models). The glmulti package 1.0.7. (Calcagno & de Mazancourt, 2010), was used to run an exhaustive analysis to all possible first order models for the 23 predictors and keeping the ones with the lower AICc (Corrected Akaike's Information Criterion (Hurvich & Tsai, 1989). This method, in addition to selecting the best models, deals with the issue of collinearity (Dormann et al., 2013).

The model selected by AICc consists of four variables (Table 1). From this model the potential litter size standardized by age was predicted for each point on the map. After this, a layer was generated by predicting the litter size for beavers at the maximum reproduction age (Payne, 1984) (9-10 years and 3.5 offspring per year). Every pixel of the layer where the model predicted that beavers could have one or more offspring was determined to be a potential establishment or a dispersant source. On the other hand, the points of the map that predicted that beavers would produce less than one offspring (on average) was determined to be a location which will not produce invasive beavers.

To assess the migration paths, the map created above was used as a voltage layer (McRae et al., 2008), which represents the probability that random walkers will leave any point on the map. As beavers disperse from their parents' lodge through bodies of water and only move overland if they cannot find an unoccupied site in their home water course (Beer, 1955; Leege, 1968; Van Deelen & Pletscher, 1996; Sun et al., 2000; Muller-Schwarze & Sun, 2003), we multiplied each pixel of the aforementioned layer by ten when it was a part of a river, lake, or lagoon, thus representing a layer of voltage times conductance (McRae et al., 2008). We extracted the areas where were ice fields where present, because beavers are not able to move across them (Lliboutry, 1988). The San Pedro river, which represents the oldest dated site in the South American continent (Graells, 2014) was set as the starting point of the migration (Starting Node). The other two nodes used for the models were the Hollemberg River (northernmost point of confirmed presence of beaver Intermediate Node), and the northernmost point where beavers could have a source population according to the GLM model (Terminal Node). The *gdistance* package (van Etten, 2012) was used to calculate the paths of least cost from San Pedro River to the terminal node with and without passing through the Hollemberg River.

5.4 Results

Sixty-six beavers were sampled, all of them on the Chilean side of Tierra del Fuego. Of these, 27 were female (Figure 1). The mean number (±SD) of uterine scars for all female beavers was 2.46 ± 1.61.

The model selected by AICc requires only climatic layers to predict the fitness of beavers; topographic layers were not selected. The four selected layers were Annual mean temperature, Mean temperature of wettest quarter, Precipitation in the driest month, and Precipitation seasonality. The model had a good fit (Nagelkerke pseudo R^2= 0.65, Pchisq= 0.99).

The projected map generates two discontinuous areas that can be source populations of beavers, separated by a non-suitable area for beaver reproduction (Figure 2). The first suitable area is located southwest of the continent, occupying the entire width of the continent up to the 52 ° S; from that point onwards it occupies a narrowing strip of land on the Pacific coast, and the northern limit of this source area is 44° S. The second area ranges from 42°S in the Atlantic coast of Argentina northward, with a minimum distance of 467 km between the two suitable areas, which is an order of magnitude larger than the longest migration registered by a beaver from its birthplace (Beer, 1955).

The connectivity analysis generates two paths shown in Figures 2 and 3. Both trajectories run overlapped for 358.97 km starting from the San Pedro River in the southeastern coast of the Brunswick Peninsula, and then cross it towards the northeastern coast. From that point onwards, the path stays relatively close to the border between Chile and Argentina. When both trajectories reach 51.75°S of latitude, they diverge (Figure 3). The least cost path continues in the northern direction for 59.74 km before intersecting again with the Hollemberg trajectory. The Hollemberg route turns southwest at the point of divergence and passes the Diana Lake (DL) and Balmaceda Lake to reach the Hollemberg River. Then it returns by the same lakes on its way north, covering 181.41 km before joining the path of least cost in latitude 51.36 °S.

After converging, both paths overlap by 1198.46 km on their way to the northernmost point where beavers can reproduce.

The least-cost path (using only the initial and terminal nodes) and the Hollemberg route overlap over 1557.43 km Both routes depart to a maximum distance of 32 km between them at the latitude of the intermediate node.

Both paths pass through confirmed presence points for beavers, such as the San Juan River and Parrillar Lagoon within the Brunswick Peninsula, without passing across any urban area. On the other hand, north of River Hollemberg, the model anticipates that beaver populations will disperse to populated areas such as Río Turbio and El Calafate in Argentina, and to Cerro Castillo, Torres del Paine, Villa O'Higgins, Chochrane and Puerto Aysen in Chile.

5.5 Discussion

Beavers are territorial animals (Aleksiuk, 1968; Welsh & Muller-Schwarze, 1989), the dispersal of subadults occurs in annual pulses (McNew & Woolf, 2005), and the juveniles --once established-- do not disperse again unless the local conditions are very unfavorable (Hill, 1982; Baker & Hill, 2003; Muller-Schwarze & Sun, 2003). It is therefore assumed that the offspring are the only dispersing agents. When building this model, each point on the map expresses the number of offspring that a beaver could have a under the conditions determined by the GLM. Because each offspring of a beaver dam must find a suitable area to settle in, it is expected that dispersal distance from a beaver lodge is proportional to the litter size generated each year. In the model this is expressed as a higher voltage, generating increased current (number of offspring). Water bodies, being preferred for the movement of the species, represent sectors of higher conductivity wherein the current moves with less resistance.

Territoriality and site fidelity of beavers have positive implications for the modeling of spatially explicit fitness. Because each individual spends most of its life in the same dam, and female fertility is density-independent (Bergerud & Miller, 1977), then the fitness of the sampled individuals depends mostly of the environmental quality, which would not happen with more vagile and migratory species.

According to the modeling results, the northernmost limit for establishing source beaver populations is at about 44° S. Because the literature has recorded a maximum dispersion for beavers of 49.6 km (Beer 1955), the migration to northern Chile could reach at the most 43°S, only managing to establish sink populations further up. The latter would fail to produce dispersing agents into the area where they could establish a second source population. Therefore, in South America, beaver populations would only be viable down to 43°S, while in its native habitat the lowest latitude in which it has been recorded is 25°N, in Mexico (GBIF, 2014). There are two possibilities as to why there are differences between the latitudes to which beavers reach in North America and what our model predicts for South America: 1) there is indeed a biological barrier for this species at this latitude in South America, which matches two predictive layers for the model (increase in mean annual temperature and decreased precipitation in the driest month), and 2) given that the model is an extrapolation, as we move away from the geographic area in which the sampling was performed, there may be higher probability of errors, which could result in latitudinal underestimates.

Another potential barrier is the southern Patagonian Ice Field, a large ice mass of approximately 13,000 km^2 (Aniya et al., 1996) which splits the suitable area for beaver reproduction at 50.60°S of latitude. This would force them to pass across many areas not suitable for reproduction (Figure 2). However, in the areas contiguous to the southern Patagonian Ice Field there are enough habitat patches where beavers could reproduce, making it still feasible for them to reach northern latitudes.

In addition, there is no information on how permeable marine areas and fjords are to beavers, making it difficult to estimate movements between the mainland and islands. But it is clear in Figure 1 that if saltwater is not a barrier for beavers, then it would be easier to go north using the islands in the fjords as stepping stones. Even if this model does not deal with saltwater areas, the sectors where the trajectory generated approaches the shoreline, could be considered more likely to become crossings into other bodies of land.

If we look at the path of least cost for beaver dispersal from the San Pedro River to the northernmost possible point for a source population, it passes at only 32 km of the Hollemberg River. Since this river is the northernmost confirmed point of presence of this species up to now, our model is biologically consistent with the potential for dispersal by this species (Beer, 1955) and the existing connectivity between the two points (Fig 3). Indeed, the proposed route for beaver dispersal passes through many known presence points of the species in the Brunswick peninsula.

Nevertheless, the failure to detect established groups of beavers between the Brunswick Peninsula and the Hollemberg River makes it difficult to validate the model. However, both routes run through uninhabited areas and away from vehicular routes until they reach the latitude of Hollemberg River. This limitations could not only explain the lack of beaver detection between these points, but by providing a likely dispersal route, it orients the possibility of a directed survey, something essential in areas of difficult access and low human population density like Patagonia.

Beyond the local issues concerning the invasion of the American beaver in Patagonia, the use of GLM models to explicitly project the fitness of a species in conjunction with models of connectivity could be promising for the study, management, and control of invasive species as well as for planning conservation strategies for endangered species. This methodology includes not only potential distribution, but also works with spatially explicit fitness patterns and dispersal routes, which gives a better picture of the species' biology. Also, since GLM models are easy to fit, any additional data obtained during management actions can be used as feedback to improve the model, which makes it ideal to work with the adaptive management recommended for invasive species (Berkes et al., 2000; Shea et al., 2002)

5.6 Acknowledgments

Thanks to FONDAP 1501-0001 Centro de Estudios Avanzados de Ecología y Biodiversidad programs 2 and 8 for funding most of the research, as well as fund Nº1162-136-SE11 of SAG for complementary funding. DC thanks CONICYT PhD Scholarship 2008. GG thanks CONICYT MSc Scholarship 2012.

5.7 Bibliography

Aleksiuk M. (1968) Scent-Mound Communication, Territoriality, and Population Regulation in Beaver (*Castor canadensis* Kuhl). *Journal of Mammalogy*, **49**, 759.

Anderson C.B., Griffith C.R., Rosemond A.D., Rozzi R., & Dollenz O. (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 C.B., PASTUR G., Lencinas M.V., Wallem P.K., Moorman M.C., & Rosemond A.D. (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.

Aniya M., Sato H., Naruse R., Skvarca P., & Casassa G. (1996) The use of satellite and airborne imagery to inventory outlet glaciers of the Southern Patagonia Icefield, South America. *Photogrammetric Engineering and Remote Sensing*, **62**, 1361–1369.

Baker B.W. & Hill E.P. (2003) Beaver (Castor canadensis). *Wild mammals of North America: biology, management, and conservation* (ed. by G.A. Feldhamer, B. Thompson, and J.A. Chapman), pp. 288–310. John Hopkins University Press, Baltimore.

Beer J.R. (1955) Movements of tagged beaver. *J. Wildl. Manage*, **19**, 492–493.

Beier P. & Barrett R.H. (1987) Beaver Habitat Use and Impact in Truckee River Basin, California. *The Journal of Wildlife Management*, **51**, 794.

Bergerud A.T. & Miller D.R. (1977) Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, **55**, 1480–1492.

Berkes F., Colding J., & Folke C. (2000) Rediscovery of traditional ecological knowledge as adaptive management. *Ecological applications*, **10**, 1251–1262.

Busher P.E. (1996) Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. *American Midland Naturalist*, 343–348.

Calcagno V. & de Mazancourt C. (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1–29.

Choi C. (2008) Tierra del Fuego: the beavers must die. *Nature*, **453**, 968–968.

Curtis P.D. & Jensen P.G. (2004) Habitat features affecting beaver occupancy along roadsides in New York state. *Journal of Wildlife Management*, **68**, 278–287.

Daleo P., Alberti J., & Iribarne O. (2009) Biological invasions and the neutral theory. *Diversity and Distributions*, **15**, 547–553.

Danilov P.I. (1995) Canadian and Eurasian beavers in Russian North-west (distribution, number, comparative ecology). 10–16.

Danilov P.I. & Kan’shiev V.Y. (1983) state of populations and ecological characteristics of European (*Castor fibe*r L.) and Canadian (*Castor canadensi*s Kuhl.) beavers in the northwestern USSR. *Acta Zoologica Fennica*, .

Darwin C. (1859) *On the Origin of Species: By Means of Natural Selection.* Dover Publications,

Van Deelen T.R. & Pletscher D.H. (1996) Dispersal characteristics of two-year-old beavers, *Castor canadensis*, in western Montana. *Canadian field-naturalist. Ottawa ON*, **110**, 318–321.

Dieter C.D. & McCabe T.R. (1989) Factors influencing beaver lodge-site selection on a prairie river. *American Midland Naturalist*, **122**, 408–411.

Dormann C.F., Elith J., Bacher S., Buchmann C., Carl G., Carré G., Marquéz J.R.G., Gruber B., Lafourcade B., Leitão P.J., & undefined others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 027–046.

Elton C.S. (1958) *The Ecology of Invasions by Animals and Plants.* University Of Chicago Press, Chicago.

Endlicher W. & Santana A. (1988) El clima del sur de la Patagonia y sus aspectos ecologicos. Un siglo de mediciones climatologicas en Punta Arenas. *Anales del Instituto de la Patagonia*, **18**, .

Van Etten J. (2012) R package gdistance: distances and routes on geographical grids. .

GBIF (2014) Available at: http://api.gbif.org/v0.9/map/point.html?&style=grey-blue&point=25.07669,-99.90083&lat=25.07669&lng=-99.90083&zoom=8.

Graells G. (2014) *Invasion de Castor canadensis en la provincia de Magallanes. Percepciones de la comunidad local contrastada con informacion de avance por datos dendrocronologicos.* Universidad de Magallanes, Punta Arenas.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**, 1965–1978.

Hill E.P. (1982) Beaver (*Castor canadensis*). *Wild mammals of North America: biology, management, and economics* (ed. by J.A. Chapman and G.A. Feldhamer), pp. 256–281. John Hopkins University Press, Michigan.

Hodgdon K.W. (1949) Productivity data from placental scars in beavers. *The Journal of Wildlife Management*, 412–414.

Howard R.J. & Larson J.S. (1985) A stream habitat classification system for beaver. *The Journal of wildlife management*, **49**, 19–25.

Hurvich C.M. & Tsai C.-L. (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Jaksic F. (2000) *Ecología de comunidades.* Ediciones Universidad Católica de Chile, Santiago, Chile.

Jaksic F.M. (1998) Vertebrate invaders and their ecological impacts in Chile. *Biodiversity & Conservation*, **7**, 1427–1445.

Lahti S. & Helminen M. (1974) The beaver *Castor fiber* (L.) and *Castor canadensis* (Kuhl) in Finland. *Acta Theriologica*, **19**, 177–189.

Larson J.S. & Van Nostrand F.C. (1968) An evaluation of beaver aging techniques. *The Journal of Wildlife Management*, 99–103.

Leege T.A. (1968) Natural movements of beavers in southeastern Idaho. *The Journal of Wildlife Management*, 973–976.

Lizarralde M.S. & undefined others (1993) Current status of the introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. *Ambio*, **22**, 351–358.

Lliboutry L. (1988) Glaciers of chile and Argentina. *Satelite image atlas of the world, South America, US, Geological survey professional paper 13861, I* (ed. by R. Williams and J. Ferrigno), pp. 109–206. US Government printing office,

Martínez Pastur G., Lencinas M.V., Escobar J., Quiroga P., Malmierca L., Lizarralde M., & Townsend P. (2006) Understorey succession in Nothofagus forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. *Applied Vegetation Science*, **9**, 143–154.

McComb W.C., Sedell J.R., & Buchholz T.D. (1990) Dam-site selection by beavers in an eastern Oregon basin. *Western North American Naturalist*, **50**, 273–281.

McNew J., LANCE B. & Woolf A. (2005) Dispersal and Survival of Juvenile Beavers (*Castor canadensis*) in Southern Illinois. *The American Midland Naturalist*, **154**, 217–228.

McRae B.H., Dickson B.G., Keitt T.H., & Shah V.B. (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, **89**, 2712–2724.

Menvielle M.F., Funes M., Malmierca L., Ramadori D., Saavedra B., Schiavini A., Volkart N.S., & undefined others (2010) American beaver eradication in the southern tip of South America: main challenges of an ambitious project. *Aliens: The Invasive Species Bulletin*, 9–16.

Muller-Schwarze D. & Sun L. (2003) *The Beaver: Natural History of a Wetlands Engineer*. Comstock Publishing Associates, Ithaca, N.Y.

Van Nostrand F.C. & Stephenson A.B. (1964) Age determination for beavers by tooth development. *The Journal of Wildlife Management*, 430–434.

Novak M. (1987) Beaver. *Wild furbearer management and conservation in North America* (ed. by M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch), pp. 283–312. Ashton-Potter Limited, Concord, Ontario, Canada.

Nummi P. (1996) Wildlife introductions to mammal-deficient areas: the Nordic countries. *Wildlife biology*, **2**, 221–226.

Parkes J.P., Paulson J., Donlan C.J., & Campbell K. (2008) Control of North American beavers in Tierra del Fuego: feasibility of eradication and alternative management options. *Landcare Research Contract Report LC0708. Available in Spanish at: www. tierradelfuego. gov. ar/s_desuamb/docs/erradica_castor. pdf and www. karukinkanatural. cl sives control*, .

Payne N.F. (1984) Reproductive rates of beaver in Newfoundland. *The Journal of wildlife management*, 912–917.

Pimentel D., Lach L., Zuniga R., & Morrison D. (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience*, **50**, 53–65.

Pliscoff P. & Luebert F. (2013) Available at: http://www.unil.ch/ecospat/page89413.html.

Retzer J.L. (1956) *Suitability of physical factors for beaver management in the Rocky Mountains of Colorado.* State of Colorado Department of Game and Fish, Robel R.J., Fox L.B., & Kemp K.E. (1993) Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. *Wildlife Society Bulletin*, 415–421.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., & undefined others (2000) Global biodiversity scenarios for the year 2100. *science*, **287**, 1770–1774.

Santana A., Butorovic N., & Olave C. (2009) Variación de la temperatura en Punta Arenas (Chile) en los últimos 120 años. 37, 85–96.

Santana A., Porter C., Butorovic N., & Olave C. (2006) Primeros Antecedentes Climatológicos de Estaciones Automáticas (AWS) en el Canal Beagle, Magallanes, Chile. First climatologic Antecedents of Automatic Weather Stations (AWS) in the Beagle Channel, Magallanes, Chile. 34, 5–20.

Saveljev A.P. & Safonov V.G. (1999) The Beaver in Russia and Adjoining Countries. *Beaver Protection, Management, and Utilization in Europe and North America* pp. 17–24. Springer,

Shea K., Possingham H.P., Murdoch W.W., & Roush R. (2002) Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications*, **12**, 927–936.

Skewes O., Gonzalez F., Olave R., Ávila A., Vargas V., Paulsen P., & König H.E. (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., González F., Rubilar L., Quezada M., Olave R., & ÁVILA V.V.Y.A. (1999) Investigación, aprovechamiento y control de castor (*Castor canadensis*) en las islas Tierra del Fuego y Navarino. *Informe Final. Servicio Agrícola y Ganadero (SAG) XII Región, Magallanes y Antártica chilena*, .

Sun L., Müller-Schwarze D., & Schulte B.A. (2000) Dispersal pattern and effective population size of the beaver. *Canadian Journal of Zoology*, **78**, 393–398.

Vázquez D.P. (2002) Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological invasions*, **4**, 175–191.

Welsh R.G. & Muller-Schwarze D. (1989) Experimental habitat scenting inhibits colonization by beaver, *Castor canadensi*s. *Journal of Chemical Ecology*, **15**, 887–893.

5.8 Figures

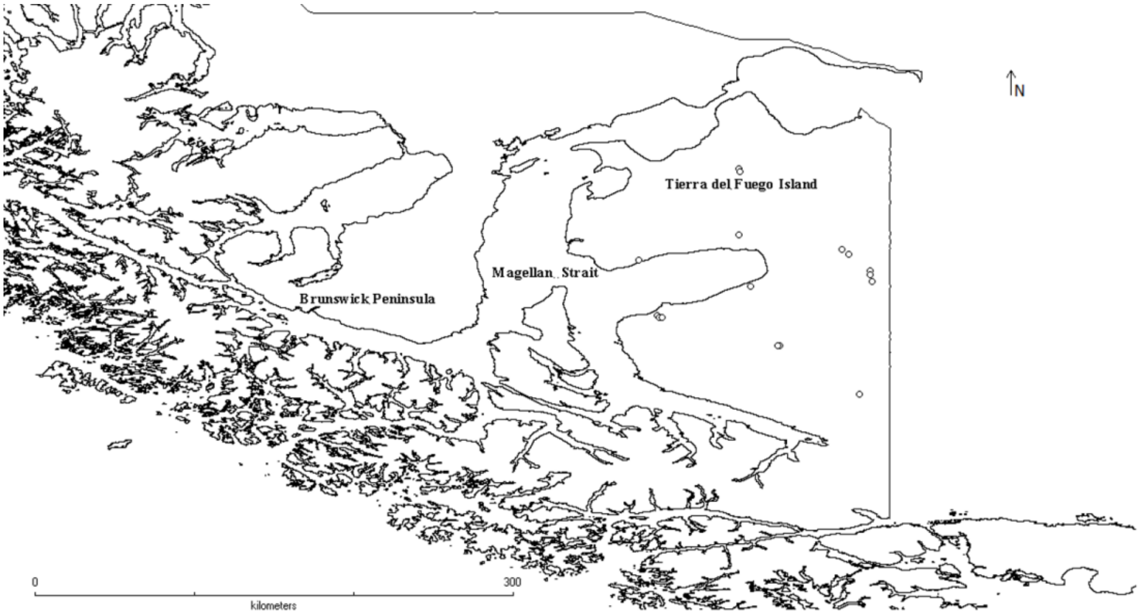

Fig. 1 Map with the sampling points for uterine scars from *Castor canadensis* females obtained from Tierra del Fuego Island.

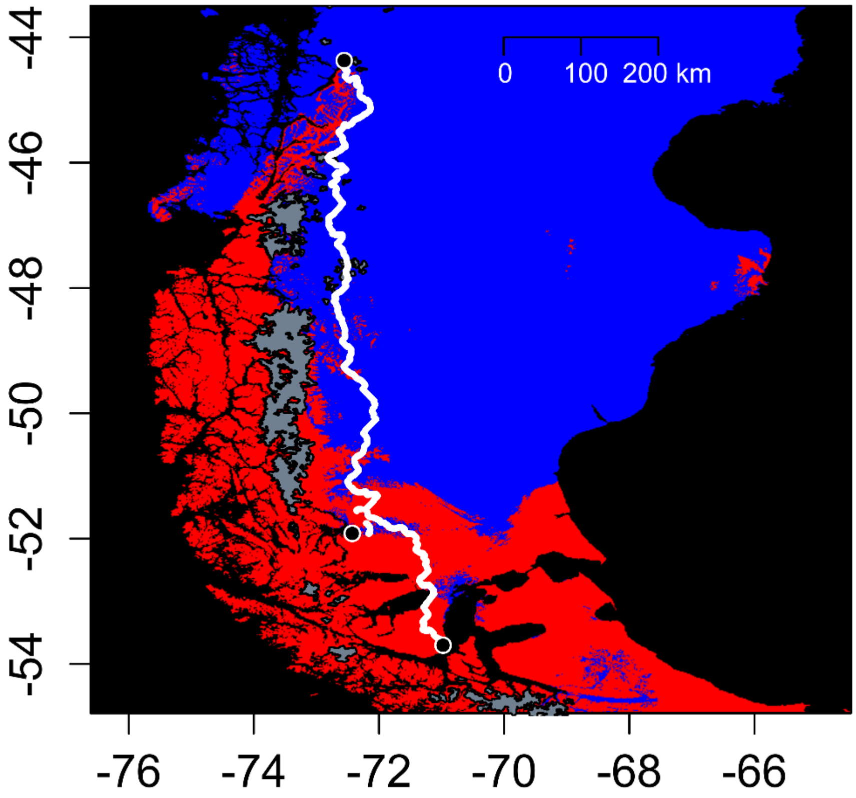

Fig. 2 Map of southern South America with the projection of the GLM model, where the red area represents where beavers can reproduce and blue areas where beavers cannot reproduce. The white lines correspond to paths traced by the model, the solid line represents the route of least cost, while the dashed line represents the same migratory movement but forcing the route to pass through the Hollemberg River. The areas in dark grey represent ice fields in South America and the black circles are from south to north: San Pedro River, Hollemberg River, and the northernmost point where beaver presence is possible.

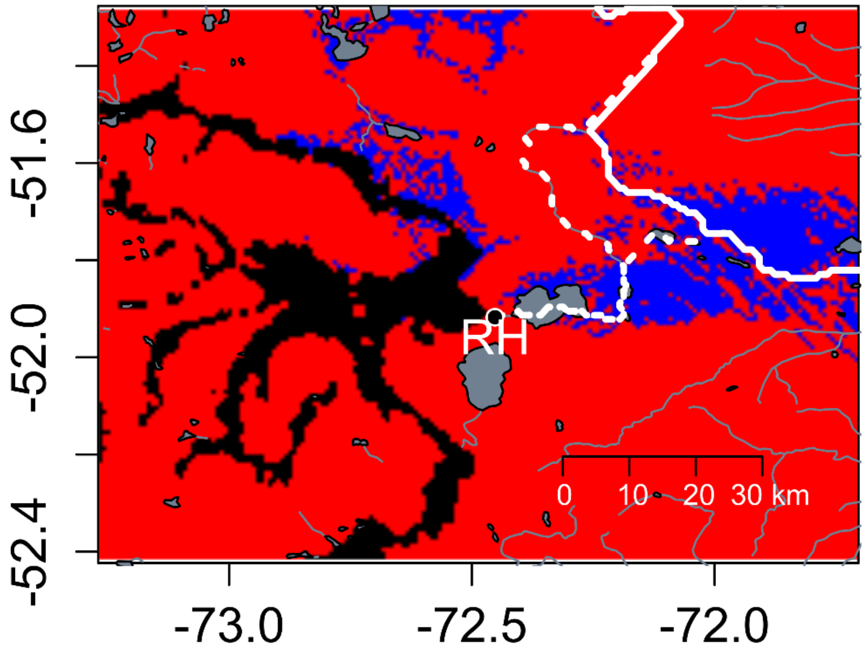

Fig. 3 Close-up to the area of the Hollemberg River showing details of the trajectories, where the red area represents where beavers can reproduce and blue areas where beavers cannot reproduce. The white solid line corresponds to the route of least cost, while the dashed line represents the same migratory movement but forcing the route to pass through the Hollemberg River. The dark gray areas represent rivers and freshwater bodies.

5.9 Tables

Table 1. Bioclimatic layers selected for the GLM model (AICc = 23,801), with the estimates of the slope and significance for each layer.

Predictors	Layer	Slope	P
Annual Mean Temperature	Bio1	-0.52875	0.00270
Mean Temperature of Wettest Quarter	Bio8	0.45639	0.00491
Precipitation of Driest Month	Bio14	0.0726	0.01349
Precipitation Seasonality	Bio15	0.19767	0.00706

VI. CONCLUSIONES GENERALES

En el contexto de la modelación de distribución de especies, se demuestra que el índice de idoneidad de hábitat no tiene una relación positiva con la adecuación biológica de la población invasora de castores en la isla de Tierra del Fuego. Sin embargo, el modelo propuesto de GLM (Generalized Lineal Model) para predecir la adecuación biológica de forma espacialmente explicita, permite estudiar la estructura espacial y frecuencias de la adecuación biológica de una especie. Los modelos de distribución basados en datos de presencia no estarían prediciendo la adecuación biológica de las especies y en el caso del estudio de las abundancias, sólo predecirían la abundancia más alta posible en un sector dado pero con un valor explicativo muy bajo, explicando como máximo un 40% de la variabilidad (VanDerWal et al. 2009; Tôrres et al. 2012). A diferencia de esto, los valores de pseudo R^2 obtenidos en este estudio mediante GLM llegan a 0,65 lo cual es un ajuste mucho mayor a pesar de tener un número muestreal más bajo.

La modelación de nicho hutchinsoniano a partir de GLM comparte algunas características propuestas para la modelación de distribución de especies que se basa en el nicho grinnelliano. Por un lado, se establecen principalmente en ejes scenopoéticos del nicho, es decir en condiciones necesarias y no en dinámicas recurso-consumidor, como las versiones más recientes de nicho eltoniano (Leibold 1995; Chase & Leibold 2003; Soberón 2007; Soberón & Nakamura 2009; Peterson et al. 2011). Ambos modelaciones estaría generando nichos fundamentales y no nichos realizados de las especies estudiadas (Peterson et al. 2011). Y por último, ambos modelos estarían pensados para ser trabajados a escala regional y no local. Sin embargo, existe una gran diferencia entre ambos modelos, la modelación de distribución basada en presencias tendría una relación triangular con la abundancia (VanDerWal et al. 2009), esto es que predeciría el valor máximo de abundancia para cada lugar. En cambio, la modelación de nicho hutchinsoniano en base a GLM, tendría una relación lineal con la adecuación biológica de la especie estudiada, por lo que determinaría promedios y no máximos. El nicho hutchinsoniano además, presenta una dualidad: un hipervolumen independiente del espacio físico o el nicho propiamente tal, y el espacio físico en el cual manifiesta o biotopo (Colwell & Rangel 2009). Los mapas obtenidos de la modelación de nicho representan el biótopo de la especie, sin embargo a través de la interpretación del GLM se puede además graficar el nicho propiamente tal, el cual puede incluir combinaciones de variables que no existen en el espacio físico (Figs. 1 a 3).

Los resultados de este estudio indicarían que al menos para especies de alta prioridad, es necesario modelar el nicho hutchinsoniano, ya que el índice de idoneidad de hábitat que ha sido propuesto para ser utilizado en esfuerzo de conservación y manejo de especies (Rodríguez et al. 2004; VanDerWal et al. 2009) entregan información con un bajo poder explicativo. Con esta metodología, se soluciona una de las principales desventajas de trabajar en base a abundancias, el determinar que valores de abundancia alta no solo se presenta por condiciones ambientales buenas, sino también por altas tasas de inmigración (Gaston 2009; Peterson et al. 2011). En este último caso, podríamos distinguir claramente cuales sectores serían potenciales fuentes y cuales potenciales sumideros.

6.1 Perspectivas

En este trabajo se realiza el primer estudio de la estructura de la adecuación biológica dentro del rango de una especie, sin embargo los patrones encontrados podrían no ser una generalidad. Para esto sería necesario estudiar estos mismos patrones preferiblemente en especies que poseen adecuaciones más sencillas de medir, tales como especies anuales.

Además de la utilización de GLM se podrían generar modelos hutchinsonianos a partir de otros algoritmos con mayor flexibilidad como el GAM (Generalized Additive Models) (Hastie & Tibshirani 1986), MARS (Multivariate Adaptive Regression Explains) (Friedman 1991) o estimación de densidad de Kernel. Estos modelos son más flexibles que los GLM al soportar relaciones no lineales, sin embargo necesitan una selección de variables para optimizar, lo cual no está aún automatizado.

6.2 Referencias

Chase, J.M. & Leibold, M. (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*, Second. University Of Chicago Press, Chicago.

Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19651–19658.

Friedman, J.H. (1991) Multivariate adaptive regression splines. *The annals of statistics*, 1–67.

Gaston, K.J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1395–1406.

Hastie, T. & Tibshirani, R. (1986) Generalized additive models. *Statistical science*, 297–310.

Leibold, M.A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology*, **76**, 1371–1382.

Peterson, A.T., Soberón, J., Pearson, R.G. & Anderson, R.P. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton, N.J.

Rodrigues, A.S., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D., da Fonseca, G.A., Gaston, K.J., Hoffmann, M. & others. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, **428**, 640–643.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters*, **10**, 1115–1123.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, **106**, 19644–19650.

Tôrres, N.M., De Marco, P., Santos, T., Silveira, L., de Almeida Jácomo, A.T. & Diniz-Filho, J.A. (2012) Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Diversity and Distributions*, **18**, 615–627.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009) Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance. *American Naturalist*, **174**, 282–291.

6.3 Figuras

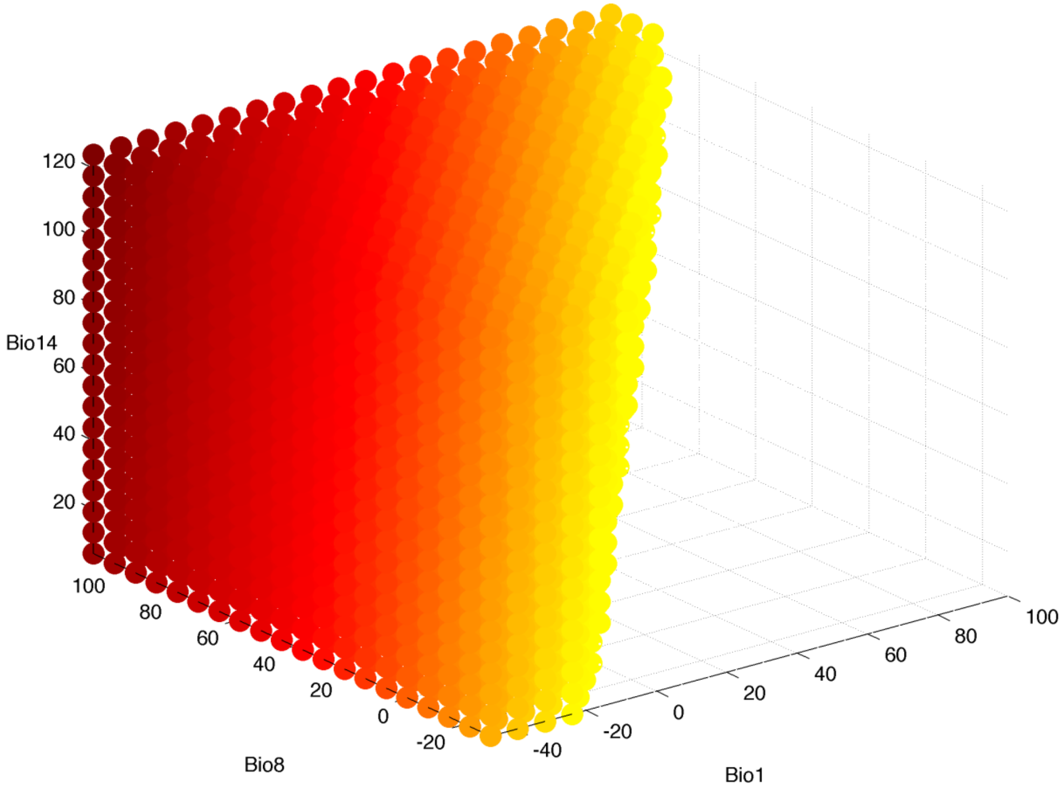

Fig. 1 Relaciones estimadas por el modelo entre las variables Bio 1, Bio 8 y Bio 14 con la cantidad de crías estandarizada por edad.

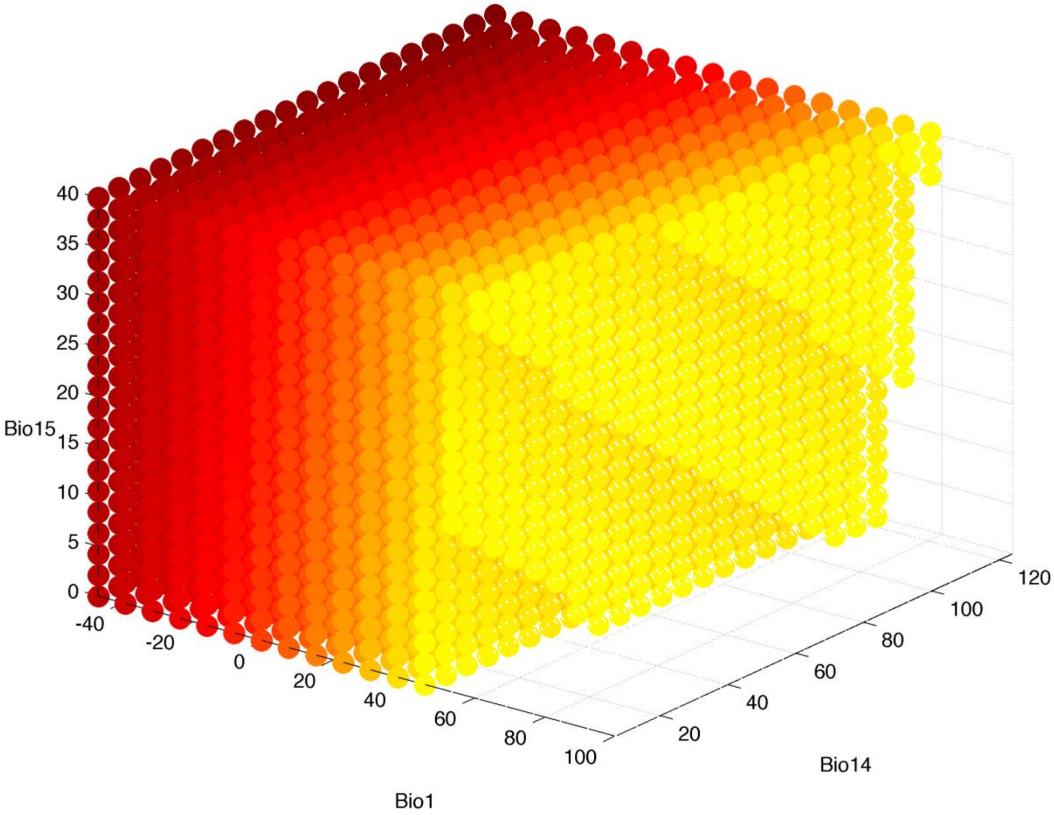

Fig. 2 Relaciones estimadas por el modelo entre las variables Bio 1, Bio 14 y Bio 15 con la cantidad de crías estandarizada por edad.

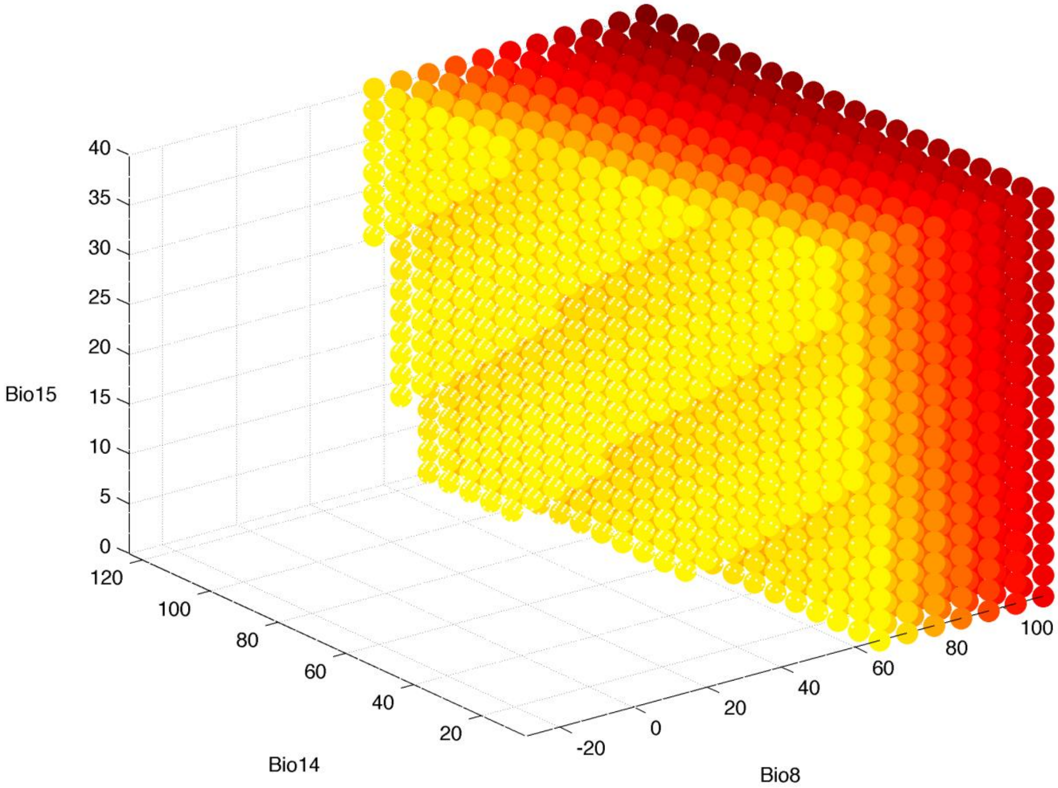

Fig. 3 Relaciones estimadas por el modelo entre las variables Bio 15, Bio 14 y Bio 8 con la cantidad de crías estandarizada por edad.