

# Coexistence between the southern river otter and the alien invasive North American mink in marine habitats of southern Chile

G. Medina-Vogel<sup>1</sup>, M. Barros<sup>1</sup>, J. F. Organ<sup>2</sup> & L. Bonesi<sup>3</sup>

<sup>1</sup> Facultad de Ecología y Recursos Naturales, Universidad Andres Bello, Santiago, Chile

<sup>2</sup> U.S. Fish and Wildlife Service, Hadley, MA, USA

<sup>3</sup> C/O Department of Earth Sciences, University of Cambridge, Cambridge, UK

## Keywords

competition; diet; habitat; alien mink; otter.

## Correspondence

Gonzalo Medina-Vogel, Universidad Andres Bello, República 252. Santiago, Chile.  
Email: gmedina@unab.cl

Editor: Andrew Kitchener

Received 10 April 2012; revised 12 November 2012; accepted 20 November 2012

doi:10.1111/jzo.12010

## Abstract

The interaction between native and introduced predators can be an important determinant of the success of introduced species and of the magnitude of their effects. In Europe, it has been shown that the American mink *Neovison vison* can be affected by native competitors; however, such evidence has not been found in South America. We studied the southern river otter *Lontra provocax* and the American mink at five marine sites, where they coexisted, and at one freshwater site, where only mink were present, in southern Chile. We used the signs of both species to study their habitat use and diet, and radio tracking to study their activity patterns. The results indicated that otters and minks tended to use different habitats in marine environments, the otter favouring littoral areas that are rocky and steep while the mink favours areas of gravel with a gently sloping intertidal zone. These differences were also reflected in their diets. At one of the coastal sites where the diet of the two species was similar, the activity pattern of minks was mostly diurnal, which is unusual. While differential habitat use may be the way through which the American mink is able to coexist with the southern river otter in coastal habitats of southern Chile, it is possible that otters are having an effect on individual minks by affecting their activity patterns, although more observations are needed to confirm this hypothesis.

## Introduction

Intraguild predation, the killing of species that use similar resources and the non-lethal effects that can ensue (Cresswell, 2008), can strongly determine the behaviour, conditions, population density and distribution of animals (Palomares & Caro, 1999; Sergio & Hiraldo, 2008), and its effects are common in carnivores (Arim & Marquet, 2004). Eurasian otters *Lutra lutra* are known to attack and kill American mink *Neovison vison* (Bonesi & Macdonald, 2004a; Simpson, 2006), and a number of studies have detected effects of otters on mink both at the population and at the individual level. For example, Eurasian otters can affect the mink's distribution and population density in the United Kingdom (Bonesi & Macdonald, 2004a; Bonesi, Strachan & Macdonald, 2006; Macdonald, O'Hara & Morrish, 2007), induce a shift in their diet (Clode & Macdonald, 1995; Bonesi, Chanin & Macdonald, 2004; Harrington, Harrington & Macdonald, 2009) and change their circadian activity patterns (Harrington *et al.*, 2009), although these effects are not always observed (Brzeziński, Świącicka-Mazan & Romanowski, 2008). The American mink, a native of the

Nearctic region, has been introduced throughout the world including southern Chile where it is now present both in freshwater and marine habitats (Medina, 1997). In coastal habitats of southern Chile, the American mink coexists with the southern river otter *Lontra provocax*, an endangered species that is slightly larger than the Eurasian otter (about 10–20%) (Sepúlveda *et al.*, 2007). As the effects of intraguild predation are strongly dependent on size differences between predator and prey (Palomares & Caro, 1999), we expect the southern river otter to have similar if not greater effects on the American mink than the Eurasian otter. In particular, at a local scale, if the larger southern river otter poses a threat to the mink, the mink should avoid close contact or intense site-use overlap (Tannerfeldt, Elmhagen & Angerbjörn, 2002). To test for the possible effects of the southern river otter on the American mink, we focused on the following questions: (1) Is the presence of American mink negatively correlated to that of the southern river otter at sites where both species are present?; (2) What role does habitat play in the coexistence of the two competitors and is this reflected in their diets?; (3) Do mink show a tendency to be more diurnal than expected when they coexist with otters?

## Materials and methods

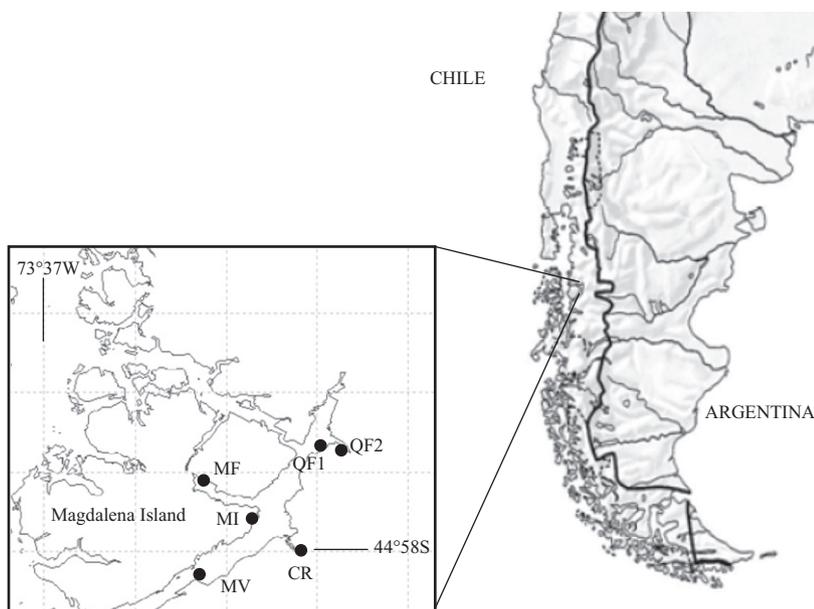
Six study sites, five marine and one freshwater, were randomly selected between 44°30'S–72°34'W and 44°51'S–72°56'W in the southern Chilean archipelago (Fig. 1). Each site was 3 km long and separated by more than 40 km from neighbouring sites for independence (Niemimaa, 1995; Sepúlveda *et al.*, 2007). The study area is covered by abundant vegetation dominated by temperate Norpatagonicus Valdivian rainforest (Veblen & Schlegel, 1982), the average annual temperature is 9°C, and up to 2973 mm of rainfalls annually. There is only low-impact human activity along the entire study site as indicated by fishing boats and a few scattered houses.

## Habitat use and overlap

Habitat characteristics of the marine study sites were assessed using 10-m-wide transects spaced at 100 m from each other

and located between the low-tide line and 50 m inland above the high-tide line. The average width of the intertidal zone varied according to the seashore gradient (range 3–50 m). The habitat characteristics that were recorded are listed in Table 1. At marine sites, vegetation distance was measured as the distance between where vegetation started above the intertidal zone and the high-tide line. At the freshwater site, this distance was calculated from the interface of the water surface and river bank to where the vegetation started. Substrata were measured in the intertidal area and classified based on the diameter of their components as: sand (<0.5 cm), gravel (0.5–10.0 cm), small rocks (10.0–25.0 cm) and large rocks (>6 m).

All six study sites (marine and freshwater) were surveyed every 3 months between May 2007 and February 2009 for a total of five to seven visits depending on weather conditions, and between 10 and 15 days were needed to complete each survey session. Each study site was surveyed along its shoreline either by boat or on foot, and mink and otter field signs



**Figure 1** Geographical locations of marine and river study sites. The sites names are: Magdalena Fjord (MF); Queulat Fjord (QF1); Queulat Fjord (QF2); Magdalena Island (MI); Marta Valley (MV) – all marine habitats; and Cisne River (CR).

**Table 1** Results of the survey of the habitat characteristics for the marine (MF, QF1, QF2, MI, MV) and the freshwater (CR) sites

Site name	Orientation	Exposure to waves	Maximum vegetation distance	Intertidal slope	Substratum <sup>a</sup>
MF	South	Protected	30 m	60% 15°–30° 40% > 80°	60% Gravel 40% Large rocks
QF1	North	Protected	10 m	100% > 80°	100% Large rocks
QF2	North	Protected	10 m	100% > 80°	100% Large rocks
MI	East	Protected	30 m	100% < 15°	100% Gravel
MV	North	Exposed <sup>b</sup>	10 m	100% < 15°	60% Sand 40% Gravel
CR	South	–	30 m <sup>c</sup>	100% > 60° <sup>c</sup>	100% Small rocks

<sup>a</sup>In the marine study sites, substratum refers to the kind of material present in the intertidal area, while in the freshwater site (CR) substratum was measured between the water level and the vegetation.

<sup>b</sup>Exposed to winter north winds.

<sup>c</sup>Vegetation cover and slope considered from or above water level.

CR, Cisne River; MF, Magdalena Fjord; MI, Magdalena Island; MV, Marta Valley; QF1, Queulat Fjord 1; QF2, Queulat Fjord 2.

(footprints and faeces) were searched for. One month before the start of the study in 2007, a preliminary survey was carried out to map otter and mink latrines (later call stations), and to collect and eliminate field signs – these samples were not used in the analyses.

Habitat use and habitat overlap between the two species were assessed by using otter and mink field signs as a proxy for their presence and by applying the index of revisitation rate (IRR) method that was developed and tested in previous studies (Medina-Vogel *et al.*, 2003; Medina-Vogel & Gonzalez-Lagos, 2007). Surveys for mink signs have been shown to be a sufficiently reliable method to detect the presence/absence of mink even when otters are present (Bonesi & Macdonald, 2004b; Harrington, Harrington & Macdonald, 2008). Moreover, an experimental study of the reaction of mink to Eurasian otters' odour has shown that mink do not avoid otter markings (Harrington *et al.*, 2009). Given these studies, we conclude that mink signs are an adequate indication of mink presence or absence. The IRR method requires IRR frequencies to be calculated by dividing the number of positive stations found in each site by the total distance (3 km) surveyed along each site, where a 'positive station' is defined as a localized small area where spraints, footprints or smears are found. Positive stations separated by more than 5 m were considered as different and counted as a single (presence/absence) case in the sample size, irrespective of the number of field signs present (Medina-Vogel *et al.*, 2003). Because signs were cleared during each survey, the IRR represents the species' habitat-use frequency at each study site that occurred in the 3 months between surveys.

IRR data were not normally distributed (Shapiro–Wilk statistic  $P < 0.02$ ), thus we used the Kruskal–Wallis one-way analysis of variance by ranks test ( $H$ ) to explore differences in site use within each species as measured by IRR and the Dwass–Steel–Critchlow–Fligner Test for all pairwise comparisons between sites (Sheskin, 2000). Thereafter, we used Mann–Whitney  $U$  tests ( $U$ ) to compare differences in site use between the two species at the marine study sites. We then used Spearman's rank correlation two-tail tests to assess whether the presence of otter and mink signs at each site and over all sites was negatively or positively correlated. All tests were performed in SYSTAT (Systat Software, Inc., Point Richmond, CA, USA). Finally, to test whether the probabilities of finding mink and otter field signs were high or low, at each of the five marine sites, we performed a static interaction analysis in which the frequencies of presence of field signs per study site were compared without reference to the temporal sequence of frequencies (Powell, 2000). Thus, the probability that an otter field sign  $i$  and mink field sign  $j$  were in the same study site was computed as:

$$I_p = \sum_{kij} P_{ki} \times \sum_{kij} P_{kj}$$

where  $I_p$  is the simple probability index, and  $P_{ki}$  and  $P_{kj}$  are the independent probabilities that at any arbitrary time an otter field sign  $i$  and a mink field sign  $j$  were in the same study site  $k$  in the same survey  $P$  (adapted from Powell, 2000).

## Diet

Spraints were collected at all six study sites during the surveys described earlier. They were washed and dried at 75°C for 48 hours (Medina, 1997). Prey remains were identified and compared with reference material at the Ecosystem Health Laboratory, Universidad Andrés Bello. Diet assessment was carried out by prey species and prey groups (fish, crustaceans, terrestrial and other aquatic species). The results were tabulated as: 'O,' occurrence (number of spraints in which a prey species or prey group occurred) and 'RF,' relative frequency (number of spraints in which a prey species or prey group occurred divided by the total occurrence of all the prey species or prey groups found). The data were not normally distributed even after transformation. Therefore, differences between prey groups were assessed by means of non-parametric tests (Pearson chi-square test, Kruskal–Wallis one-way analysis of variance and Mann–Whitney  $U$  tests). Niche breadth was determined by the Levins (1968) equation:

$$B = 1 / \sum_i p_i^2$$

where  $p_i$  is the relative frequency of each prey species  $i$  in the diet. Niche overlap was calculated with the equation:

$$\alpha = \frac{\sum_i p_i q_i}{\sqrt{\sum_i p_i^2 \sum_i q_i^2}}$$

where  $p_i$  is the proportion of the  $i$ th prey species in the diet of predator  $p$ , and  $q_i$  is the proportion of the  $i$ th prey species in the diet of predator  $q$  (Pianka, 1973). Diet diversity was assessed by the Shannon–Wiener diversity index (Magurran, 1988):

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

where  $s$  is the total number of species in the diet and  $p_i$  the frequency of the  $i$ th species.

Values of  $H'$  between otter and mink were compared by means of the Hutcheson  $t$ -test (Magurran, 1988). 'Undetermined prey species' were not included in the calculation of the indices while assuming that they were roughly proportional to the determined ones.

## Activity pattern

To verify whether mink in the presence of otters tended to be active at different times of the day, we conducted a radio-tracking study at the marine study site with the highest overlap between mink and otters in terms of IRR (Magdalena Fjord study site, Table 2) and at the Cisne River. To compare otter and mink daily patterns of activities, we divided the day into four blocks of 6 hours starting at midnight. To compare night versus day activities within each species, we divided the day into two: 6:00 AM–6:00 PM (day) and 6:00 PM–6:00 AM (night). Non-parametric tests were used to test for differences.

**Table 2** Mean index of revisitation rate frequencies, indicating site use by otter *Lontra provocax* and mink *Neovison vison*, and Mann–Whitney *U* tests for differences in site use between the two species

Study site	IRR				Mann–Whitney <i>U</i> test			Probability index ( $I_p$ ) $n$ ( $X \pm SD$ )	Spearman's ( $r$ )
	Total		Mink		Total				
	Mean	SE	Mean	SE	Otter rank-sum	Mink rank-sum	<i>P</i>		
Magdalena Fjord	0.48	0.08	0.51	0.08	69.0	36.0	0.04	7 0.26 $\pm$ 0.10	–0.59
Magdalena Island	0.03	0.08	1.0	0.08	32.5	72.5	0.01	6 – <sup>a</sup>	– <sup>a</sup>
Marta Valley	0.67	0.08	0.30	0.08	67.0	38.0	0.05	5 0.02 $\pm$ 0.03	–0.54
Queulat Fjord 1	0.62	0.08	0.36	0.08	71.0	34.0	0.02	6 0.08 $\pm$ 0.11	–0.66
Queulat Fjord 2	0.71	0.08	0.27	0.08	71.5	33.5	0.01	6 0.02 $\pm$ 0.04	–0.68
Overall*	0.60	0.07	0.37	0.07	1,411	1,074	0.04	30 0.09 $\pm$ 0.11	–0.64* <sup>b</sup>

<sup>a</sup>Statistics were not calculated due to the too small frequency of otter signs.

<sup>b</sup>Level of significance of Spearman's rank based on two-tailed tests.

\* $P < 0.01$ .

Probability index showing the probability that otter and mink signs would be found during the same survey; Spearman's correlation coefficient test results of the correlation between otter and mink signs for each site and over all sites.  $n$  represents the number of times that each site has been surveyed.

SD, standard error; SE, standard error.

An animal was considered to be active when moving outside the den.

Minks were trapped using wire double-entrance cage traps. Traps were spaced between 500 and 1000 m at the marine shore (range 5–36 traps per night for a total of 957 trap nights) or along the river (range 8–21 traps per night for a total of 251 trap nights). We also deployed traps inland up to 500 m from the shore in the marine area and up to 3 km from the Cisne River. However, we never trapped a mink under these conditions. Otters were trapped using Victor soft-catch foothold traps (1.5 Soft Catch, Litz, PA, USA). Trapped animals were anaesthetized (Ketamine-Xylazine; Ketamine, Ketostop®, Drag-pharma Invetec S.A., Santiago, Chile; Xlazine: Rompun®, Bayer, Leverkusen, Germany), equipped with implantable transmitters with activity switches, measured, and then released at the point of capture. The radio-tracking study took place in April 2009, October 2010 and November 2010. Tagged animals were located by triangulation from two mobile stations and, where possible, by homing in. A strong signal was received up to 800 m away. The position was estimated for each individual every 10 minutes for one continuous period of 24 hours, and when it was possible once a week every 10 minutes for 1 hour twice a day for 12 days until a circadian cycle was completed. To avoid biases due to time in captivity, only radio locations obtained 5 days after mink and otters were released were analysed. Trapping and radio-tracking methods for both otter and mink were approved by the bioethical committee of the Universidad Andrés Bello.

## Results

### Habitat use and species overlap

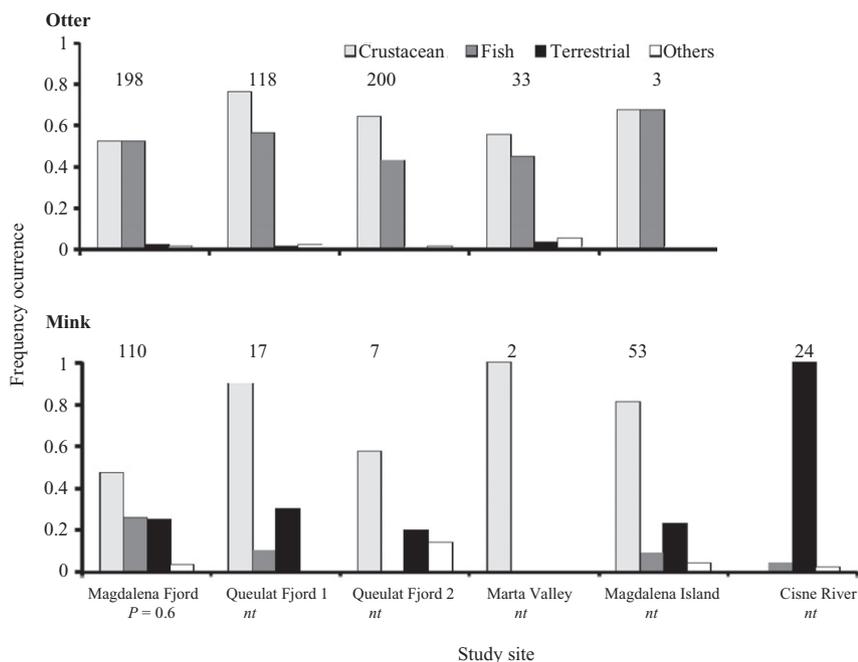
From a total of 30 surveys at the marine sites, we recorded 332 mink- and 212 otter-positive sites and collected 189 mink and

552 otter faeces. All spraints, footprints or smears found were located no further than 60 m from the high-tide line. The five marine study sites differed markedly in their habitat characteristics, except for Queulat Fjord 1 and Queulat Fjord 2 (Table 1). The most heterogeneous site was Magdalena Fjord (Table 1).

Otters' signs were recorded significantly more often (i.e. higher IRR) than those of minks' at all marine sites, except at Magdalena Fjord and Magdalena Island (Mann–Whitney *U* tests – Table 2). The ratio between the IRR of otters and minks was 1.6 ( $n = 5$  sites, range = 0.03–2.6), indicating that overall otters tended to scent mark marine sites more often than minks.

For otters, IRR was significantly different between marine sites [ $H = 11.8$ , degrees of freedom (d.f.) = 4,  $P = 0.02$ ] as Marta Valley, Queulat Fjord 1 and Queulat Fjord 2 recorded significantly higher IRR than the other sites (Dwass–Steel–Critchlow–Flinger Test  $P < 0.05$ ). Although there were significant differences in IRR for mink between the five marine sites ( $H = 20.73$ , d.f. = 4,  $P < 0.01$ ) (Table 2), there was no significant difference in the pairwise comparisons with the Dwass–Steel–Critchlow–Flinger Test. The probability ( $I_p$ ) that otter and mink field signs were found in the same study site during the same survey was low at all sites, except for Magdalena Fjord (Table 2). It was not possible to calculate the probability index and the Spearman's correlation coefficient for Magdalena Island as there were only two surveys in which we found very few otter signs (IRR = 0.13 and 0.09), so that there were too few data to perform the analyses.

Furthermore, the frequencies of otter and mink field signs were negatively correlated at each of the sites (Table 2), and the negative correlation was significant when all sites were considered together (Spearman's  $r = -0.64$ ,  $n = 24$ ,  $P < 0.01$ ) (Table 2).



**Figure 2** Frequency of occurrence of prey groups in otter and mink faeces. The numbers above the histograms indicate sample sizes. *P* indicates the statistical significance of the Pearson chi-square tests when comparing the diets of otter and mink in terms of prey groups at each site; *nt* indicate that no test was performed due to small sample sizes.

## Diet

At the Cisne river, mink scats contained mainly rodents (80%), whereas at the marine sites the most common prey group was crustaceans (51%) (Fig. 2). Otter diet in the marine sites comprised mainly crustaceans (51%) followed by fish (46%) (Fig. 2; Table 3), but otters ate significantly more fish than minks ( $U = 25.0$ ,  $d.f. = 1$ ,  $P < 0.01$ ). When considering otters and minks separately and the prey groups taken by them at the different sites, we found that there was a significant difference from site to site for both species (otter –  $H = 28.8$ ,  $d.f. = 3$ ,  $P < 0.01$ ; mink –  $H = 32.6$ ,  $d.f. = 3$ ,  $P < 0.01$ ), and that the otter's diet diversity index ( $H' = 2.622$ ) was significantly higher than that of the mink's ( $H' = 2.186$ ) ( $t = 54.2$ ,  $d.f. = 2-262$ ,  $P < 0.01$ ). Consequently, otters demonstrated a larger niche breadth ( $B = 0.9$ ) than minks ( $B = 0.4$ ).

A relatively low Levins niche overlap index between the two species was recorded ( $\alpha = 0.263$ ), when considering the marine study sites with the highest number of recorded faeces (Magdalena Fjord and the two Queulat fjords). At Magdalena Fjord, which was the site with the highest probability of finding otter and mink signs together (Table 2), there were no significant differences between the diets of otters and minks (Fig. 2). At the two Queulat fjords, where the probability of finding otter signs was greater than that of finding mink signs (Table 2), the diets of otters and minks were significantly different (Fig. 2).

## Activity patterns

A total of 15 mink (eight males and seven females) were trapped in January 2009 and in January 2011 at Magdalena Fjord. Of these, two individuals, a male and a female, were

radio-tagged and 11 and 69 radiolocations were recorded, respectively. On the Cisne River, a total of 11 minks (nine males and two females) were trapped, five in February 2010 and six in November 2010. Of these, five males were radio-tagged (193 radiolocations in total – average per individual =  $43 \pm 18$  standard deviation). At Magdalena Fjord, an adult male otter, whose home range overlapped with that of the female mink, was trapped and radio-tagged (122 radiolocations).

The male otter showed no significant differences between night and day activity ( $U = 72.5$ ,  $d.f. = 1$ ,  $P = 0.98$ ), but the male and female minks were significantly more active during the day ( $U = 36.5$ ,  $d.f. = 1$ ,  $P = 0.04$ ). Conversely, in the freshwater habitat, where otters and minks did not coexist, minks showed no difference between night and day activities ( $U = 232$ ,  $d.f. = 1$ ,  $P = 0.82$ ).

## Discussion

We found that in the coastal area, the presence of minks, as inferred by their field signs, tended to be inversely correlated to that of the southern river otter, but this pattern seemed to be strongly determined by the characteristics of the habitat. Previous studies, conducted in freshwater areas, showed that habitat heterogeneity may play an important role in determining the likelihood of coexistence of the American mink with the Eurasian otter (Bonesi & Macdonald, 2004c), and that habitat diversity is positively associated with the presence of both the American mink and the Eurasian otter (Lundy & Montgomery, 2010). In our case, habitat heterogeneity, coupled with the physiological constraints of the two species that leads them to exploit different habitats, is possibly also one of the factors that may explain the presence or absence of

**Table 3** Occurrence (O), frequency of occurrence (FO) and relative frequency (RF) of prey species in southern river otter *Lontra provocax* ( $n = 552$ ) and American mink *Neovison vison* ( $n = 189$ ) faeces from five marine sites in southern Chile

Prey species	Otter diet			Mink diet		
	O	FO	RF	O	FO	RF
<b>Crustaceans</b>						
<i>Cancer setosus</i>	12	0.02	0.02	0	0.00	0.00
<i>Cancer</i> sp.	52	0.09	0.08	0	0.00	0.00
<i>Munida</i> sp.	22	0.04	0.03	0	0.00	0.00
<i>Hemigrapsus crenulatus</i>	56	0.10	0.08	26	0.14	0.11
<i>Acanthocyclus hassleri</i>	38	0.07	0.06	19	0.10	0.08
Undetermined	194	0.35	0.29	87	0.46	0.38
Total	341	0.62	0.51	116	0.61	0.51
<b>Fish</b>						
<i>Pinguipes chilensis</i>	36	0.07	0.05	2	0.01	0.01
<i>Eleginops maclovinus</i>	49	0.09	0.07	0	0.00	0.00
<i>Sebastes capensis</i>	54	0.10	0.08	0	0.00	0.00
<i>Salilota australis</i>	8	0.01	0.01	0	0.00	0.00
<i>Genypterus</i> sp.	3	0.01	0.00	0	0.00	0.00
<i>Sprattus fueguensis</i>	5	0.01	0.01	1	0.00	0.00
Salmonidae	0	0.00	0.00	0	0.00	0.00
<i>Odontesthes</i> sp.	0	0.00	0.00	1	0.00	0.00
Merlucciidae	8	0.01	0.01	0	0.00	0.00
<i>Agonopsis chiloensis</i>	5	0.03	0.02	1	0.00	0.00
<i>Prolatilus jugularis</i>	11	0.02	0.02	0	0.00	0.00
Undetermined	139	0.25	0.21	33	0.17	0.15
Total	307	0.56	0.46	35	0.19	0.14
<b>Insects</b>						
<i>Chiasognathus granti</i>	5	0.01	0.01	27	0.14	0.12
Total	5	0.01	0.01	27	0.14	0.12
<b>Rodents</b>						
<i>Oligoryzomys longicaudatus</i>	0	0.00	0.00	37	0.20	0.16
Total	0	0.00	0.00	37	0.20	0.16
<b>Birds</b>						
Undetermined	0	0.00	0.00	8	0.04	0.03
Total	0	0.00	0.00		0.04	0.03
<b>Echinoderms</b>						
<i>Loxechinus albus</i>	4	0.01	0.01	0	0.00	0.00
Total	4	0.01	0.01	0	0.00	0.00
<b>Bivalves</b>						
Mytilidae	3	0.01	0.01	0	0.00	0.00
Total	3	0.01	0.01	0	0.00	0.00
<b>Gastropods</b>						
Undetermined	3	0.01	0.01	0	0.00	0.00
Total	3	0.01	0.01	0	0.00	0.00
<b>Amphibians</b>						
Undetermined	0	0.00	0.00	6	0.03	0.03
Total	0	0.00	0.00	6	0.03	0.03

coexistence at the marine sites. Indeed, we observed a relatively small trophic niche overlap of just 0.26, comparable with the smallest recorded between American minks and Eurasian otters by Bonesi *et al.* (2004) in a freshwater habitat in winter (0.23; range: 0.23–0.92). The site with the greatest degree of overlap between the two species, Magdalena Fjord, was also the site with the greatest diversity of suitable habitats,

having similar proportions of gravel–gentle and rocky–steep seashores (Table 1). Gravel–gentle areas are good hunting grounds for minks, because they can find small crustaceans that are probably too small for otters to be considered as suitable prey (Castilla, 2008). On the other hand, rocky–steep seashores are probably the best hunting grounds for otters, because in the sublittoral zone, larger crustaceans and fish are found that the minks are not able to hunt (Castilla, 2008). Indeed, our dietary analysis show that otters were able to exploit fish and both large (*Cancer* spp.) and bottom-dwelling crustaceans (*Munida* spp.) that we did not find in the minks' diet. However, mink tended to hunt more often species found in the intertidal zone like the hairy-handed crab *Hemigrapsus crenulatus* and the crab *Acanthocyclus hassleri*. These observations suggest that habitat segregation between otter and mink may occur at the habitat scale within a single site. We were not able to assess the degree to which exploitation of different habitats by mink was due to the distribution of the prey it was capable of hunting or to disturbance by otters. However, during this study we received two reports from local people of aggressive encounters between otters and minks, which ended after mink fled, suggesting that it is possible that otters may play a role in limiting the mink's access to different habitats (cf. Sidorovich & Macdonald, 2001; Brzeziński *et al.*, 2008).

While the most heterogeneous site hosted both otter and mink signs, coastal sites that were almost exclusively rocky and steep, like Queulat Fjords 1 and 2, showed relatively fewer signs of mink, while showing an abundance of otter signs (Table 2). On the contrary, the single site hosting exclusively a gravel–gentle habitat, Magdalena Island, presented very few signs of otters and abundant signs of minks. Marta Valley was characterized by a gently sloping intertidal area with sand and gravel and was apparently inhospitable for both species because very few signs of either species were found there. Although there are no replicates for each of the habitat combinations (except for the Queulat Fjords), these results fit the known prey and habitat preferences of the two predators. Our data are in accordance with a study conducted in a coastal area of Scotland that predicted that minks should live at higher population densities in coastal areas with heterogeneous shores that provide a wide intertidal zone with few or no areas comprising sand or shingle (small gravel < 2 cm in diameter) (Bonesi, Dunstone & O'Connell, 2000). Our data also accord with observations on habitat preferences of *L. canadensis* and American minks made by Ben-David, Bowyer & Faro (1995) in a coastal area of Alaska. While it is possible that in areas where the intertidal zone is not heterogeneous and where otters are present, minks may move inland to exploit more terrestrial-based resources (e.g. Clode & Macdonald, 1995), our trapping results indicate that this was not the case in our study area. Indeed, no minks were trapped up to 500 m inland at Magdalena Fjord, probably owing to the fact that inland areas were mostly made up of steep cliffs that were unsuitable for mink.

Like in the marine habitats, crustaceans play a key role in the diet of the southern river otter in freshwater habitats as well (Cassini *et al.*, 2009; Sepúlveda *et al.*, 2009), and lack of

this kind of prey in southern Patagonian freshwater systems (Oyandel *et al.*, 2008) explains why otters were absent from the Cisne River study area, where minks resorted to hunting almost exclusively terrestrial prey, which comprised mostly one species of rodents, the long-tailed colilargo *Oligoryzomys longicaudatus*.

Regarding our third question, our study seems to suggest that otters may impact mink by inducing a shift in their activity patterns. Mechanisms of spatial segregation can indeed be complemented by mechanisms of temporal segregation to allow coexistence with a stronger competitor (Berryman & Hawkins, 2006). In our study, and similar to Harrington *et al.* (2009), we have found that when coexisting with otters, mink tended to be more diurnal in spite of their diet being rather similar (Magdalena Fjord) to that of the otter (Fig. 2). On the basis of diet, we would expect a similar circadian pattern of activity as in both species, because this is driven mostly by hunting. Instead, we observed that the otter's activity was more evenly distributed throughout the day, while the mink was predominantly diurnal. In a study of mink activity patterns in a coastal area where fish and crustaceans made up about 50% frequency of occurrence in the mink's diet (Dunstone & Birks, 1987), the mink tended to be predominantly crepuscular or nocturnal (Dunstone & Birks, 1985). Given the similarity in the diets of mink and otter at our site and the predominant crepuscular and nocturnal activity observed in the coastal study by Dunstone & Birks (1987), it is possible mink activity was predominantly diurnal at the marine site, because minks were probably avoiding otters rather than selecting the best times to hunt. However, our radio-tracking data are limited, especially to a single otter, so that our results should be treated with caution and further data are required to confirm this observation.

In conclusion, our study has found that in coastal areas of southern Chile, there is habitat segregation between the southern river otter and the American mink at a local scale, albeit we could not discern whether this was due to the physiological constraints of the species or to the minks avoiding areas of high predation risk. However, a shift in the activity pattern by minks, as our study seems to suggest, may help reduce the use of areas of high predation risk and fits with predictions of the intraguild predation hypothesis (Palomares & Caro, 1999). Moreover, given the relatively large difference in size between the southern river otter and the American mink and predictions of the intraguild predation hypothesis, it is possible that at least some of the habitat-use patterns that we observed are due to mink trying to avoid areas of higher predation risk (Palomares & Caro, 1998). Unlike Fasola *et al.* (2009), who found that in the freshwater habitats of Patagonia, resource use by mink was more similar to that of otters where the species occurred sympatrically than when they were allopatric, in our case minks tended to have a more diverse and terrestrial diet at the site where they coexisted with otters than at the sites where they were allopatric, where they tended to eat almost exclusively crustaceans. This difference may be explained by the fact that in the freshwater habitats of Patagonia, there is less prey diversity than in our coastal study, and also possibly by the fact that otters are likely to be found at higher

population densities in coastal habitats, forcing minks to shift their niche to a greater extent.

## Acknowledgements

This research was funded by project DGI 01-01-09/R of the Universidad Andrés Bello, radio collars, mink trapping and radio tracking funded by FONDECYT project 1100130 and Servicio Agrícola y Ganadero (SAG). We are very grateful to Mr. René Monsalve and Vicente Celedón for field assistance.

## References

- Arim, M. & Marquet, P.A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.* **7**, 557–564.
- Ben-David, M., Bowyer, R.T. & Faro, J.B. (1995). Niche separation by mink and river otters: coexistence in a marine environment. *Oikos* **75**, 41–48.
- Berryman, A.A. & Hawkins, B.A. (2006). The refuge as an integrating concept in ecology and evolution. *Oikos* **115**, 192–196.
- Bonesi, L. & Macdonald, D.W. (2004a). Impact of released Eurasian otters on a population of American mink: a test using an experimental approach. *Oikos* **106**, 9–18.
- Bonesi, L. & Macdonald, D.W. (2004b). Evaluation of sign surveys as a way to estimate the relative abundance of American mink (*Mustela vison*). *J. Zool. (Lond.)* **262**, 65–72.
- Bonesi, L. & Macdonald, D.W. (2004c). Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink. *Oikos* **106**, 509–519.
- Bonesi, L., Dunstone, N. & O'Connell, M. (2000). Winter selection of habitats within intertidal foraging areas by mink (*Mustela vison*). *J. Zool. (Lond.)* **250**, 419–424.
- Bonesi, L., Chanin, P. & Macdonald, D.W. (2004). Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* **106**, 19–26.
- Bonesi, L., Strachan, R. & Macdonald, D.W. (2006). Why are there fewer signs of mink in England? Considering multiple hypotheses. *Biol. Conserv.* **130**, 268–277.
- Brzeziński, M., Świącicka-Mazan, A. & Romanowski, J. (2008). Do otter and mink compete for access to foraging sites? A winter case study in the Mazurian Lakeland, Poland. *Ann. Zool. Fenn.* **45**, 317–322.
- Cassini, M.H., Fasola, L., Chehébar, C. & Macdonald, D.W. (2009). Scale-dependent analysis of an otter-crustacean system in Argentinean Patagonia. *Naturwissenschaften* **96**, 593–599.
- Castilla, J.C. (2008). *Una guía para la observación del Litoral Chileno*. Santiago, Chile: Pontificia Universidad Católica de Chile.
- Clode, D. & Macdonald, D.W. (1995). Evidence for food competition between mink (*Mustela vison*) and otter (*Lutra lutra*) on Scottish island. *J. Zool. (Lond.)* **237**, 435–444.

- Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis* **150**, 3–17.
- Dunstone, N. & Birks, J.D.S. (1985). The comparative ecology of coastal, riverine and lacustrine mink *Mustela vison* in Britain. *Z. Angew. Zool.* **72**, 59–70.
- Dunstone, N. & Birks, J.D.S. (1987). The feeding ecology of mink (*Mustela vison*) in a coastal habitat. *J. Zool. (Lond.)* **212**, 69–83.
- Fasola, L., Chéhébar, C., Macdonald, D.W., Porro, G. & Cassini, M.H. (2009). Do alien North American mink compete for resources with native South American otter in Argentinean Patagonia? *J. Zool. (Lond.)* **277**, 187–195.
- Harrington, L.A., Harrington, A.L. & Macdonald, D.W. (2008). Estimating the relative abundance of American mink *Mustela vison* on lowland rivers: evaluation and comparison of two techniques. *Eur. J. Wildl. Res.* **54**, 79–87.
- Harrington, L.A., Harrington, A.L. & Macdonald, D.W. (2009). The smell of new competitors: the response of American mink, *Mustela vison*, to the Odours of Otter, *Lutra lutra* and Polecat, *M. putorius*. *Ethology* **115**, 421–428.
- Levins, R. (1968). *Evolution in changing environments*. Princeton, NJ: Univerity Press.
- Lundy, M.G. & Montgomery, W.I. (2010). A multi-scale analysis of the habitat associations of European otter and American mink and the implications for farm scale conservation schemes. *Biodiver. Conserv.* **19**, 3849–3859.
- Magurran, A.E. (1988). *Ecological diversity and its measurement*. London: Croom Helm Limited.
- McDonald, R.A., O'Hara, K. & Morrish, D.J. (2007). Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*). *Divers. Distrib.* **13**, 92–98.
- Medina, G. (1997). A comparison of the diet and distribution of Southern river otter (*Lutra provocax*) and mink (*Mustela vison*) in southern Chile. *J. Zool. (Lond.)* **242**, 291–297.
- Medina-Vogel, G. & Gonzalez-Lagos, C. (2007). Habitat use and diet of endangered southern river otter in a predominantly palustrine wetland in Chile. *Wildl. Biol.* **44**, 979–982.
- Medina-Vogel, G., Kaufmann, V., Monsalve, R. & Gomez, V. (2003). The relationship between riparian vegetation, woody debris, stream morphology, human activity and the use of rivers by southern river otter in Chile. *Oryx* **37**, 422–430.
- Niemimaa, J. (1995). Activity patterns and home range of the American mink *Mustela vison* in the Finnish outer archipelago. *Ann. Zool. Fenn.* **32**, 117–121.
- Oyandel, A., Valdovinos, C., Moya, C., Azocar, M., Mancilla, G. & Figueroa, R. (2008). Patrones de distribución espacial de los macroinvertebrados bentónicos de la cuenca del río Aisén. *Gayana* **72**, 241–257.
- Palomares, F. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *Am. Nat.* **153**, 492–508.
- Pianka, E.R. (1973). The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**, 53–74.
- Powell, R.A. (2000). Animal home range and territories and home range estimators. In *Research techniques in animal ecology: 65–110*. Boitani, L. & Fuller, T.K. (Eds). New York: Columbia University Press.
- Sepúlveda, M.A., Bartheld, J.L., Monsalve, R., Gómez, V. & Medina-Vogel, G. (2007). Habitat use and spatial behaviour of the endangered southern river otter (*Lontra provocax*) in riparian habitats of Chile: conservation implications. *Biol. Conserv.* **140**, 329–339.
- Sepúlveda, M.A., Bartheld, J.L., Meynard, C., Benavides, M., Astorga, C., Parra, D. & Medina-Vogel, G. (2009). Landscape features and crustacean prey as predictors of the southern river otter (*Lontra provocax*) distribution in Chile. *Anim. Conserv.* **12**, 522–530.
- Sergio, F. & Hiraldo, F. (2008). Intraguild predation in raptor assemblages: a review. *Ibis* **150**(Suppl. 1), 132–145.
- Sheskin, D.J. (2000). *Handbook of parametric and nonparametric statistical procedures*. 2nd edn. Boca Raton: Chapman & Hall/CRC.
- Sidorovich, V. & Macdonald, D.W. (2001). Density dynamics and changes in habitat use by the European mink and other native mustelids in connection with the American mink expansion in Belarus. *Neth. J. Zool.* **51**, 107–126.
- Simpson, V.R. (2006). Patterns and significance of bite wounds in Eurasian otters (*Lutra lutra*) in southern and south-west England. *Vet. Res.* **158**, 113–119.
- Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002). Exclusion by interference competition? the relationship between red and arctic foxes. *Oecologia* **132**, 213–220.
- Veblen, T.T. & Schlegel, F. (1982). Reseña ecológica de los bosques del sur de Chile. *Bosques (Valdivia)* **4**, 73–115.