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Habitat use and diet of endangered southern river otter *Lontra provocax* in a predominantly palustrine wetland in Chile

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The southern river otter *Lontra provocax* is an endangered species. It has a patchy distribution in southern Chile and Argentina, inhabiting both freshwater and marine habitats. While most studies of their diet and habitat use have been carried out in freshwater habitats, our study is the first one on these aspects in a predominantly palustrine wetland. In southern Chile, the Boroa wetland may be the only wetland with southern river otters and five different subsystems: palustrine open water, swamp forest, seasonal and permanent marshes, and riverine associated with open farm fields. We studied these five different subsystems during April 2003 - May 2004, and collected and analysed 194 spraints in order to assess the effect of rainfall and subsystems on the diet and sprainting behaviour of southern river otter. The river otter's diet primarily consisted of crustaceans; however, rainfall and wetland subsystems influenced the frequency of fish and especially amphibians in the spraints collected. This is the first study documenting the helmeted water toad *Caudiverbera caudiverbera* as a prey of southern river otter. Southern river otter visited latrines located within the swamp forest more frequently, as this subsystem may provide refuge for latrines and dens as well as an important supplementary feeding resource. Our study provides insights into the role of coastal wetlands in predation processes, and highlights the importance of ecosystem services derived from wetland for biodiversity conservation. However, it is of concern that these wetlands are increasingly affected by drainage for agriculture and other landscape changes in southern Chile.

Key words: fish, helmeted water toad, *Lontra provocax*, otter, swamp forest

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Marshes and swamp forest wetlands across Chile are considered economically useless, and consequently, they are being changed in composition and in area (Hauenstain et al. 2005). Pollution from pulp factories, residential developments, logging and drainage are part of the activities that are affecting Chilean wetlands severely (Hauenstain et al. 2005). River and stream canalisation and drainage as well as other wetland changes and overharvesting have effectively eliminated the southern river otter *Lontra provocax* (nutria de río or huillín) from much of its former range (Medina 1996, Medina-Vogel et al. 2003). As a result, the southern river otter of southern Chile and Argentina is categorised as endangered on the IUCN Red List of Threatened Species (IUCN 2003). Historically, in Chile, the distribution of the species was more extensive including rivers, streams and fjords from the Cauquenes and Cachapoal rivers (34°S) in the north to the Magellan region (53°S) in the south (Medina 1996). At present, river otter populations in freshwater habitats have been confirmed in few isolated areas, from 39°S to 44°S (Medina 1996). Southern river otters use a wide range of freshwater ecosystems, ranging from deepwater Andean lakes and wide deep rivers to narrow and shallow streams, seasonal marshes and swamp forests (Chehébar et al. 1986, Medina 1997, 1998, Medina-Vogel et al. 2003, Aued et al. 2003). However, depending on the habitat characteristics, the freshwater ecosystems are not all equally important (Medina-Vogel et al. 2003). Previous diet studies indicate that in riverine and lacustrine wetlands, southern river otters primarily feed on invertebrates contrasting European otter *Lutra lutra*, American river otter *Lontra canadensis*, Neotropical otter *L. longicaudis*, giant otter *Pteronura brasiliensis* and spotted-necked otter *Lutra maculicollis*, which all feed mostly on fish (Duplaix 1980, Melquist & Hornocker 1983, Chehébar 1985, Chehébar et al. 1986, Heggberget & Moseid 1994, Reid et al. 1994, Carss 1995, Spinola & Vaughan 1995, Medina 1997, 1998, Taastrøm & Jacobsen 1999, Perrin & Carugati 2000, Quadros & Monteiro-Filho 2001, Medina-Vogel et al. 2003). However, significant differences in prey species, including seasonal variation in the fish consumed by southern river otter, have been recorded between lakes and their river outlets, and between Andean rivers and lowland rivers (Medina 1997, Medina-Vogel et al. 2003). In spite of this, there is no information about the ecology of southern river otters in coastal palustrine wetlands, even though

there are few studies about aspects such as the effect of rain or flood seasons on the diet and sprinting behaviour of the species in different wetlands habitats. Nevertheless, based on an Index of Revisitation Rate (IRR), it has been suggested that swamp forests make up a preferred habitat for southern river otter (Medina-Vogel et al. 2003).

Wetlands are one of the most productive ecosystems in the world, with high levels of biodiversity, in which seasonal events such as floods may generate post-flood seasonal peaks in fish availability (Theiling et al. 1999), and therefore variations in prey availability to otters between seasons (Taastrøm & Jacobson 1999, Perrin & Carugati 2000). We studied the Boroa wetland, which includes five subsystems (palustrine open water, swamp forest, permanent and seasonal marshes and open farm field) that often occur within the range of one otter home range (Medina 1996, Medina-Vogel et al. 2003, Medina-Vogel 2005). The Boroa wetland complex also remains minimally altered by agriculture and pollutants from pulp factories (Hauenstain et al. 2005, Marcotte 2006). Our objectives were to examine: i) the relationship between diet, rainfall and wetland subsystems, and ii) wetland subsystem use by southern river otters in terms of an Index of Revisitation Rate (IRR) within the Boroa wetland. To assess the importance of wetland subsystems as habitat for southern river otters, we tested the following alternative hypotheses: a) the southern river otter diet is affected by rainfall; b) the southern river otter diet is different in the different wetland subsystems; and c) southern river otter latrines are concentrated in the swamp forest subsystem, indicating a greater use of this wetland subsystem in terms of an Index of Revisitation Rate (IRR).

Material and methods

Our study area covered 15.4 km², including approximately 30 km of river courses from the Pacific Ocean, situated at 0-25 m a.s.l., 6.4 km from the seashore (Fig. 1), and within the borders of the county of Tolten, IX Region (39°17'S, 73°05'W). The maximum flow of the associated watercourses can be up to 14 times the minimum flow, and during times of high water levels, the adjacent plains and riparian zones are flooded. Our study area is located in a region with a humid-temperate climate with an annual mean temperature of 12°C and a mean rain-

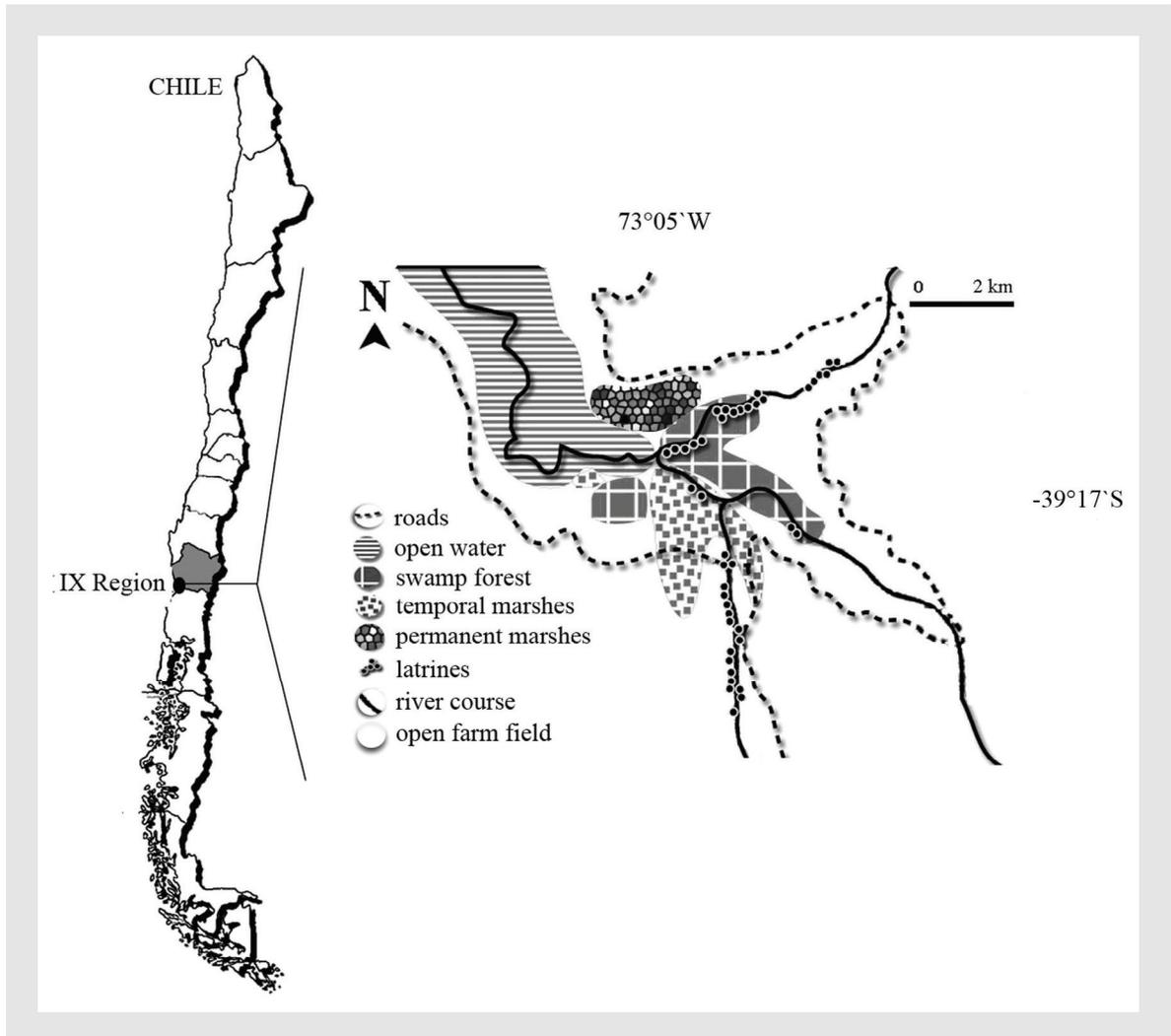


Figure 1. Location of the study wetland in the IXth region in Chile.

fall of 1,553 mm, with minimum levels of rainfall in summer (January - March) and maximum levels in winter (June - August; Campos 1985, Escalona 2001). In the studied wetland, the following five subsystems occurred (see Fig. 1): palustrine open water (24% of the total study area), riverine associated with open farm fields (34%), riverine associated with permanent marshes (7%), riverine associated with seasonal marshes (16%), and riverine associated with swamp forests (19%). The vegetation community is composed of *Juncos procerus*, *Lotus uliginosus*, *Holcus lanatus*, *Dichondra sericea*, *Agrostis capillaries*, *Eleocharis macrostachya*, *Eleocharis pachycarpa*, *Cyprus eragrostis*, *Carex acutata*, *Scirpus californicus*, *Sagittaria montevidensis*, *Alisma plantago-aquatica*, *Myriophyllum aqua-*

ticum, *Potamogeton linguatus*, *Ludwigia peploides*, and the tree species *Myrceugenia exsucca*, *Temu divaricatum*, *Blepharocalyx crukshanksii* and *Drimys winteri* (Ramirez et al. 1983, Escalona 2001, Hauenstein et al. 2005).

During April 2003 - May 2005, most of the shoreline of the studied wetland was surveyed for two days on foot for river otter field signs (footprints, smears and spraints). During the rainy season, surveys took two to four hours more than in the dry season on average. Therefore, the survey route changed between surveys according to changes in the water levels; however, survey routes always followed the shoreline contour and covered the entire considered area of each wetland subsystem studied. First order and intermittent streams

were not surveyed. Surveys were made on 45-65 days depending on weather conditions and accessibility. One month before the first survey, a preliminary survey was conducted in order to find and map otter latrines, and to collect and eliminate all possible spraints, smears and footprints to have only spraints no older than 65 days for the diet analysis. Thereafter, all spraints and footprints were collected or recorded (Medina 1998). Latrines were shoreline locations where river otters exited the water to defecate, urinate, scent mark and groom. A 'positive site' was defined as a site where dens/shelters, latrines or sandy shores with new (not >65 days old) otter field signs (spraints, smears or footprints) were found (Medina 1996, Medina-Vogel et al. 2003). Positive sites separated by >5 m were considered to be different. Collected spraints were washed and dried at 75°C for 48 hours, and stored in paper bags for later analysis (Medina 1998). Prey remains in the dried spraints were identified and compared with reference material collected and maintained at the Instituto de Zoología, Universidad Austral de Chile. Fish remains in collected spraints were identified using operculae and vertebrae, and their sizes were estimated by comparing the size of abdominal and caudal vertebrae with previously measured reference material (Medina 1997, 1998). The results were tabulated as: 'O' occurrence (number of spraints in which a species occurred) and 'RF' relative frequency (number of spraints in which a species occurred divided by the total occurrence of all the species tested; Brzezinski & Marzec 2003). Benthic freshwater invertebrate fauna were sampled five times in each subsystem using a Surber sampler dragged <1.2 m deep, no further than 4 m from the shore and for 3 m at a time. Stones, gravel, sand and sediment were removed. This was done the first time during spring of 2004 and a second time during the summer of 2005. An Index of Revisitation Rate (IRR) was applied to compare habitat use in terms of sprainting behaviour by southern river otter between wetland subsystems (Medina-Vogel et al. 2003). The IRR was calculated by dividing the number of positive sites in each survey and wetland subsystem by the actual distance walked along each subsystem as a proportion of the total number of kilometres surveyed. Each positive site was treated in the same way: presence/absence (1 or 0), irrespective of the number of spraints and smears or footprints (Newman & Griffin 1994, Medina-Vogel et al. 2003).

Rainfall was recorded at the Toltén meteorological station and classified according to the data obtained per month of study into two categories: a) dry season (months with <150 mm of rain) and b) wet season (months with >150 mm of rain). Our data were non-normally distributed so multiple-comparison procedure using Pearson χ^2 -test and Wilcoxon signed-rank test were used to compare IRR (dependent variable) as a function of the different independent variables (two rainfall categories and five wetland subsystems). The Wilcoxon signed-rank test was also used to compare the diet between season and wetland subsystems. Significance was set at $P < 0.05$ throughout, and all statistical tests were carried out using SYSTAT version 11. Prey diversity in the diet was assessed using the Shannon-Wiener diversity index (Krebs 1989).

Results

Wetland subsystem use by southern river otter

We recorded no footprints, smears, urine, spraints, otter dens, shelters or latrines in the ca 24 km of shorelines surveyed of the palustrine open water and riverine habitats associated with permanent marsh subsystems during the 18 surveys. Therefore, the data analysis was concentrated on the other three subsystems. From a total of 18 surveys made along 8 km of riverine associated with open field and seasonal marsh subsystems and 2.5 km of riverine associated with the swamp forest subsystem, we collected 194 spraints in 42 latrines with a total of 109 positive sites (see Fig. 1). Of the latrines and spraints, 14 (33%) and 85 (44%), respectively, were located in 2.5 km of surveyed swamp forest (34 spraints/km), which had 0.5 km associated with permanent marshes. Twenty-eight (66%) latrines with 109 (56%) spraints were found in 8 km of surveyed riverine associated with open farm fields (13.7 spraints/km), which had approximately 1.3 km riverine associated with seasonal marsh subsystem (see Fig. 1). The riverine associated with open farm fields and seasonal marsh subsystems concentrated 61% (66) of positive sites within the 18 surveys. There was a great variation in the number of spraints collected by months: during the wet season, the maximum number of spraints collected per survey was 23 (minimum three) and the average was 10 (SD = 6.8), and during the dry season the maximum was 42 (minimum six)

Table 1. Total and mean number of spraints collected per survey in the rainfall categories low (<100 mm), medium (100-250 mm) and high (250-500 mm) between April 2003 and May 2005, at the Boroa wetland in IX Región, Chile.

| Months | Rainfall category | | |
|------------------------------------|-------------------|-----------------|-----------|
| | Low | Medium | High |
| | January-May | August-December | June-July |
| Mean rainfall | 68 mm | 195 mm | 374 mm |
| Total number of collected spraints | 127 | 49 | 18 |
| Number of survey months | 8 | 7 | 3 |
| Mean number of spraints | 15.9 | 7 | 6 |

and the average was 22 (SD = 16.4). Therefore, there was no significant difference in the number of spraints collected between months with less or more than 150 mm of rain (Wilcoxon $Z = -1.3$, $P = 0.21$). When months were classified according to low (<100 mm), medium (100-250 mm) or high (250-500 mm) rainfall, a clear effect of rainfall on the number of spraints collected was observed (Table 1). The density of spraints collected over the total study area and study period was 5.6 spraints/km (average: 0.3 spraints/km/survey) and 18.5 spraints/km (average: 1.0 spraints/km/survey) if we consider only the surveyed distance of the subsystems where spraints and latrines were found.

As positive sites were found only in the riverine associated with swamp forests and the riverine associated with open farm fields and seasonal marsh subsystems (see Fig. 1), the IRR was calculated from the total surveyed distance of 10.5 km, and a total of 189 surveyed km in the 18 surveys in these three subsystems. This resulted in a mean IRR recorded by the riverine associated with swamp forest of 10.4, which was significantly higher (Wilcoxon $Z = -2.8$, $P < 0.01$) than the IRR recorded by the riverine associated with open farm fields and seasonal marsh subsystems (4.8; Table 2). Within the swamp forest, the IRR obtained for the dry season was significantly higher (15.4; Wilcoxon $Z = 2.03$, $P = 0.04$) than that obtained for the wet season (5.3), and also higher (Wilcoxon $Z = -2.23$, $P = 0.02$) than that of the riverine associated with open farm fields and seasonal marsh subsystems (6.0). During the wet season, results could in part be explained by the diet variations as described below. No significant differences were observed between subsystems during the wet season (see Table 2).

Otter diet variation by season and wetland subsystem

We collected 15 samples for benthic invertebrates in river courses associated with the five wetland subsystems; the macrocrustaceans *Samastacus spi-*

nifrons and *Aegla* sp. and insects from the orders Plecoptera and Odonata were identified as the aquatic invertebrates in all river courses. Spraint analysis revealed that macrocrustaceans were the most frequent prey (70%RF), followed by fish (15%RF), others (such as mussels, mammals, birds and unidentified; 6%RF), amphibians (4%RF) and insects (4%RF; Table 3), with significant difference ($\chi^2 = 34.3$, $df = 12$, $P < 0.01$) among the relative frequency of prey between the dry and the wet seasons (see Table 3). Macrocrustaceans were also the most frequent prey in both the riverine associated with the swamp forest (64%RF) and the riverine associated with open farm fields and seasonal marsh subsystems (76%RF), but the relative frequency of identified prey between both subsystems was significantly different ($\chi^2 = 25.0$, $df = 10$, $P < 0.01$). In fact, amphibians were less (Wilcoxon $Z = 2.2$, $P = 0.03$) frequent (2.0%RF) in the swamp forest than in the riverine associated with open farm fields and seasonal marsh subsystems (10.0%RF).

Only two fish remains from spraints were from fish > 15 cm long. The estuarine fish *Odonthesthes regia* was recorded, confirming the influence of sea

Table 2. Number (N) and mean Index of Revisitation Rate (IRR) for the riverine associated to swamp forest (A) and riverine associated to open farm fields and seasonal marsh subsystems (B) in the dry season (December-May; <150 mm) and wet season (June-November; >150 mm) in the Boroa wetland during April 2003 - May 2005.

| | Dry season (December-May) | | | | Wet season (June-November) | | | |
|------|------------------------------|------|-----|------|-------------------------------|-----|-----|-----|
| | A | | B | | A | | B | |
| | N | IRR | N | IRR | N | IRR | N | IRR |
| | 4 | 17.4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| | 6 | 26.1 | 2 | 2.6 | 0 | 0.0 | 1 | 1.3 |
| | 2 | 8.7 | 3 | 3.9 | 1 | 4.3 | 2 | 2.6 |
| | 7 | 30.4 | 14 | 18.4 | 1 | 4.3 | 6 | 7.9 |
| | 4 | 17.4 | 12 | 15.8 | 1 | 4.3 | 2 | 2.6 |
| | 3 | 13.0 | 6 | 7.9 | 2 | 8.7 | 5 | 6.6 |
| | 0 | 0.0 | 2 | 2.6 | 2 | 8.7 | 3 | 3.9 |
| | 4 | 17.4 | 0 | 0.0 | 2 | 8.7 | 5 | 6.6 |
| | 2 | 8.7 | 2 | 2.6 | 2 | 8.7 | 1 | 1.3 |
| Mean | 3.6 | 15.4 | 4.6 | 6.0 | 1.2 | 5.3 | 2.8 | 3.7 |

Table 3. Occurrence (O) and relative frequency (RF) expressed as a percentage of prey species or families in the total number of 194 spraints collected during the dry season (December-May; N=134, <150 mm) and wet season (June-November; N=60, >150 mm).

| Prey | Dry season | | Wet season | |
|----------------------------------|------------|------|------------|------|
| | O | RF | O | RF |
| Macrocrustacean | | | | |
| <i>Samastacus spinifrons</i> | 87 | 44.8 | 37 | 48.1 |
| Not identified | 45 | 23.2 | 21 | 27.3 |
| Fish | | | | |
| <i>Odonthestes regia</i> | 1 | 0.5 | 0 | 0.0 |
| <i>Oncorhynchus</i> sp. | 2 | 1.0 | 0 | 0.0 |
| <i>Percichthys trucha</i> | 1 | 0.5 | 0 | 0.0 |
| Perciformes | 2 | 1.0 | 0 | 0.0 |
| Osteichthyes, not identified | 31 | 16.0 | 5 | 6.5 |
| Amphibians | | | | |
| <i>Caudiverbera caudiverbera</i> | 1 | 0.5 | 6 | 7.8 |
| Not identified | 4 | 2.1 | 1 | 1.3 |
| Insects | | | | |
| Plecoptera | 3 | 1.5 | 0 | 0.0 |
| Coleoptera | 2 | 1.0 | 0 | 0.0 |
| Dysticidae (Coleoptera) | 1 | 0.5 | 0 | 0.0 |
| Chelometheridae | 0 | 0.0 | 1 | 1.3 |
| (Pseudoescorpionido) | | | | |
| Aeshnidae (Odonata) | 1 | 0.5 | 0 | 0.0 |
| Odonata | 1 | 0.5 | 0 | 0.0 |
| Not identified | 0 | 0.0 | 1 | 1.3 |
| Mussels | | | | |
| <i>Chilina</i> sp. | 3 | 1.5 | 1 | 1.3 |
| <i>Astrodiscus twomeyi</i> | 3 | 1.5 | 1 | 1.3 |
| Vertebates | | | | |
| Not identified | 3 | 1.5 | 1 | 1.3 |
| Mammals | | | | |
| <i>Abrothrix</i> sp. | 0 | 0.0 | 1 | 1.3 |
| Roedor not identified | 0 | 0.0 | 1 | 1.3 |
| Not identified | 1 | 0.5 | 0 | 0.0 |
| Birds | | | | |
| Not identified | 2 | 1.0 | 0 | 0.0 |
| Total | 194 | | 77 | |

tides in the studied wetland. The diet diversity in the wet season was slightly smaller (Shannon-Wiener $H' = 0.666$) in relation to the dry season ($H' = 0.737$), and higher in the swamp forest ($H' = 0.74$) in relation to the riverine habitat associated with open farm fields and seasonal marsh subsystems ($H' = 0.70$). The overall diet diversity for the study was $H' = 0.753$. In addition, 11 (5%) spraints were found with seeds from vegetation of the palustrine open water and permanent marsh subsystems (i.e. *Cyprus eragrostis*, *Scirpus californicus* and *Eleocharis pachycarpa*).

Discussion

During our study, the average density of spraints collected over the total surveyed distance and the

study period was lower than recorded by Medina (1998) in Andean lakes (ca 0.80 spraints/km), and that recorded by Medina et al. (2003) in rivers close to this research study area (ca 1.5 spraints/km). However, if only the surveyed distance of the wetland subsystems where latrines were found is considered, the density of spraints collected was within the densities of the previously mentioned studies and higher than that recorded by Quadros & Monteiro-Filho (2001) in their study of Neotropical otter (0.71 spraints/km), but similar to the number of spraints considered for analysis in other studies of southern river otter, Neotropical otter and African clawless otter (78-202 spraints; Medina 1996, Quadros & Monteiro-Filho 2001, Parker et al. 2005, Watson & Lang 2003).

In our study, water depth and conditions experienced during the rainy season affected the number of otter spraints found negatively. Further studies using the same survey method as applied in our study should consider that flooding and water levels can affect the surveyor's ability to find field signs, as well as the ability of the otters to find good marking sites (Medina-Vogel et al. 2003).

The use of spraints to assess habitat use by river otters is controversial. Kruuk (1992) suggested that sprainting serves to communicate to other otters the use of key resources, so a higher number of positive sites would be expected in those habitats with the greatest use by otters. However, depending on the studied species, studied habitat and methodology, spraints may not necessarily reflect habitat use within a home range (Madsen & Prang 2001). Medina-Vogel et al. (2006) demonstrated that for the particular habitat conditions where marine otters live, spraints do not represent otter population density within one seashore habitat type. However, when using an index of absence/presence of otter field signs such as an Index of Revisitation Rate (IRR; Newman & Griffin 1994, Medina-Vogel et al. 2003), or presence/absence frequencies of field signs to compare different study sites, habitats or regions, the index as well as the frequencies are reliable results to compare habitat use as an indicator of otter and other mustelids' visits of each surveyed stretch, patch or habitat during a determined period (Hutchings & White 2000, Madsen & Prang 2001, Virgos & García 2002, Medina-Vogel et al. 2003, Bonesi & Macdonald 2004).

In our study, as well as in that of Medina-Vogel et al. (2003), the highest IRR was obtained by the

riverine habitat associated with the swamp forest subsystem, followed by the riverine habitat associated with open farm fields and seasonal marsh subsystems, and no data were obtained for the other wetland subsystems. Southern river otters are able to move 5 km per day, have a home range up to 15 km long in average; in riverine and lacustrine habitats their densities have been estimated to be up to 0.3 otters/km (Medina-Vogel 2005). Thus the open palustrine and riverine associated with permanent marsh subsystems were within the range of one southern river otter's home range, either resident in the riverine associated with the swamp forest or riverine associated with open farm fields and seasonal marsh subsystems. Additionally, the differences in the diet and the IRR between the swamp forest and riverine associated with open farm fields and seasonal marsh subsystems could also be a consequence of spraints coming from different otters that were using the three subsystems in different proportions. In comparison to other study sites in rivers and lakes, at least two to no more than four otters must have been resident or partially resident in the study area (Medina-Vogel 2005). Nevertheless, the evidence that in only two of the five studied wetland subsystems were otter field signs recorded, the evidence of higher IRR recorded by the swamp forest subsystem, the absence of a difference in IRR between the swamp forest subsystem and the riverine associated with open farm field and seasonal marsh subsystem during the wet season, the fact that different diets were described from spraints collected in the swamp forest and the riverine associated with open farm field and seasonal marsh subsystems, and the variations in fish and amphibians remains in spraints collected between wetland subsystems and seasons, support the rejection of the null hypothesis that the wetland subsystems were used equally and that no effect of rainfall existed in the habitat use and diet of southern river otter.

Our study confirms previous observations in as far as southern river otters select riparian sites of confined watercourses with a low density of riparian vegetation, combined with mature trees and exposed roots for marking and latrines (Medina-Vogel et al. 2003). Marking behaviour is also displayed by other otter species (Macdonald et al. 1978, Andrews 1989, Kruuk 1995, Ruiz-Olmo & Gonsálbez 1997).

Seasonal variation in the diet of southern river otters has been recorded only in riverine habitat

(Medina 1998), where fish (i.e. *Percichthys trucha*) were more frequent in the southern river otter diet during the dry season than during the wet season, as recorded in our study. Macrocrustaceans have been recorded in all freshwater subsystems studied, without seasonal variations but with differences in the main species consumed between lakes and their rivers' outlets (Medina 1998). The macrocrustaceans *Samastacus spinifrons* and *Aegla* sp. are the most frequent prey in the southern river otter diet in freshwater habitats (Chehébar 1985, Chehébar et al. 1986, Medina 1997, 1998, Medina-Vogel et al. 2003). In only a few studied sites where fish were recorded > 35% (RF), the Shannon-Wiener diversity index was $H' > 0.8$ (Medina 1997, 1998). However, in our and in previous studies in rivers and swamp forest habitats where *Samastacus spinifrons* and *Aegla* sp. were present, *Aegla* sp. did not occur in the southern river otter diet (Medina-Vogel et al. 2003). Crustaceans have been described as a lower quality food (in terms of energy) for otters than fish (Kruuk 1995, Medina-Vogel et al. 2004). Otters are opportunistic predators; marine otter *Lontra felina* feeds mainly on prey that is most abundant and easy to catch and consume (Medina-Vogel et al. 2004), and in marine habitats European otter eat bottom-dwelling fish during most of the year, but change to other fish species during winter (Kruuk & Moorhouse 1990, Kruuk 1995). In Belarus, European otter varies its diet in response to an increase in fish availability during spawning (Sidorovich 2000). In South Africa, African clawless otter and spotted-necked otter eat fewer crustaceans during winter, when these are less available (Perrin & Carugati 2000). Indeed, in our study, higher IRR and Shannon-Wiener diversity indices were recorded in the swamp forest and during the dry season, where both habitat and season were associated with increased relative frequency of fish in the diet. When the number of fish decreased during the wet season, amphibians and other vertebrates increased; this suggests that the flooding season and therefore confined river courses associated with palustrine wetlands and marshes are important in the amphibian's ecology, and for complementary food resources to the southern river otter. The large helmeted water toad can weigh up to 0.5 kg, and one toad can contribute 340 kcal, 10 times more than one 30 g adult macrocrustacean *S. spinifrons* (Rudolph 2002, FAVET 2004). Amphibians, together with fish, insects and other vertebrates (mammals, birds and undetermined) constituted

30%(RF) $((81/271) \times 100$; see Table 3) of the diet in our study, more than the 20% (fish and amphibians) in the diet recorded by Medina (1997) in different riverine and lacustrine wetlands of islands and continental southern Chile, and is comparable to the relative frequencies of fish (12-43% RF) in the diet described for Andean riverine and lacustrine habitats (Medina 1998).

Within our studied wetland, sections of the swamp forest and seasonal marsh subsystems were affected by drainage and river canalisation. Such landscape changes effectively eliminated North American river otter from much of its range in North America (Towell & Tabor 1982, Melquist & Dronkert 1987). Similar causes have been suggested for the decline of European otter and European mink *Mustela lutreola* in Europe (Foster-Turley et al. 1990, Macdonald et al. 2002), and southern river otters in Chile (Medina 1996, Medina-Vogel et al. 2003). Our results suggest a need to discontinue the destruction of swamp forests and marshes associated with rivers and streams in southern Chile. As previous studies suggested (Medina-Vogel et al. 2003), we demonstrate that swamp forest and also in our study, river courses associated with marshes, could be key habitats for this endemic and endangered species of otter.

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