

Understanding the inter-specific dynamics of two co-existing predators in the Tierra del Fuego Archipelago: the native southern river otter and the exotic American mink

Alejandro E. J. Valenzuela · Andrea Raya Rey ·
Laura Fasola · Adrián Schiavini

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Abstract Knowledge about interactions between endangered native southern river otters (*Lontra provocax*) and introduced American mink (*Neovison vison*) is essential for effective management of both species. We evaluated competition for spatial and trophic niches between otter and mink in overlapping and non-overlapping areas, comparing distribution, habitat preference, diet and mink marking behavior. We surveyed otter and mink signs along 250 km of Beagle Channel coastline. Habitat suitability models were constructed based on species presence/absence and habitat characteristics, using generalized linear models. Feces were collected for diet analyses. Otters used forested coasts with 12°–32° shoreline slope and without human influence, and our evidence suggests

they were not affected by mink presence. Mink preferred forested and shrubland coasts with 10°–28° shoreline slope. Neither human influence nor otter presence affected mink habitat occupation, but in the presence of otters, mink left fewer signs. Otters consumed more aquatic prey than mink, and mink modified their diet in the presence of otters, consuming more exotic small terrestrial mammals and less fish as well as shifting to smaller and shallower fish species that are less consumed by otters. Mink showed more plastic, generalist behavior than otters, being more tolerant of human presence, using more habitat types and having greater diet breadth. At the same time, otters apparently affect mink adversely and could help limit their invasion in sympatric areas. Conservation and recovery of otters, therefore, may produce a secondary benefit of simultaneously reducing the effect of mink, thereby providing an additional way to control this exotic predator's population.

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A. E. J. Valenzuela · A. Raya Rey ·
L. Fasola · A. Schiavini
Centro Austral de Investigaciones Científicas (CADIC),
Consejo Nacional de Investigaciones Científicas y
Técnicas (CONICET), Bernardo Houssay 200,
9410 Ushuaia, Tierra del Fuego, Argentina

Present Address:

A. E. J. Valenzuela (✉)
Southern Patagonia Coordination Unit, Argentine
National Parks Administration, San Martín 1395,
9410 Ushuaia, Tierra del Fuego, Argentina
e-mail: ale.alevalenzuela@gmail.com

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Introduction

Introduced carnivores affect native predators through competition, disease and parasite transmission, direct aggressive interactions, and hybridization (Macdonald and Harrington 2003; Manchester and Bullock 2000).

These impacts can be magnified in isolated environments such as archipelagos (Courchamp et al. 2003). Furthermore, complex interactions among predators can lead to cascading trophic effects (McDonald et al. 2007), and therefore, understanding the inter-specific relationship between native and introduced carnivores is crucial to comprehend the community ecology of this new assemblage and modified ecosystem (Bonesi and Macdonald 2004a; Carlsson et al. 2010).

According to optimal foraging and habitat selection theories (see Rosenzweig 1981), two competitors can coexist in a heterogeneous habitat if one species is a specialist (particularly the dominant competitor) and the other is a generalist (Bonesi and Macdonald 2004a; Rosenzweig 1987). Then, introduced and native carnivores would be expected to coexist when the habitat is: (1) heterogeneous and (2) the exotic species is both subordinate and opportunistic (Clode and Macdonald 1995; Delibes et al. 2003). The subordinate competitor should modify its behavior, habitat use, and/or trophic habits towards suboptimal conditions to adapt to the presence of the dominant native predator (Bonesi et al. 2004). However, little or no change is expected in these same factors for the dominant competitor.

The southern river otter (*Lontra provocax*) is an endemic, endangered species from both the Argentine and Chilean portions of Patagonia (Chehébar 1985; Sepúlveda et al. 2008; Sielfeld 1989). It was decimated in the past century due to over hunting and other human activities (Aued et al. 2003; Cassini et al. 2010; Medina-Vogel et al. 2003; Sielfeld and Castilla 1999). This species uses freshwater habitats in the northern part of its distribution, but occupies the marine coastline towards the south (Fasola et al. 2009). In the Tierra del Fuego (TDF) Archipelago, shared between Chile and Argentina, the southern river otter is found throughout the interior fjords and channels (Massoia and Chebez 1993; Sielfeld 1992). In the Argentine (eastern) portion of the archipelago, there are two previously reported subpopulations: on the Beagle Channel's (BC) coasts in TDF National Park and on Staten Island (Centrón et al. 2008). Otter distribution is known to be determined by prey availability (Aued et al. 2003; Cassini et al. 2009; Fasola et al. 2009), and their presence is associated with rocky shores covered by ample vegetation (Chehébar et al. 1986; Medina-Vogel et al. 2003; Sepúlveda et al. 2007). In coastal environments

specifically their diet is dominated by fish and crustaceans and does not have seasonal fluctuations (Gómez et al. 2010; Sielfeld 1989; Sielfeld and Castilla 1999).

The American mink (*Neovison vison*) is a semi-aquatic carnivore native to North America. It was released from fur farms onto TDF Island around 1950 (Lizarralde and Escobar 2000) and currently has invaded several islands in the archipelago (Anderson et al. 2006; Davis et al. 2012). As with otters, the mink also is associated with vegetated coastlines, but their diet and habitat use are broader, including both aquatic and terrestrial prey and environments (Dunstone 1993). Introduced mink are reported to have negative effects on native species in Europe (Bonesi and Palazón 2007), principally small prey items such as rodents and water birds via depredation (Banks et al. 2004). Furthermore, exotic mink are also known to out-compete native intra-guild species including the European mink (*Mustela lutreola*; Sidorovich and Macdonald 2001) and Eurasian polecat (*Mustela putorius*; Bonesi and Palazón 2007).

The interactions of introduced and native species are often very complex. It is usually difficult to determine the direction of impacts when ecologically similar species are involved, but situations have been documented whereby the native predator can control the introduced one (Carlsson et al. 2010), or alternatively, there can be a sustained coexistence (Bonesi and Macdonald 2004a). For example, the Eurasian otter is the only native European carnivore that has been shown to have a negative effect on the distribution and abundance of exotic American mink (Bonesi et al. 2006). Furthermore, otters were observed directly attacking mink (Bonesi and Macdonald 2004b) and also stealing food from them (Bonesi et al. 2000). In northern Patagonia, the southern river otter and American mink showed both habitat and trophic overlap (Chehébar et al. 1986; Previtali et al. 1998), which could lead to competitive interactions. However, Fasola et al. (2009), Gómez et al. (2010) and Medina (1997) found no evidence of competition for food, due to resource partitioning between these two species in continental Patagonia and TDF.

In addition to the theoretical and conceptual issues regarding the community ecology of novel assemblages, there is also acute concern among TDF's natural resource managers of the potential impacts this introduced carnivore may have on native and endangered species. This concern further justifies the need to

understand the inter-specific dynamics of these two species. In this context, mink invasion on TDF represents an ideal opportunity to study community interactions between a native and introduced predator in light of current theories on competition and invasive species on islands, as well as serving as a platform to better understand and manage native biodiversity. We, therefore, set out to detect evidence for competition at the levels of spatial and trophic niches between otter and mink along the BC, comparing between areas where these species are found together and where they are not. We analyzed: (1) distribution of both species in the study area, (2) their habitat requirements, (3) changes in mink marking behavior in the presence of otters, and (4) diet of both mustelids in the absence and presence of the other. We conclude by discussing the implications of these results for conservation and wildlife management of both the southern river otter and the American mink in the TDF Archipelago.

Methods

Study area

The TDF Archipelago comprises South America's southernmost group of islands. TDF Island is the largest in the archipelago. It is separated from the continent by the Strait of Magellan and is delimited to the south by the BC, which occupies a submerged glacial valley and connects the Atlantic and Pacific Oceans at about 55°S. The climate along the BC is cold oceanic (Rabassa et al. 2000) with prevailing winds from the southwest, low annual thermal fluctuation (<5 °C), a mean annual temperature of 6 °C, and an annual precipitation of 467.3 mm (Bujalesky 2007). The human populations situated along the Argentine north coast of the BC include the city of Ushuaia and the small fishing village of Puerto Almanza. On the Chilean southern shore, we find the town of Puerto Williams. Other human settlements are limited to isolated ranches and naval stations. The core study area extended for 250 km of the coast line on the Argentine sector of the BC from the international border with Chile in the west to Moat Point in the east. Otter feces samples were also obtained for diet analysis from Staten Island, which is 29 km to the east of TDF Island across the Le Maire Strait. This was the only available site for determining otter diet in the absence of mink.

Survey

Fifty transects (600 m each) separated by 4.4 km were conducted along the BC study area. Each transect was surveyed for otter and mink signs (scats, tracks, dens and latrines) within 50 m of the water line (as per Harrington and Macdonald 2008; Yamaguchi et al. 2003) twice a year, during warm (spring-summer) and cold (fall-winter) seasons from 2005 to 2009. In each transect, we recorded the following relevant habitat variables and area characteristics based on previous literature: (1) vegetation type, including forest, shrubland, grassland, peatland or flat beach; (2) coastal slope, measured as the average inclination of the shoreline; and (3) human influence, ranked on a 0–4 scale with 0—no human influence, 1—little evidence of human activity, cattle, dog or cat signs and no human settlements, 2—frequent signs of human, cattle, dog or cat presence, small human settlements (ranches), 3—very frequent signs of human, cattle, dog/cat presence, settlements with less than 2,000 residents, and 4—constant human and dog/cat presence, settlements with more than 2,000 residents.

Distribution and habitat preference

We studied the distribution of otter and mink along the BC based on signs that indicated presence/absence. A transect was considered positive only if signs were found in two consecutive years (i.e. 4 consecutive surveys) during the sampling period to avoid recording transient animals' temporary occupation. To assess whether the habitat characteristics explained the presence of both species, we used generalized linear models (GLMs). Our response variable was presence/absence (binary) of otter/mink signs in each transect. Therefore, the Bernoulli binomial error distributional family was used with a canonical logit link function in the GLMs. We tested all models that had a biological basis arising from the possible combinations of the explanatory variables (vegetation type, shoreline slope, human influence, and presence of mink in otter's models and vice versa). Akaike Information Criterion (AIC) for small sample sizes was used for model selection (Akaike 1974); models with less than 2 AIC units of difference with the best model obtained were considered significant. Differences in the number of mink signs found in transects with and without otters were evaluated with a Kruskal–Wallis test,

using transects as replicates, under the assumption that the abundance of mink signs was similar between the same habitat types. Statistical analyses were performed using R 2.9.1 software (R Development Core Team 2009); P values were considered significant when <0.05 .

Diet

Otter and mink diets were determined by analyzing feces collected during surveys. Scats were attributed to each species based on size, shape and smell, as per Bonesi et al. (2004). The total numbers of samples collected were 268 and 85 for mink and otter respectively. In addition, 28 otter feces were collected from Crossley Bay and San Juan de Salvamento Port on Staten Island, where otters occur in the complete absence of mink.

Feces were stored in 70 % ethyl alcohol to preserve samples and to keep delicate remains (e.g., fish skull bones) wet to avoid damage by desiccation. Before analysis, each sample was washed with warm water through a sieve (0.3 mm mesh) to facilitate separation. Undigested remains were identified to the lowest possible taxonomic level and sorted using a dissecting scope (10 \times) into eight main categories (mammals, fish, birds, crustaceans, insects, polychaetes, chitons and cephalopods). Also, items were classified according to origin (native or exotic) and the habitat type where they were likely taken (aquatic or terrestrial). Identification was based on our own reference collection (Wildlife Ecology and Conservation Laboratory, CADIC) and supplemented with published descriptions and identification keys (Chehébar and Martín 1989; Gosztonyi and Kuba 1996; López et al. 1996; Pearson 1995; Tapella and Lovrich 2006; Volpedo and Echeverría 2000). We identified mammalian remains from teeth, jaws and medullar and cuticle scale patterns of hair. Fish species were identified from cranial bones, otoliths and scales. Digestion caused sufficient damage to feathers as to prevent further identification. Crustaceans were classified on the basis of shape, texture and color of appendages and exoskeletal fragments. Identification of insects was done from exoskeletons (elytra, jaws, legs, wings and heads). Cephalopods were classified from lower beaks, polychaete from setae and chitons from plates. Otter or mink hairs in feces were considered to be the result of grooming and therefore disregarded in

analyses. Plant material and crustaceans less than 5 mm in length also were excluded from analyses as they were considered to be secondary prey, incidental intake or adhesion after defecation.

For each scat, we recorded the items present and the volume (V) of each main category, as percentage of the total sample volume. We estimated V visually by placing each feces per category uniformly in a Petri dish that was divided into eight portions (each portion corresponded to 12.5 % of total volume). We calculated the following indexes for each prey category to describe the diet of the two mustelids and make comparisons: (1) frequency of occurrence (FO: number of feces where a prey category was found divided by the total number of feces multiplied by 100), (2) relative frequency of occurrence (RFO: number of occurrences of a prey item in relation to the sum of occurrences of all prey items multiplied by 100), (3) mean percentage of estimated volume (AV: average of V estimated in each sample for a give prey category), and (4) frequency of occurrence as a dominant category (DOM: number of occurrences of each prey category when the category is dominant in feces, considering the prey item with largest V in each feces as dominant). Each index has benefits and disadvantages (see Fasola et al. 2010), and so it is therefore necessary to use all indexes to describe the species' diet (Raya Rey and Schiavini 2005). However, if the indexes are correlated, descriptions and comparisons could be continued relying only one of them. So, we used Spearman's rank correlations to compare between the calculated indexes (FO, RFO, MV and DOM), finding that all were significantly correlated to one another ($P < 0.01$). Therefore, further comparisons were done with RFO, as it is the most frequently used in the literature (Carss and Elston 1996). The diet of otters was evaluated in the presence (BC) and absence (SI) of mink, and mink diet was compared in the presence and absence of otters along the BC. RFO differences were assessed using a Chi-square test and Fisher's exact test, when 20 % or more of the expected frequencies were below five (Zar 1984). To enhance the comparison of trophic behavior between otter and mink, the following indexes were calculated based on the main categories: (1) Shannon and Weiner (1963) diversity index (H') to assess the diversity of diet items for each species under co-occurrence or not; (2) trophic niche breadth (B), calculated according to Hurlbert's standardization of

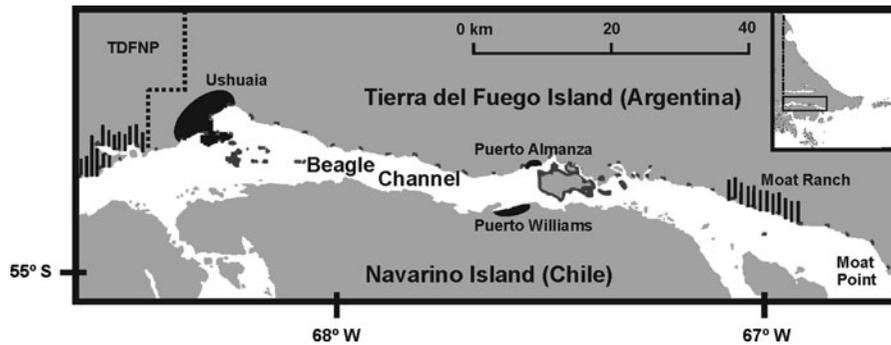


Fig. 1 Map of study area showing survey transects (dark grey lines) along the Beagle Channel coast and the two coastal areas with signs of southern river otter (*L. provocax*) presence (vertical stripes): (1) Tierra del Fuego National Park (TDFNP) and (2) Moat Ranch

Levins' index (Hulbert 1978; Levins 1968) as $[(1/\sum p_i^2) - 1]/[n - 1]$, where p_i is the RFO of each prey category and n is the total number of prey categories; and (3) diet overlap (α), using the Pianka (1973) index calculated as $\alpha_{j,k} = \sum(p_{ij} \cdot p_{ik}) / (\sum p_{ij}^2 \cdot \sum p_{ik}^2)$, where p_i is the RFO of prey category i for species j (otter) and k (mink). B and α values range between zero and one, where a B equal to one indicates the broadest possible niche. For diet overlap (α), a value of zero indicates no overlap, and a value of one signifies complete overlap. All statistical analyses were conducted in R version 2.9.1 (R Development Core Team 2009), and statistical significance was accepted at $P < 0.05$.

Results

Distribution and habitat preference

Mink signs were found throughout the surveyed area along the BC, but only in preferred habitats, while otter presence was observed only in two zones (Fig. 1): (1) TDF National Park from the border with Chile in the west to Mount Susana in the east, and (2) the coastal zone from Navarino Point in the west to the area next to the Becasses Islands in the east. This second area corresponds to a new range for confirmed otter presence on TDF Island. American mink presence overlapped with transects that had otter signs ($n = 11$). Additionally, mink signs, but not those of otter, were found in a total of 19 transects, and in the remaining 20 transects we found no signs of either species. All transects with mink and/or otter presence had signs in at least 3 of 5 years, while all transects with their absence never had signs during the entire study period.

We compared 24 possible habitat suitability models for otter and mink presence (Online Resource 1). The GLM that best explained (i.e. lowest AIC) the presence of otters along the BC included vegetation type, shoreline slope (with a quadratic function) and human presence (Table 1). Otter presence was unrelated to mink presence. This best model explained 84 % of the variance. The probability of finding otters was higher in forested habitats with coastal slopes that ranged from 12° to 32° and were free of human influences (Fig. 2). On the other hand, the GLM that best fit the mink data included vegetation type and shoreline slope (with a quadratic function); this model excluded human influence and otter presence and explained 66 % of the variance (Table 1). Like otters, the mink was associated with forested habitats, but also with shrublands, and their presence probability was greater when the coastal slope ranged between 10° and 28° (Fig. 2). The probability of otter presence was higher than the mink's in the absence of people (Fig. 2a), but under human influence, the introduced species showed a higher probability of presence than the native one (Fig. 2b). Despite mink being found in the presence of otter, the abundance of their signs in transects with co-occurrence of the two species was lower (one per transect on average) than when mink were found alone (seven per transect on average) (Kruskal–Wallis rank sum test, $K = 11.89$, $df = 1$, $P < 0.001$).

Diet

The feces content analysis showed that in the TDF Archipelago the diet of both mustelid species was significantly different ($\chi^2 = 83.30$, $df = 5$, $P < 0.001$),

Table 1 Significant (i.e. lower AIC) habitat suitability models that best explained the presence of southern river otter (*L. provocax*) and American mink (*N. vison*) on the Beagle Channel

Species model	Variable	Coefficient	SD
Southern river otter	Intercept	-7.9638	4.1245
	Vegetation type		
	Forest	5.8804	3.2574
	Shrubland	0.1287	0.2114
	Grassland	0.0701	0.2052
	Shore slope	0.8267	0.4165
	Shore slope ²	-0.0184	0.0099
	Human influence	-3.3431	1.7914
	American mink	Intercept	-8.2281
American mink	Vegetation type		
	Forest	4.5661	1.2449
	Shrubland	3.2625	1.2067
	Grassland	0.5291	1.5242
	Shore slope	0.8104	0.1862
	Shore slope ²	-0.0217	0.005

For each variable included in the models, the coefficient and standard deviation (SD) are indicated

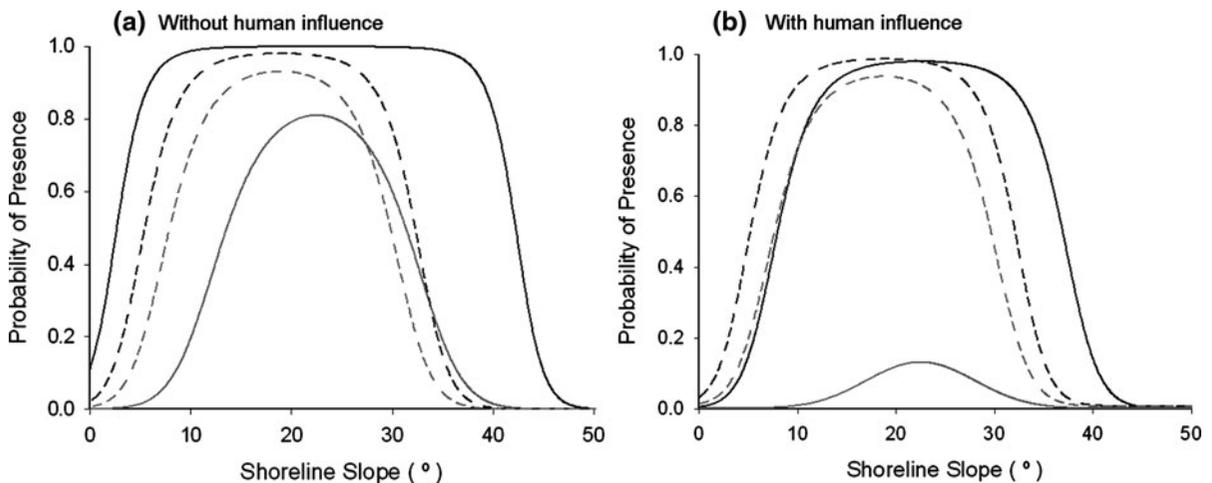


Fig. 2 Probability of southern river otter (*solid lines*) and American mink (*N. vison*, *dotted lines*) presence for forest (*black lines*) and shrubland (*grey lines*) habitats along the

Beagle Channel, as a function of shoreline slope in areas without human influence (a) and areas affected by humans (b)

with otters consuming more aquatic prey items (95.4 % RFO) than mink (56.5 % RFO). However, no differences were found between the two species regarding consumption of the main diet categories. However, the otter showed lower prey diversity and niche breadth than the mink's diet (Table 2). Furthermore, diet overlap between both species was lower when they co-occurred ($\alpha = 0.611$), compared to mink diet when found in the absence of otters ($\alpha = 0.801$).

Otters fed mainly on fish and crustaceans, occasionally consuming small mammals, birds, cephalopods and

polychaetes (Table 3). There was no significant difference in otter diet between the BC and SI (Fig. 3a; $\chi^2 = 0.27$, $df = 3$, $P = 0.97$). Moreover, otter diet from both of those areas had similar values of diversity ($H_{BC} = 0.93$ and $H_{SI} = 0.91$) and niche breadth ($B_{BC} = 0.234$ and $B_{SI} = 0.254$). Only native prey was found in the otter's feces.

Small mammals and fish together represented over 70 % RFO of the mink's diet along the BC (Table 3). The consumption of crustaceans and birds was similar, each category representing around 10 % of the diet.

Table 2 Trophic niche breadth (B) and Shannon–Weiner diversity index (H') calculated for diet of southern river otter and American mink (in presence/absence of otters) from sites along the Beagle Channel

	Otter	Mink (with otters)	Mink (without otters)
H'	0.927	1.384	1.352
B	0.234	0.466	0.443

Occasional consumption of insects, polychaete and chitons was found. Mink diet changed significantly, though, in the presence of otters (Fig. 3b; $\chi^2 = 13.16$, $df = 4$, $P < 0.05$). The exotic mink consumed more terrestrial prey (mainly exotic, small mammals such as European rabbits, *Oryctolagus cuniculus*, and muskrats, *Ondatra zibethicus*), and less fish (mainly from the family Nototheniidae) in areas where the otter was present. Additionally, fish species and sizes preyed upon by mink in areas influenced by otters were both more inshore and smaller than those eaten in the absence of the native mustelid.

Discussion

Understanding the inter-specific factors affecting distribution and trophic dynamics of otter and mink in Tierra del Fuego

Native southern river otter and introduced American mink are sympatric predators along the BC coast of

TDF Island. Forested coastal habitats had most of the records for both mustelids. However, mink also used shrublands, revealing a greater flexibility of habitat use compared to the otter. Furthermore, mink habitat use was not affected by humans, unlike the response demonstrated by otters, which avoided coastal stretches with even moderate anthropogenic disturbance. The habitat preferences found in our study for the southern river otter largely coincide with conditions previously described for this species in northern Patagonia (Aued et al. 2003; Chehébar 1985; Chehébar et al. 1986) and in the TDF Archipelago before mink invasion (Sielfeld 1990, 1992). These facts would render invalid the hypothesis that the presence of American mink has affected the habitat use or probability of presence of otters. Also, this finding agrees with results described for similar systems involving American mink and the Eurasian otter (Bonesi and Macdonald 2004a; Bonesi et al. 2004; Ruiz-Olmo et al. 1997; Sidorovich and Macdonald 2001).

On the other hand, the relationships described elsewhere between the native otter and exotic mink indicated that otters negatively impact mink distribution and abundance (Aued et al. 2003; Bonesi and Macdonald 2004a; Bonesi et al. 2006; McDonald et al. 2007). Based on our results along the entire BC, we cannot conclude definitively that a similar situation is taking place in the whole study area. Indeed, mink habitat use along the BC was consistent with the general pattern found for the entire island (Valenzuela, unpublished data) and for northern Patagonia (Fasola et al. 2009,

Table 3 Relative frequency of occurrence calculated for the diet of southern river otters in the presence (Beagle Channel-BC) or absence (Staten Island-SI) of American mink

	Prey	Otter (BC)	Otter (SI)	Mink (w/)	Mink (w/o)	
Mammals	Mammals	1.74	–	42.7	28.57	
	Native (Cricetidae)	1.74	–	17.3	16.39	
	Exotic	–	–	25.4	12.18	
	Fish	Fish	56.52	54.29	30.27	44.96
		<i>Patagonotothem</i> spp.	22.83	18.08	11.17	22.21
		<i>E. maclovinus</i>	13.23	21.39	3.54	8.9
		<i>H. bispinis</i>	13.23	6.57	11.38	3.19
	Unidentified	7.23	8.25	4.18	10.66	
	Crustaceans (<i>Munida</i> spp.)	37.39	37.14	12.43	10.92	
	Birds	2.61	–	9.73	12.19	
Polychaetes	–	5.71	–	1.68		
Mink diet values on BC were calculated in presence (w/) or absence (w/o) of otters	Insects (beetles)	–	–	3.78	1.26	
	Chitons	–	–	1.09	0.42	
	Cephalopods	1.74	2.86	–	–	

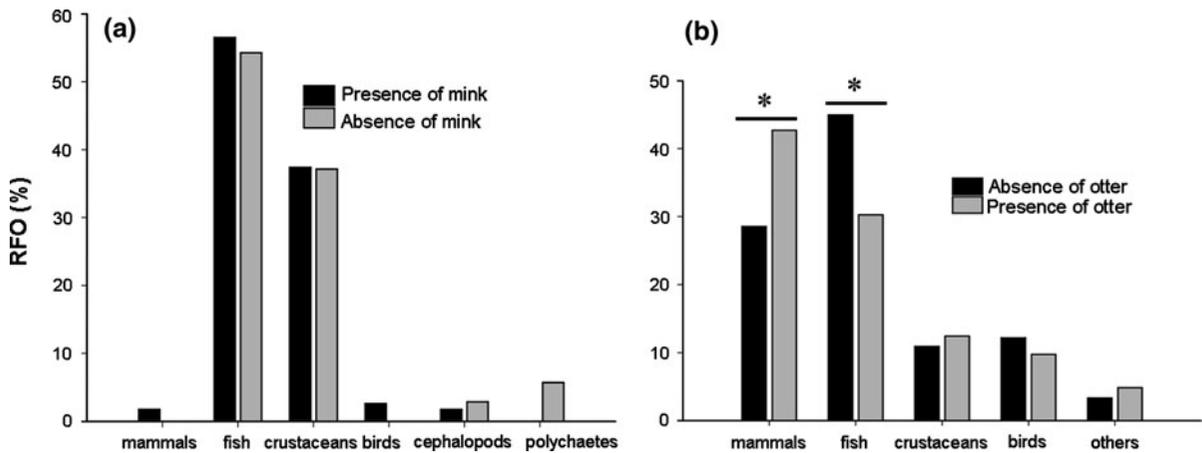


Fig. 3 Diet of both mustelid species expressed as relative frequency of occurrence (RFO) in areas where **a** southern river otter overlap (Beagle Channel) and do not overlap (Staten

Island) with American mink and where **b** mink are found along the Beagle Channel in the presence and absence of otter. (*) indicates significant differences ($P < 0.05$)

2010; Previtali et al. 1998), while otters were distributed in only two disjunct areas along the BC. Yet, at the same time, the otter on a smaller scale indeed seemed to affect mink, causing it to leave fewer signs (potentially indicating a lower abundance) and change its trophic behavior (to more terrestrial prey items).

In Spain, mink likewise have been shown to change their marking behavior by decreasing the number of signs deposited in the presence of Eurasian otters to avoid interference (García et al. 2009). In England, Bonesi et al. (2006) found that mink moved away from aquatic environments inhabited by otters, and therefore decreased their local abundance, which explains the absence of mink signs in those sectors. However, a later study in the same area based on captures found that the abundance of mink in the presence of otters did not decrease (Harrington et al. 2009), which reinforces the idea that the mink may modify its behavior in the presence of otters, even while maintaining its occupation of the sites. In our study system, though, we found few mink signs along freshwater or wetland habitats inland from the BC areas with otters, indicating that mink are not simply moving inland to avoid otters. In summary, our results suggest that otter presence on the BC could impact mink through changing their marking behavior and/or affecting their abundance, but live trapping studies would be needed to discern between these two scenarios.

Looking at another niche dimension to explore inter-specific effects, Gómez et al. (2010) postulated that coexistence between otter and mink on the BC

was facilitated by the high availability of marine prey. However, these authors compared the diet of both species without differentiating when species were found together or not, a key design requirement when evaluating competition and possible mechanisms under coexistence scenarios. We found that mink modified their diet in the presence of otters, consuming more terrestrial prey. In addition, diet overlap decreased when both species co-occurred. A similar behavior has been described for the relationship between Eurasian otter and American mink (Bonesi et al. 2004; Clode and Macdonald 1995; Melero et al. 2008; Palazón et al. 2008). We conclude that trophic segregation, instead of the high availability of marine prey from the BC, is likely a more important mechanism for the coexistence of these two species.

We also discovered that trophic differentiation of mink diet in the presence of otter was operating at two different levels: (1) mink consumed more terrestrial prey, and (2) mink shift the species and sizes of fish consumed. Both situations favor a decrease of diet and spatial overlap between the two mustelids to avoid exploitation and interference-mediated competition, respectively. First, an increase in consumption of mammals by mink probably supplants the decrease of fish intake and also allows avoidance of direct interference with otter along the marine coast. Second, in the presence of otter, mink consumed more *Harpagifer bispinis* and less *Patagonotothen* spp. and *Eleginops maclovinus* (family Nototheniidae). *H. bispinis*' average size is less than those of species of the family

Nototheniidae that were preyed upon, and also it is more usually found in intertidal or shallow water areas (Froese and Pauly 2011; López et al. 1996; Vanella et al. 2007). Mink, therefore, appeared to be using inshore areas under scenarios of co-existence with the native predator, avoiding foraging zones frequently used by otter (Kruuk 2006). On other hand, our results indicated that mink presence did not affect the otter's diet. Therefore, these data suggest that otters affect the foraging behavior of mink on the BC coast.

However, considering that mink diet diversity and trophic niche breadth did not change in the presence of otters, the plasticity of the introduced mustelid still allows coexistence, dodging some negative effects of competition. Such coexistence responds to theoretical predictions for habitat selection (Rosenzweig 1981) with the otter acting as the native specialist and the dominant species, and the mink playing the role of an exotic generalist and the subordinate species. Similar results were found by Bonesi and Macdonald (2004a) for coexistence between the Eurasian otter and the American mink in England. Future studies should focus on other ecological aspects not considered in our work, such as effects on reproductive success and activity patterns, that would elucidate more subtle effects of coexistence.

In conclusion, rather than finding negative effects of introduced mink on the native otter, their co-existence along the BC could instead be unfavorable for the mink. Bonesi et al. (2006) and Ruiz-Olmo et al. (1997) suggested that native otters offer biotic resistance to rates of expansion by mink, which could also be the case in the TDF Archipelago. Additionally, results reported in Anderson et al. (2006) also support this line of argument, since these authors found that mink have not yet been recorded in Yendegaia Bay (Chile), which is immediately west of the TDF National Park and the area where the highest density and frequency of otters signs were found. In this context, increased otter density from TDF National Park to the west may create conditions whereby the otter out-competes the mink and could potentially be somewhat limiting its westward expansion and invasion along the BC coastline into the Chilean Agostini National Park.

Southern river otter conservation in the TDF Archipelago

Knowledge about the spatial use, behavior, habitat requirements, diet and relevance of anthropogenic

influence for the endangered southern river otter is still scarce (Sepúlveda et al. 2007). Therefore, the results of this study are important not only to understand basic community ecology, but also to better determine the ecology of the southernmost population of this rare species and provide background information to support its conservation. An effective otter conservation strategy requires the determination of factors that affect its distribution (Barbosa et al. 2003). Despite having highly productive and abundant marine resources throughout the BC (Almandoz et al. 2011; Raya Rey and Schiavini 2000; Tapella 2002; Vanella et al. 2007), otter were found in only two restricted areas separated by more than 80 km, indicating that its distribution is not limited by prey availability, but rather other habitat variables. Moreover, no signs of otter presence were found along extensive areas with habitats that should be preferred by otters (i.e. forest with shoreline slopes range between 12° and 32°). Consequently, human influence (hunting history, current human settlement, maritime activities, contamination, feral animals) appears to be the crucial factor that constrains the southern river otter's distribution along the BC coast.

Indeed, otter distribution in the study area was interrupted by a zone that includes the few main urban settlements (Ushuaia, Puerto Williams and Puerto Almanza), and otters are also not found along the adjacent, north-central coast of Navarino Island (Anderson et al. 2006). Several authors have indicated that otter species in general and *L. provocax* in particular are especially sensitive to human influences, such as habitat degradation and fragmentation, pollution, disturbance in coastal and offshore waters, and the presence of dogs (Aued et al. 2003; Kruuk 2006; Medina-Vogel et al. 2003; Melquist et al. 1981; Sepúlveda et al. 2007; Sielfeld 1992; Ruiz-Olmo and Jiménez 2008). Therefore, given the vulnerable conservation status of southern river otters, we recommend that recovery actions for this species along the north shore of the BC should be focused on preserving areas (coastlines and adjacent waters) with habitats preferred by otters that still remain relatively free of human influence and also to decrease human influences on these specific areas to minimize effects on preferred habitats or prey. In this sense, also considering the possible limiting effect of native otter on invasive mink, human influence could have interfered with the natural ecosystem's antagonistic response

against the mink's invasion (i.e. the mink invades as a commensal with humans, but would be more restricted if it only dealt with the biotic interactions with otter).

Additionally, protection, conservation and eventual recovery of the native otter could contribute to the recovery of the TDF ecosystem. Juliano et al. (2010) suggested that the presence of an intact assemblage of native predators (higher trophic levels) and their native prey may reduce the success of an introduced predator, limiting their effects on local species. In Europe, the recovery of the Eurasian otter is expected to reduce the impact of American mink in the long run (Bonesi and Macdonald 2004a; Harrington et al. 2009; McDonald et al. 2007). Consequently, promoting the conservation of the southern river otter in the TDF Archipelago not only would benefit the recovery of this endangered native species, but it also has the potential to be a synergistic and complementary way of limiting the impact of American mink in the area. Furthermore, we have shown that mink increased their consumption of other exotic mammals in the presence of otters. Therefore, a secondary effect of otter recovery could be the reduction of other exotic species such as rabbits and muskrats. Finally, future management plans to control American mink in TDF should prioritize an initial strategy of trapping them in areas where they co-occur with otters, such as TDF National Park and Moat Ranch, where culling can be expected to provide an additive effect on the exotic species' population by acting in synergy with the native one.

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Could the native southern river otter limit the invasion of the exotic American mink? Understanding the inter-specific dynamics of two co-existing predators in the Tierra del Fuego Archipelago

Biological Invasions

Alejandro E.J. Valenzuela*, Andrea Raya Rey, Laura Fasola, Adrián Schiavini

* E-mail: ale.alevalenzuela@gmail.com

Habitat suitability models (# = 24) tested to explain the presence of southern river otter (*Lontra provocax*) in Beagle Channel sorted by Akaike Information Criterion for small sample size (AICc). Likelihood log values (logLik), number of parameters involved (k) and weight (w_i) of each model are presented. Δ_i : AICc values difference; v: vegetation type (forest, shrubland, grassland, peatland or flat beach); s: coastal slope; h: human influence; m: presence of exotic American mink (*Neovison vison*).

Model	logLik	k	AICc	Δ_i	w_i
v-s-s ² -h	-7.2069	7	27.86	0.0	0.619
v-s-s ² -h-m	-6.9465	8	32.46	4.6	0.062
v-h-m	-9.5500	6	32.55	4.7	0.059
v-h	-10.7978	5	32.61	4.8	0.058
v-s-s ²	-9.6338	6	32.72	4.9	0.055
s-s ² -h	-12.3069	4	33.28	5.4	0.041
v-s-s ² -m	-9.1284	7	34.22	6.4	0.026
v-s-h	-10.4434	6	34.34	6.5	0.024
v-s-h-m	-9.4803	7	34.93	7.1	0.018
s-s ² -h-m	-12.3069	5	35.63	7.8	0.013
v	-14.1107	4	36.89	9.0	0.007
s-h	-15.3342	3	37.06	9.2	0.006
v-m	-13.2432	5	37.50	9.6	0.005
s-h-m	-14.6194	4	37.91	10.0	0.004
v-s	-14.0091	5	39.04	11.2	0.002
v-s-m	-13.2319	6	39.91	12.1	0.001
h	-21.7050	2	47.60	19.7	0.000
h-m	-20.8526	3	48.10	20.2	0.000
s-s ²	-26.5577	3	59.51	31.6	0.000
s-s ² -m	-26.1052	4	60.88	33.0	0.000
s	-31.3341	2	66.86	39.0	0.000
s-m	-31.3116	3	69.02	41.2	0.000
m	-43.1200	2	90.43	62.6	0.000
Null	-44.4295	1	90.92	63.1	0.000

Habitat suitability models (# = 24) tested to explain the presence of American mink (*Neovison vison*) in Beagle Channel sorted by Akaike Information Criterion for small sample size (AICc). Likelihood log values (logLik), number of parameters involved (k) and weight (w_i) of each model are presented. Δ_i : AICc values difference; v: vegetation type (forest, shrubland, grassland, peatland or flat beach); s: coastal slope; h: human influence; o: presence of native southern river otter (*Lontra provocax*).

Model	logLik	k	AICc	Δ_i	w_i
v-s-s ²	-36.3750	7	85.30	0.0	0.628
v-s-s ² -o	-36.5300	7	87.80	2.5	0.180
v-s-s ² -h	-36.9540	7	88.60	3.3	0.118
v-s-s ² -h-o	-36.3100	8	89.60	4.3	0.074
v	-55.2060	4	118.70	33.4	0.000
v-s	-54.7990	5	120.00	34.7	0.000
v-o	-54.9260	5	120.20	34.9	0.000
v-h	-55.1960	5	120.80	35.5	0.000
v-s-o	-54.7850	6	122.10	36.8	0.000
v-s-h	-54.7990	6	122.10	36.8	0.000
v-h-o	-54.9230	6	122.40	37.1	0.000
s-s ² -h	-57.1660	4	122.60	37.3	0.000
s-s ² -h-o	-56.5170	5	123.40	38.1	0.000
v-s-h-o	-54.7840	7	124.30	39.0	0.000
s-s ²	-59.5680	3	125.30	40.0	0.000
s-s ² -o	-58.9790	4	126.20	40.9	0.000
s-o	-90.5340	3	187.20	101.9	0.000
s-h-o	-89.5810	4	187.40	102.1	0.000
s-h	-94.2310	3	194.60	109.3	0.000
s	-95.2910	2	194.70	109.4	0.000
Null	-110.1020	1	222.20	136.9	0.000
h	-109.6220	2	223.30	138.0	0.000
o	-109.6430	2	223.40	138.1	0.000
h-o	-109.1350	3	224.40	139.1	0.000