

Do alien North American mink compete for resources with native South American river otter in Argentinean Patagonia?

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Abstract

American mink *Mustela vison*, originally bred in fur farms, have become established in areas occupied by native endangered Southern river otter *Lontra provocax*, in Patagonia. In accordance with European experience, this biological invasion in South America raises questions about the interaction between invasive mink and native otter, from the viewpoints of both community assembly and conservation. We set out (1) to find which aspects of habitat structure were related to the distribution of signs of both this invasive species and Southern river otter *Lontra provocax*, in Argentinean Patagonia and their most common prey and (2) to test general predictions of niche partitioning between these two species. Based on surveys of 447 of 600 m transects for otter and mink scats/footprints along the waterside of lakes and rivers in the Andean Patagonian region, we compared diet composition (from scat analysis) and micro-habitat preferences (from field signs) of the two species. Otters were more specialist than mink in habitat use and diet. Mink used different habitats in other river basins where otters were absent. Where they occurred together in the basin of the Limay River, the distributions of their signs were similar, and mink diet was more similar to that of otters. There was no detectable difference in otter diet before and after mink arrival in the Limay basin. Contrary to the prediction of niche partitioning, and to the findings of European studies, resource use by mink was more similar to that of otters where the species occurred sympatrically than where they were allopatric.

Introduction

The introduction of exotic species is considered the second main threat, globally, to biodiversity after habitat destruction (Macdonald & Thom, 2001). One aspect of this threat arises where invasive species compete with the native ones for resources (Pimentel *et al.*, 2000).

The American mink *Mustela vison*, was introduced to Europe and South America for fur farming in the first half of the last century. Following escapes and releases, feral mink populations are now established in Britain, continental Europe and South America (Macdonald & Harrington, 2003). Mink predation has been responsible for declines in native birds (Craik, 1997) and mammals (Barreto *et al.*, 1998). This invasive species also has serious negative impacts on native competitors (e.g. the European mink *Mustela lutreola*, Macdonald *et al.*, 2002). In Europe and South America, mink have spread, and their distribution now overlaps with the natural range of native otter species (*Lutra lutra* and *Lontra provocax*, respectively).

The similarities between mink and otter in terms of prey and habitat use have led researchers to test predictions of competition theory, not only to assess the potential impact of mink on otter (or vice versa) but also to improve the understanding of the mechanisms underlying community assembly.

In North America, within the mink's natural range, coexistence between otter *Lontra canadensis* (8–10 kg), and mink is thought to be possible due to differences in foraging strategies and because of the more generalist characteristics of the latter in terms of habitat use (Melquist, Whitman & Hornocker, 1981). These differences are presumably a result of past competition. However, in Great Britain, where the co-occurrence of the two species is more recent, there is evidence of competition between American mink and Eurasian otter *L. lutra* (5–11 kg) (Clode & Macdonald, 1995; Bonesi, Chanin & Macdonald, 2004; Bonesi & Macdonald, 2004a,b). Bonesi *et al.* (2004) found a shift in American mink diet after otters recovered in their study area (from a predominance of aquatic prey to a higher frequency of

terrestrial items). Also, mink signs decreased in an area where otter numbers increased after a reintroduction programme (Bonesi & Macdonald, 2004a). Coexistence persisted longer where habitat heterogeneity was high enough to provide mink with sufficient terrestrial prey in response to the increasing presence of otters (Bonesi & Macdonald, 2004a,b). Elsewhere in the United Kingdom, Harrington (2007) found Eurasian otters and American mink coexisting with no evidence of habitat partitioning, but with a phase shift in the activity rhythm of mink, which were predominantly diurnal in the presence of otters. Clode & Macdonald (1995) reported a shift in the diet of mink, but not that of otter on Scottish Islands. Additionally, there is evidence of otters outcompeting mink in direct contests (Bonesi & Macdonald, 2004b). In summary, unlike native prey species, Eurasian otters have apparently not suffered due to the arrival of the American mink in Britain. In fact, some authors have proposed a hypothesis that the presence of otters may cause mink to decline (Bonesi & Macdonald, 2004a; McDonald, O'Hara & Morrish, 2007) and there is evidence that the presence of Eurasian otters in Spain slows the colonization of the invasive mink (Ruiz-Olmo *et al.*, 1997).

The huillín or Southern river otter is an endemic (Cabrera, 1957), endangered species from Argentinean and Chilean Patagonia (IUCN, 2007). In Argentina, the largest known population occupies freshwater bodies in the west of the basin of the Limay River in Patagonia, where they feed predominantly on two genera of macrocrustaceans (Chehébar, 1985). American mink have spread prodigiously in the Andean-Patagonian region of Argentina, since they were first seen in the wild in the 1960s. In just 40 years, they have expanded their range to occupy most of the forest strip formed by the Andean-Patagonian region, and between 1983 and 1995 mink invaded the huillín's range in the Limay River basin (Chehébar *et al.*, 1986; Porro & Chehébar, 1995). The principal prey of American mink in Patagonia are small rodents and lagomorphs, but a large proportion of their diet can be macrocrustaceans (Medina, 1997; Previtali, Cassini & Macdonald, 1998).

The balance of competition and coexistence varies depending on the availability of resources, the level of resource use overlap and the time since the species started to co-occur. But another relevant factor is the ability of the species to respond to a novel competitor (Keddy, 2001) (in this case, a native species receiving an invasive potential competitor). In the case of the huillín, the species in Argentina has faced a drastic reduction in its distribution due to hunting. The population in the Limay River basin has been monitored over the last 20 years and is now slowly recolonizing sites (Chehébar, 1985; Porro & Chehébar, 1995; Fasola *et al.*, 2006). Also, this population showed less genetic variability than the coastal otters, probably due to isolation (Centrón *et al.*, 2008). Therefore, it is also possible that huillín, given their population characteristics in the Limay basin, will be in a different competitive balance with mink than that studied in Britain.

This study is based on surveys of the presence of otter and mink, as evidenced by droppings and footprints, along 600 m waterside transects bordering lakes and rivers in the Andean Patagonian region. Firstly, we compared (1) the frequency of sites with American mink signs between aquatic habitats grouped by circumstances (aquatic habitat type, presence/absence of crustaceans, presence/absence of South American river otter); (2) the diet of the American mink between these same pairs of circumstances; (3) the diet of south American river otter before and after the arrival of the American mink. In one river basin, that of the Limay River, both mink and otters were found, so there we sought to describe local characteristics associated with defaecation (scent-marking) sites chosen by each species. The results enabled us to test the prediction that two predator species, known to use two resources (space and prey) similarly, would have negative effects on each other and exhibit a shift in the use of these principal resources where they occur sympatrically.

Methods

Study area

We surveyed a strip of forest (38°52'S–54°52'S) that fringes most of the length of the east side of the Andes, running north–south through Patagonia. Within this, we visited freshwater bodies in 10 different river basins where the climate is cold-temperate and humid, and precipitation occurs mainly in winter (June–September), as either rainfall or snow (Cabrera, 1971). The forest is dominated by *Nothofagus* spp. (Cabrera, 1971).

Potential prey along this strip of forest include 20 species of native rodents (families: Cricetidae, Ctenomyidae, Caviidae, Myocastoridae), two exotic murid rodent species, two exotic lagomorph species, four native opossums (Redford & Eisenberg, 1992), seven native fish species of which three are abundant, three frequent exotic fish species (Milano *et al.*, 2006), two genera of aquatic macrocrustaceans (one species and two subspecies) (Morrone & Lopretto, 1994) and more than 75 species of waterfowl (Christie, Ramilo & Bettinelli, 2004). There are other carnivores present throughout the area: two species of skunks, two other mustelid species, two fox species and four felid species (all of which are thought to be terrestrial) (Redford & Eisenberg, 1992).

Field survey

Between January and May 2005, and January and February 2006, 447 survey sites (each separated by a distance of more than 4 km; Chehébar, 1985) were visited along the edges of 67 lakes and 62 rivers and streams. At each site, two or more people intensively (50–150 min) surveyed 600 m of waterside (following Macdonald, 1983) for mink and otter signs (footprints and scats). Scats found were collected and various environmental variables recorded. At river sites, only one bank was surveyed (because in our generally remote study areas there were few bridges, so crossing the

rivers was hazardous). The assumptions in two aspects of the methodology of our survey deserve comment. Firstly, despite the careful evaluation of this genre of survey by Bonesi & Macdonald (2003), there is no doubt that it can be less revealing than the tracking rafts described by Reynolds, Short & Leigh (2004). Indeed these two techniques are specifically compared by Harrington, Harrington & Macdonald (2007). Therefore, and despite the great intensity of our sign searches, the possibility of false negatives cannot be excluded (particularly as we surveyed only one bank in rivers). Secondly, because the home range sizes of these two mustelids have not been documented yet in our study areas, and nor have their dispersal distances, it is possible that the 4 km separation between the sample sites was insufficient to rule out the possibility that the same individual was detected in neighbouring sites, to that extent diminishing the statistical independence of our samples. Further studies will shed light on the validity of these assumptions regarding these aspects of space use by mink and otter in Patagonia.

In addition, in 1982 and 1983, before mink arrived, Claudio Chehébar and members of the Nahuel Huapi National Park visited lakes and rivers of the Park following the same type of transects, and collected otter spraints. Scats of other carnivores were only rarely found along the waterline, and were readily distinguished from those of otter and mink.

Diet analysis

We submerged scats in water to facilitate the separation of the faecal contents. Undigested prey remains were sorted into five categories: bird (feathers, bone fragments); mam-

mal (hair, teeth and bone fragments); crustaceans (external skeleton fragments) and fish (vertebrae, scales, skull bone fragments and otoliths). To describe the diet and make comparisons, we calculated: (1) the prey occurrence (the number of faeces in which the prey class was identified) and (2) the relative frequency of occurrence (number of occurrences of a prey class in relation to the sum of occurrences of all prey classes). We described and compared the diet of mink in the presence/absence of crustaceans and presence/absence of the potential competitor. The diet of otter was evaluated before and after mink arrival. We calculated the Shannon–Wiener diversity index (H) for the diet of both species.

Aquatic habitat use – local habitat use analysis

Firstly, we described general patterns regarding the use of lakes and rivers in different situations. For mink, we calculated the frequency of sites where signs were found for basins categorized into the following four types: with crustaceans and without otter; without crustaceans, without otters; and with crustaceans and with otter. For otters, the only category observed was ‘with crustaceans and mink’.

Secondly, we analysed factors associated with the distribution of otter and mink signs in lakes within the Limay River basin (the only basin where both species are sympatric). We applied a principal component analysis (PCA) to eight environmental variables recorded for each of the 172 transects surveyed in the south-west of the Limay River basin. This subarea within the Limay basin (Fig. 1) can be divided into two, a southern portion inhabited by both otter

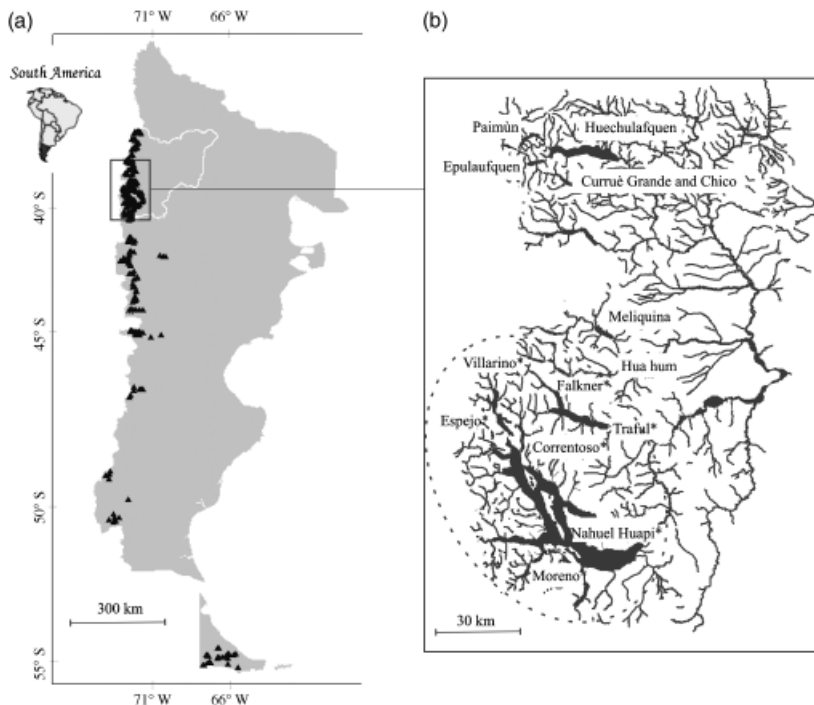


Figure 1 (a) Study area. Grey points: 447 sites surveyed. The Limay River basin (where both species overlap) is delimited by a white border. (b) Detail of the south-west of the Limay River basin, depicting lakes included in the analysis. The dotted oval encompasses lakes that are occupied by both the Southern river otter and the American mink.

Table 1 Results of the logistic regression conducted with the first three factors of the principal component analysis (PCA) and their interactions as independent variables and the presence or absence of signs of minks or otters in the transects, as dependent variables

Species	Context	Variable	Coefficient	Wald test	P-value	2LL
Mink	With otter	PC1	0.37 (0.17)	4.90	0.027	5.1^a
	Otter absent	PC2	-1.35 (0.99)	5.22	0.022	6.79^a
Otter	With mink _a	PC1a	0.88 (0.21)	18.11	<0.001	28.84^b
		PC3a	-0.58 (0.21)	7.53	0.006	
	With mink _b	PC1b	0.96 (0.22)	18.49	<0.001	28.89^b
		PC3b	-0.59 (0.22)	7.08	0.008	

2LL: log-likelihood ratio; the critical values of χ^2 against which the 2LL value was compared to assess the goodness of fit, bold numerals indicate $2LL > \chi^2_{\text{critical value}}$.

PCa: logistic regression model built with factors from PCA indicated as 'a' in Table 2; PCAb: logistic regression model built with factors from PCA indicated as 'b' in Table 2.

^a $\chi^2_{\text{cv,d.f.}=2,0.05} = 4.60$.

^b $\chi^2_{\text{cv,d.f.}=1,0.05} = 3.84$.

and mink ($n = 141$ transects) and a northern portion with only mink ($n = 31$ transects). The variables were as follows: (1) *Bottom material size*: mean of bottom material values (1–6) with 50% or more cover, where mud or bare ground = 1, sand = 2, smooth pebble (<5 cm) = 3, stones (5–20 cm diameter) = 4, medium rocks (20–40 cm diameter) = 5 and large rocks (≥ 40 cm) = 6.

(2) *Coast width (three categories)*: between (1) 0 and 10 m, (2) 10 and 20 m and (3) ≥ 20 m.

(3) *Coast slope (four categories)*: slope between (1) 0 and 25°, (2) 25 and 45°, (3) 45 and 60° and (4) 60 and 90°.

(4) *Human activity*: sum of the presence/absence of human footprints, faeces of domestic ungulates, sightings of people, dogs or cattle.

(5) *Shelter quality*: sum of the presence/absence of hanging vegetation, holts under exposed roots, fallen trunks and dens.

(6) *Tree cover*: 0 (<33%), 1 (33–66%) and 2 (>66%).

(7) *Vegetation complexity*: ranked 1–3 on the basis of the number of strata (herbs and grasses, shrubs and trees) (each stratum defined as present only where cover was $\geq 33\%$).

(8) *Aquatic vegetation*: presence/absence of underwater vegetation.

Variables with a loading of greater than |0.63| were considered as important contributors for the PCA factors (Tabachnick & Fidell, 2001). The first three PCA factors, which explained more than 75% of the variance, were then included in logistic regression analyses to study the relationships between the factors and the distribution of otter and mink signs (presence/absence as dependent variable for each species) (Manly 1993; Guichón & Cassini, 1999; Aued *et al.*, 2003). We partitioned the data according to the presence or absence of the competitor. In this way, three logistic regression models were built. In the first one, presence/absence of mink signs was the dependent variable and it considered sites only within the otter's distribution (Nahuel Huapi, Traful, Espejo, Correntoso, Villarino, Falkner and Moreno lakes). The second model used the same dependent variable but considered sites where mink signs were found beyond the otter's distribution limit (Lolog, Paimún, Epulafquen, Huechulafquen, Meliquina, Hua hum, Currué Chico and

Currué Grande lakes). Finally, in the third model, presence/absence of otters was the dependent variable and only sites within otters' range were considered (Nahuel Huapi, Traful, Espejo, Correntoso, Villarino, Falkner and Moreno lakes) (Table 1). In our study area, there were no locations with otter and without mink. In all the lakes studied, the two species had been known to coexist for at least 5 years. The variables tested in the models included the first three factors of the PCA. The goodness of fit of the models was evaluated using the log-likelihood ratio criteria and the correct inclusion of variables using the Wald test (Agresti, 2002). The outcomes from the logistic regression models were used, firstly, to test for associations between the locations of signs of the species and the PCA factors and, secondly, to compare the associations found for mink in the presence and in the absence of otters. For the purposes of statistical analysis of the associations between the detection of each species and the recorded environmental variables, we make the assumption that our data from all sites are statistically independent. Therefore, conclusions should be drawn cautiously until further evidence is available.

Finally, we sought to describe the sites where signs were found in terms of the habitat variables recorded. As a way to describe more accurately the associations between the variables and otter sprainting sites, we repeated the PCA using environmental data from only those transects (141 transects) within the otter's range (seven lakes, Table 2b). By doing this, we ensured that the factors from the second PCA were exclusively absorbing the variability of the sites within the otter's range. We then built a second logistic regression model for otters, using the presence of their signs as the dependent variable and the first three factors of the second PCA as independent variables. We used the results of this analysis to interpret associations between the likelihood of finding otter signs and the derived habitat variables (Table 1). To investigate associations between signs of American mink and the environmental variables, we used the original regression models (that is to say, the complete dataset of 172 transects located in 15 lakes) (Table 2a).

Table 2 Coefficients of correlations (loadings) between the variables recorded and the first three factors of the principal component analysis (PCA) conducted with data measured on (a) 172 transects of 600 m transects located in 15 lakes of the Limay River basin and (b) 141 transects of 600 m transects located in seven lakes of the Limay River basin (otter range)

Variable	PC1		PC2		PC3	
	a	b	a	b	a	b
Bottom substrate size	0.88	0.89	0.41	0.36	0.22	0.25
Coast width	-0.55	-0.55	0.28	0.30	0.01	0.04
Coast slope	0.62	0.64	0.12	0.04	0.16	0.19
Human activity	-0.73	-0.76	0.08	0.04	0.66	0.64
Shelter quality	0.54	0.55	-0.78	-0.77	0.27	0.26
Tree cover	0.18	0.16	-0.21	-0.29	-0.15	-0.16
Vegetation complexity	0.11	0.17	-0.37	-0.34	-0.15	-0.12
Aquatic plants	0.12	-0.10	-0.27	-0.39	0.01	-0.02
Eigenvalue	3.05	3.46	1.39	1.29	0.82	0.89
Variance explained (%)	46.01	50.17	21.09	18.77	12.48	12.98

The major contributors for each of the PCA factors are in bold.

Results

Signs of otters and mink were found in 73 and 164 (of 447) transects, respectively.

Outside the range of otters, mink signs were found at similar frequencies in both lakes and rivers where macrocrustaceans were present (contingency analysis, $\chi^2 = 1.29$, d.f. = 1, $P = 0.255$) (Fig. 2a). In contrast, in basins where macrocrustaceans were absent, mink were more frequently present in rivers than in lakes ($\chi^2 = 24.18$, d.f. = 1, $P < 0.001$) (Fig. 2a).

Otters fed principally on crustaceans, whereas mink diet was more diverse (Fig. 2b). Diet diversity for mink ($H = 1.14$) was more than twice that for otters ($H = 0.46$) where they are sympatric. The diet of mink was slightly less diverse in the absence of crustaceans ($H = 1.03$) and was most diverse when other basins with crustaceans were included ($H = 1.31$) (in this case, the index was higher than that for the Limay basin alone because prey classes were present in more equitable proportions).

The main variation between locations was due to the fact that mink ate crustaceans when these prey were available (Fig. 2b). There was no significant difference in mink diet between the southern and northern parts of the Limay River basin, where otters are, respectively, absent and present ($\chi^2 = 2.13$, d.f. = 3, $P = 0.546$) (similarly, there was no difference in mink diet between these sections of the Limay basin when only aquatic prey were considered: $\chi^2 = 0.18$, d.f. = 1, $P = 0.668$).

Comparison of prey remains in otter spraints collected in the Limay basin in summer 1982 and 1983 (before the invasion by mink) and in summer 2005 (when mink were present) also showed no significant differences ($\chi^2 = 1.88$, d.f. = 2, $P = 0.39$).

In summary, we could detect no difference in the diet of either mink or otter when comparing situations where the two species coexisted and where they occurred separately.

The salient elements of environmental variation throughout transects taken in the Limay River basin were categor-

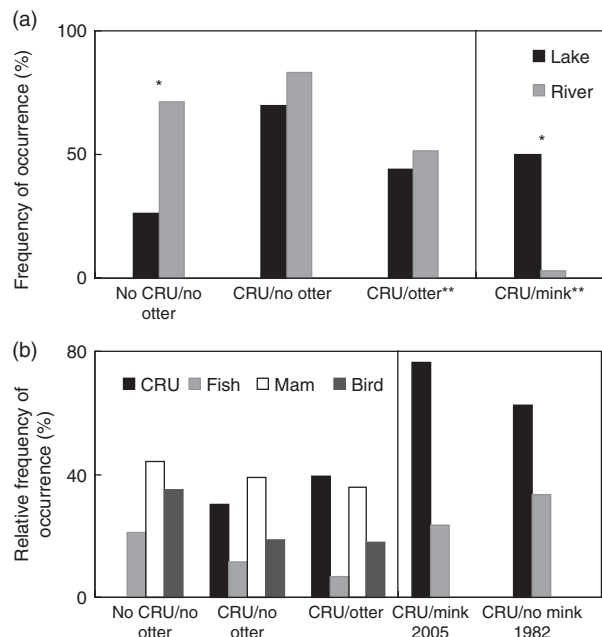


Figure 2 (a) Frequency of positive sites/total sites visited with mink (left)/otter (right) signs recorded in different environments. *Significant differences; **Source: Aued *et al.* (2003). (b) Left: diet of mink in different environments [freshwater environments separated into those with crustaceans (indicated with CRU) and without these sort of prey] expressed as frequency of occurrence (%) of each type of prey. Right: diet of otter in freshwater, with crustaceans, in the presence of mink (2005) and in the absence of the latter (1982).

ized using PCA. The first three factors of the PCA explained 79.6% of the variance found in the variables recorded along transects. The variables with high loadings were 'size of the bottom substrate' for PC1; 'shelter quality' for PC2; and 'human activity' for PC3 (Table 2).

The logistic regression model which best fitted the occurrence of otters (in the presence of mink) included PC1 and

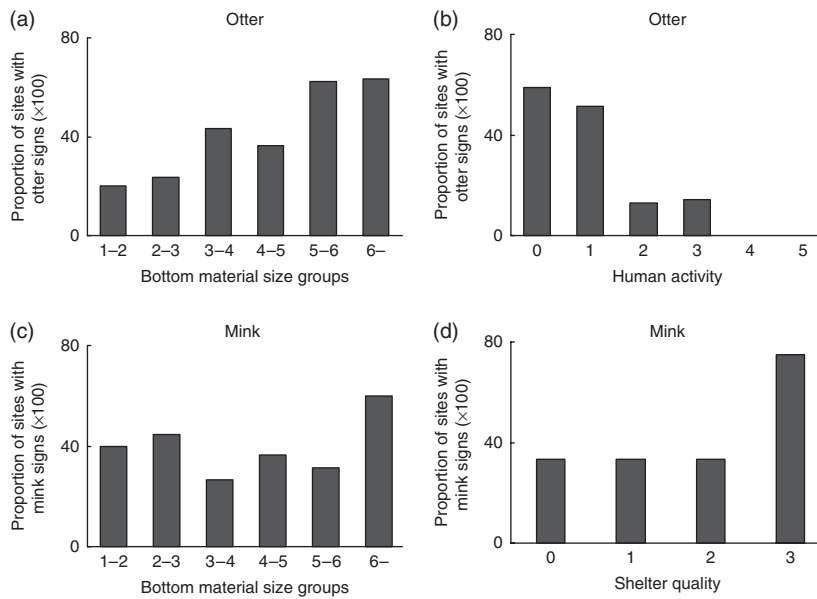


Figure 3 Proportion of sites with (a) otter signs in groups of size of bottom material (groups formed for the purposes of this graph), (b) otter signs in groups of increasing signs of human activity, (c) mink signs in groups of size of bottom material and (d) mink signs in groups of increasing availability of sites for shelter.

PC3 (Table 1). Where both species occurred, the model that best predicted the signs of mink included the first (PC1) factor. Where mink occurred without otters, PC2 helped us to predict mink sign presence.

In short, where mink and otters were sympatric, PC1 was a predictor of the presence of both species. In contrast, where mink occurred in the absence of otters, only PC2 predicted the presence of their signs.

The second PCA conducted specifically for the otter distribution area showed the same variables to be major contributors to the first factors as in the former PCA (Table 2b). The nature of the correlations between factors and the variables was also similar, and consequently, we obtained the same outcome from the logistic model using the results of this PCA (see Table 2b for the results for the second PCA). The presence of otter was predicted by PC1 and PC3, which were entered into the logistic regression model with a positive and a negative coefficient, respectively. The correlation between PC1 and 'size of the bottom material' was positive and it resulted negative with 'human activity'. Correlation between PC3 and 'human activity' was positive. Although PC1 correlated positively with 'coast slope', the value was in the limit.

Summarizing, sites with otter signs tend to be found where bottom material is larger and where fewer signs of human activity are found (Figs 3a, b and 4a).

In the case of mink, within the distribution of the otter, the best predictors of the presence of their signs were also PC1, with a positive coefficient in the logistic regression model. Thus, sites with mink signs (within the range of the otter) tended to be found in places with large bottom material and with fewer signs of human activity (coinciding with the association between otter sign and local habitat characteristics) (Fig. 3c). Where mink are alone (beyond the range of the otter), only PC2 with a negative coefficient was included in the model, showing in this situation that sites

with mink signs tend to be found in places with more shelter (the correlation between PC2 and its best contributor 'shelter quality' was negative) (Figs 3d and 4b).

Discussion

Otters occurring sympatrically with American mink had a more specialized diet than did mink. Mink showed, in all the situations considered here, a more diverse diet than otters in Patagonia, consistent with what has been found elsewhere (Melquist *et al.*, 1981, also Clode & Macdonald, 1995; Bonesi *et al.*, 2004; Bonesi & Macdonald, 2004b). Mink fed on a greater number of prey types than did otters, and where the two species co-occurred, their diets converged because crustaceans (the otter's main prey) became as important as mammals in mink's diet.

Aued *et al.* (2003), in the same area, found that Southern river otters frequented lakes more than rivers and lagoons, and found that macro-crustaceans also occur mainly in lakes. When they compared the occurrence of otters between water bodies, otters favoured those with abundant macro-crustaceans. Within lakes, these authors found a negative effect of human activity, because human settlements in the vicinity were negatively associated with otter signs within lakes. Also, Aued *et al.* (2003), and more recently M. H. Cassini, B. Aued, L. Fasola, C. Chehébar and D. Macdonald (unpubl. data), found that the density of the otter's main prey in the Limay River basin (crustaceans) was greater in bottoms formed of rocks than those characterized by stones, sand or gravel. With a different strategy for variable recording, and including more local habitat variables (i.e. size of the bottom material) as potential predictors of the otter's presence, our analysis formalized the association between large-sized bottom material and the presence of otter signs, a result that is explicable in terms of crustacean abundance. Additionally, the analysis showed that

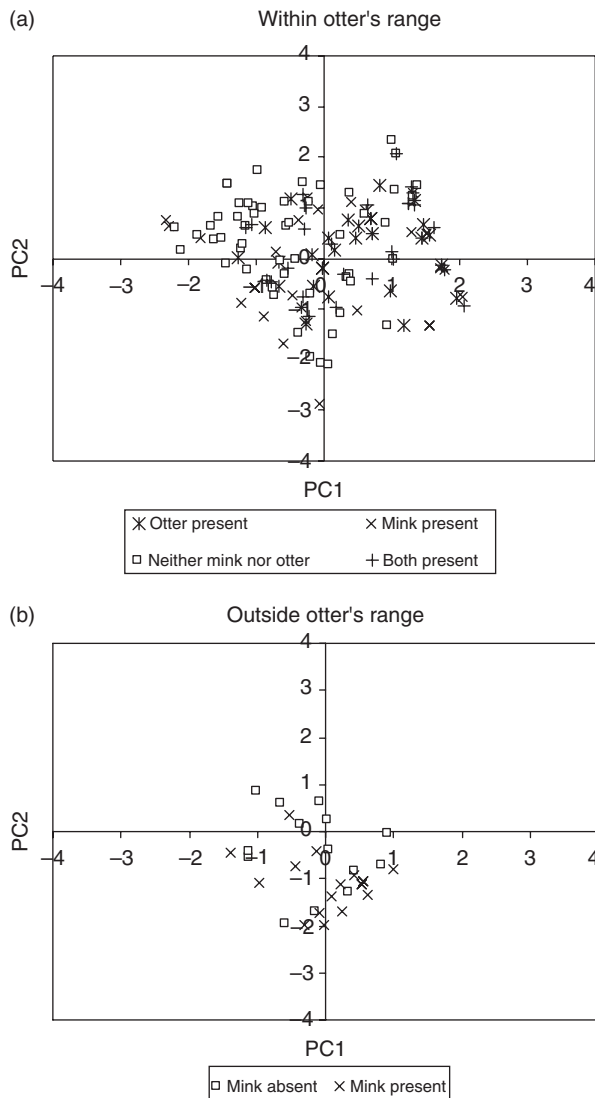


Figure 4 (a) Sites surveyed within the otters' range (the south of the Limay River basin) with respect to factors 1 (PC1) and 2 (PC2): +, sites with signs of both species (correlated positively with PC1); X, sites with signs only of otters; x, sites with signs only of mink; □, sites with neither mink nor otter signs. (b) Sites surveyed outside the otters' range (the north of the Limay River basin): x, sites with signs of mink (associated with lower values of PC2); □, sites without signs.

signs of human activity were associated with an absence of otter signs. Thus, our results support and extend those of Aued *et al.* (2003). Sites with a steep coast tended also to be associated with otter presence. In short, the association between otter signs and substrate characterized by larger rocks and boulders is explicable in terms of crustacean abundance.

The distribution of mink signs differed between river basins when comparing types of aquatic environments. The frequency of occurrence of mink signs was higher for rivers than for lakes in those basins lacking crustaceans, whereas

mink were equally likely to be found along rivers and lakes in basins where crustaceans occurred. Aued *et al.* (2003) found the same trend for mink in the Limay River basin, where macro-crustaceans and otters are present. At a finer scale, within the water bodies of the Limay River basin where otters occurred, mink, like otters, were found in association with rocky bottoms. Beyond the otter's range, the probability of finding mink signs was dictated solely by the availability of bank-side shelter.

Competition, one of the main forces structuring communities, is expected to occur when two ecologically similar species coincide in time and space. Otter and mink typically overlap in prey type and in preferred habitat to varying degrees. When resources are limiting, the extent of overlap generally determines the interaction intensity. Competition intensity and the relative competitive abilities of the competitors determine the outcome of the system (exclusion or simple coexistence without niche differentiation; Keddy, 2001).

Contrary to predictions, we found no evidence suggesting that the use of either prey or habitat by mink and otters diverged when they occurred together in our study area. We did record a change in prey and habitat use in mink, yet, unexpectedly, in the presence of otters, the changes resulted in convergence rather than divergence. This is the opposite of what has been found in Britain, where otters are dominant to mink, and mink change their diet in the presence of otters (Clode & Macdonald, 1995; Bonesi & Macdonald, 2004a; Bonesi *et al.*, 2004).

Possible explanations for our findings include (1) the relationship between the two species was (at the time of the study) still unresolved; (2) species densities are low, and the shared resources are not limiting; (3) the resources were sufficiently abundant so that the competition was alleviated; (4) partitioning of resources was occurring at a scale or dimension not considered in our study (e.g. size of prey, daily activity); (5) the species are so similar that differentiation is not possible (Keddy, 2001) and the negative effects of coexistence may be impacting other aspects of their life histories (e.g. population parameters such as reproductive success) that we did not study or (6) the ability of otters to exert dominance over mink is depressed, given the characteristics of the Limay population (i.e. recovering population, etc.).

By the time of this survey, mink and otters had been present together in the Limay River basin for 10–22 years (Chehébar, 1985; Porro & Chehébar, 1995; Fasola *et al.*, 2006). Bonesi *et al.* (2004) found a shift in mink diet between 1973 and 1999 but in their study area it was not possible to determine the time that elapsed until a shift in mink diet became evident. Nevertheless, it is plausible that the period of coexistence in our study area was insufficient to allow competition to be expressed but this will become clear only over time.

Densities of species were not studied here, but sign surveys in 1983 (Chehébar *et al.*, 1986), 1995 (Porro & Chehébar, 1995), 2000 (Aued *et al.*, 2003) and the present study identified re-colonization of new sites by both species.

This does not support the idea that densities are too low for negative interaction to arise, because dispersal events are generally triggered by density-dependent factors (Lambin, Aars & Pieltney, 2001).

There are, however, two observations that may lend support to the second explanation (2) above. First, where otter and mink coexist, mink feed more heavily on crustaceans (the dominant prey of otters) than they do elsewhere. Second, under these circumstances, mink, like otters, are associated with the rocky bottoms where crustaceans abound. So, crustaceans may be sufficiently abundant to facilitate otter and mink coexistence without detectable dietary competition. Nahuel Huapi is one of the largest lakes in Patagonia, and supports the highest density of macro-crustaceans of all the lakes where otters occur (M. H. Cassini, B. Aued, L. Fasola, C. Chéhébar and D. Macdonald, unpubl. data). Indeed, at Lake Nahuel Huapi, we often found signs of both species at the same dens, although the behavioural implications of this are unknown.

On the marine coast of Tierra del Fuego, mink have recently invaded Lapataia Bay, and there they are now using the same dens that have been recorded as being occupied by otters during the previous 7 years. Kruuk (2006) has also recorded mink using shelter also used by *L. lutra* in Europe and by *L. canadensis* in North America. The consequences of sharing refuges, however, and whether or not den sites are indeed limiting, remain unknown.

Although an unhappy exemplar, due to its negative impact on indigenous species, the American mink provides a 'natural' experiment for unraveling the rules of community assembly. In some places, American mink invading a predatory community with otters shift their diet (Clode & Macdonald, 1995; Bonesi *et al.*, 2004). In Britian, mink appear to be able to coexist for longer with otters in heterogeneous habitats, presumably to accommodate this dietary shift (Bonesi & Macdonald, 2004a,b). In Patagonia, they appear to do neither.

Questions are now open towards the role of prey and time since coexistence in defining the direction of this new non-natural assemblage.

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