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Review

The marine otter *Lontra felina* (Molina, 1782): A review of its present status and implications for future conservation

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A B S T R A C T

The marine otter *Lontra felina* is an endangered and little known species living in a fragmented habitat: the coast of Peru and Chile. The smallest marine mammal's presence is unclear in Argentina and southern Tierra del Fuego and the current limits of the distribution are still under discussion. Recent population genetic studies suggest certain levels of gene flow despite a disjunct population. In the 20th century intensive hunting was the major threat to *L. felina*. This top predator still faces an uncertain future due to the impact of human activities (urbanization, pollution, and intensive fisheries). There is a need of further studies deepening the knowledge on population genetics, population numbers and migration behavior. Environmental education work, law enforcement and monitoring of protected areas are suggested to secure the survival of the species.

Introduction

As observation of *Lontra felina* is challenging, information on the species has been very scarce. Studies on behavior, diet, reproduction and/or ecology were made in the second part of the 20th century. The first genetic studies were published in 2010 (Valqui et al. 2010; Vianna et al. 2010). However, further information on population numbers, migration and genetics are still needed to achieve a better understanding and to provide arguments for conservation measures of this top predator.

Due to intensive hunting in the 20th century and the increasing human impact on marine ecosystems, the marine otter is listed as Endangered by the IUCN, in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), in Appendix I of the Convention on Migratory Species (CMS). Additionally, it is protected by Peruvian and Chilean law.

Considering implications for future conservation, this review summarizes the results of the most important peer-reviewed publications related to the marine otter and further presents important information from grey literature. Controversies created due to the lack of information or poor documentation about the species are presented. Within the scope of "Proyecto *Lontra felina*" the author has executed exhaustive field trips along the Peruvian coast between 2008 and 2011, sampling non-invasively and evaluating the marine otter populations in over 80 locations. New observations and unpublished information on behavior gained in those field trips are also presented.

Species description

Otters are divided into seven genera and thirteen species (Wilson and Reeder 2005). The three primary lineages are: (i) the first lineage comprising the European, Asian and African river otters (*Aonyx*, Hydrictis *Lutra*, *Lutrogale*) and the sea otter (*Enhydra*), (ii) the second lineage composed of the American otters (*Lontra*, separated from *Lutra* by Van Zyll de Jong 1987) and (iii) the third and basal lineage, the monotypic giant otter (*Pteronura*) (Koepfli and Wayne 1998; Koepfli et al. 2008). The genus *Lontra* is monophyletic and comprises four species, three of them occurring inside South America (Koepfli et al. 2008). *L. felina* is the only species of its genus living in exclusively marine habitats and is presumably the most recently evolved mammal adapted to this habitat (Estes 1986). The smallest marine mammal of the world weighs 3.2–5.8 kg and measures 87–115 cm in total length. The fur is dark brown on the back and sides and slightly lighter on the underside. The species has large vibrissae and fully webbed feet and shows no sexual dimorphism in size or color (Larivière 1998 and references therein) (Fig. 1). *L. felina* is relatively unknown and perhaps it is for that reason that it has several names. Spanish: chungungo, gato marino, lobito marino, nutria de mar (in all regions), chinchimén, chingungo, gatuna, huallaque (only in Chile and Argentina), anzumo, zorrillo, pejegato (only in Peru); English: South American Sea otter, marine otter, sea cat.

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Fig. 1. The marine otter *Lontra felina* ©www.kevinschafer.com.

Distribution and abundance

The marine otter *L. felina* was first described in 1782 in Chile by the Jesuit priest Juan Ignacio Molina who described many species to science (Molina 1782). Subsequent registers of the occurrence were scarce and few were published. In 1835, during his five-year journey on HMS Beagle, Charles Darwin recorded abundance of marine otters at the Chonos Archipelago, Chile (Darwin 1889). In 1844, the Swiss naturalist Johann Jakob Tschudi, who travelled through Peru from 1836 to 1842, reported very frequent sightings of *L. felina* in every coastal location, speculating that it could be present up to Ecuador (Tschudi 1844)–a fact that was never confirmed. Gay (1874) carried out descriptive studies on the species. In the mid 20th century, several authors documented reproduction, behavior and morphology (Osgood 1943; Yañez 1948; Housse 1953). In the 80s and 90s, the Chilean biologist Walter Sielfeld did research on conservation status, relative abundance, habitat characteristics, diet and also on niche overlap with *L. provocax* in southern Chile. These represent the most thorough studies on *L. felina* up to date (Sielfeld 1989, 1990a,b, 1992; Sielfeld and Castilla 1999). Cabrera (1957) reported frequent sightings in scientific expeditions in Tierra del Fuego and Isla de los Estados. In 1959, the German naturalist Ernst Schweigger travelled along the Peruvian coast and documented marine otters up to Isla Lobos de Tierra (6°26′S), representing the northernmost record of *L. felina* (Schweigger 1964). Later studies registered the species only up to Chimbote (9°00′S), Peru (Brack 1978; Brownell 1978; Larivière 1998; Apaza et al. 2004; Sánchez and Ayala 2006; Valqui et al. 2010). Recent records of the marine otter in Salaverry (8°13′S) (Santillán and Caro 2007) and Huanchaco (8°04′S) (Alfaro-Shigueto et al. in press), Peru, suggest that occasional events of colonization may occur north of 9°00′S, but several factors may hinder the establishment of populations in those areas: (1) rocky shore patches have been occupied by dogs, cats and rats; (2) lack of food availability exists due to a higher competition of the species with a more intensive fishery (Apaza et al. 2004); (3) the distances between suitable habitat patches may impede gene flow.

Between Chimbote and the limit to Chile, the Peruvian coast encompasses ~1600 km of about 100 rocky shore patches offering suitable conditions for marine otters alternated by patches of unsuitable habitat (e.g. sandy beaches and/or shoreline without caves). Interruptions average 9.1 km in length and are maximal 98.4 km long (calculation by the author). Some conspicuous groups of marine otters are present in Pucusana (12°28′S), Punta Corrientes (12°57′S), San Gayán Island (13°50′S), Morro Sama (17°59′S) and Vila Vila (18°07′S) (Sánchez 1992; Apaza et al. 2004; Valqui 2004; Ruiz 2009; Mangel et al. 2010; Valqui et al. 2010). See

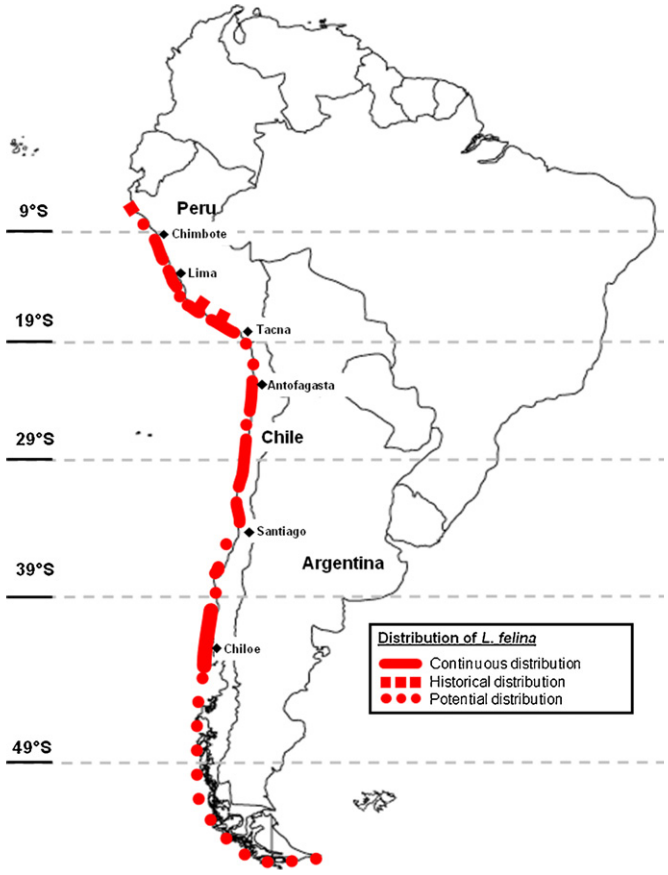

Fig. 2. Historical, potential and current distribution of *Lontra felina* at the Pacific coast.

Table 1 (online appendix) for a complete list of locations with marine otter presence and abundance numbers.

Between its northern limit to Peru and Chiloé, the Chilean coast is fragmented similarly to the Peruvian coast and it encompasses ~3000 km of areas with marine otter presence alternated by marine otter free areas. In a larger scale, patches are separated increasingly, from northern Chile to central-south Chile, where in two shore line areas of 427 km between Algarrobo (33°22′S) and Peninsula Tumbes (36°36′S) and 273 km between Arauco Bay (37°10′S) and Queule (39°23′S) no marine otters were reported (Vianna et al. 2010 and references therein). Very little is known about the populations south of Chiloé Island (43°26′S) and the species has been nearly exterminated from the regions of Cape Horn and southern Tierra del Fuego, the southern limits of its distribution (Brownell 1978; Chéhebar 1990). Conspicuous groups are reported for Soldado (26°10′S), Arrayán (29°43′S), Panul (30°03′S), Palo Colorado (32°01′S), Puquén (32°11′S), Papudo (32°26′S), Quintay (33°11′S), Colcura (37°07′S) and Punhihuil (41°55′S) (Vianna et al. 2010) (Table 1).

In Argentina *L. felina* originally occurred in a 400 km segment of coast, but there are no recent studies or reliable records about distribution and population numbers. The last record was 25 years ago (Massoia and Chebez, 1993 in: Cassini 2008; Parera 1996) (Fig. 2).

Interestingly, marine otters have sometimes been observed in rivers, feeding on shrimps in river farms of Camaná and Ocoña (Peru) up to 650 m above sea level (Hvindberg-Hansen 1970; Tello 1972; Viacava et al. 1978; Brownell 1978). There is one report of a marine otter in the Majes River, 40 km away from the ocean (Grimwood 1968). The last report in a river was done in the river Cañete (13°07′S) in 2003 (Apaza et al. 2004). Presumably, the growing human presence and better guarding in aquaculture shrimp farms (Apaza et al. 2004) is causing the retrieval of the marine otter to solely oceanic waters.

Most studies assessing the marine otter population only covered limited regional areas, while the use of several different methodologies made it difficult to determine the total population and hinders an approximation today. Sielfeld (1992) stated that the elusive behavior is an intrinsic obstacle for accurate population estimates and underlined the strong fluctuation of density values obtained in several studies done in past years. Population number for larger regions were proposed by Castilla and Bahamondes (1979), who estimated about 200–300 individuals for the Peruvian coast, without specifying how they obtained these numbers. Vaz Ferreira (1979) proposed the population of Peru, Chile and Argentina to consist of 1000 individuals, but Sielfeld and Castilla (1999) noted that no methodology was explained in that calculation. According to density numbers frequently found in the field, Sielfeld and Castilla (1999) stated that Vaz Ferreira's population number must be a sub-estimation. Along 1300 km of the Peruvian coast, from Lima (12°30′S) to the border of Chile (18°00′S), Apaza et al. (2004) proposed a total of 312 km of potential marine otter habitat. Multiplication with the average density of 2.21 ± 1.97 individuals per kilometer (ind/km) resulted in a population estimate of 691 ± 76 individuals for central and southern Peru. In a regionally more limited study, Mangel and Alfaro-Shigueto (2004) registered 22–28 individuals in 15.6 km of coast between Ilo (17°42′S) and Vila-Vila (18°07′S) in southern Peru. The population in 55 km of rocky shore was estimated at 88 (±11) individuals.

The densities calculated in these and several other studies vary from 0.04 to 10.0 ind/km (12 studies, mean density = 3.3 ind/km), although densities between 1.0 and 2.7 ind/km are more consistently recorded (Castilla and Bahamondes 1979; Castilla 1982; Cabello 1983; Rozzi and Torres-Mura 1990; Ebensperger and Castilla 1991; Sánchez 1992; Sielfeld 1992; Medina 1995; Apaza et al. 2004; Mangel and Alfaro-Shigueto 2004; Medina-Vogel et al. 2006, 2007). Based on the authors' research done between 2008 and 2011 in Peru, further areas with occurrence of otters were determined (via direct sightings, scat occurrence or references by other studies or by local fishermen), resulting in new calculations: 789 km (c.a. 50%) of a 1800 km stretch of the Peruvian coast are proposed as habitat of *L. felina*. Considering the most frequently reported densities of 1.0–2.7 ind/km the population is estimated to range from 789 to 2131 individuals at the Peruvian coast. Molecular analysis revealing high levels of mitochondrial DNA (mtDNA) variability (Valqui et al. 2010; Vianna et al. 2010) and further data on occurrence might support this data, indicating that the population numbers reported in the last years were underestimated. Medina-Vogel et al. (2006) discuss the uncertainty of the methodology in most surveys done in the last decades, while they propose minimum abundance indices rather than total survey numbers. Rarefaction analysis based on fecal genotyping (Kohn et al. 1999) could allow more accurate population size estimates.

Ecology

Habitat

The Humboldt Current System (HCS) flows from southern Chile (~42°S) for over 4000 km north-westward along the west coast of South America, up to Ecuador (Thiel et al. 2007). The cool upwelling system with coastal water temperatures ranging from 14 °C to 20 °C (Swartzman et al. 2008) shows high marine productivity and allows the presence of huge populations of seabirds, sea lions and cetaceans (Majluf et al. 2002). Paradoxically, this system creates desert conditions at the coast (Bertrand et al. 2004; Bertrand 2008). The nearest 150 m of the cold and productive waters and the characteristic heterogeneous alternation of sandy beaches, rocky shores and islands of the littoral compose the habitat of the marine otter (Larivière 1998; Sánchez and Ayala, 2006). They may inhabit islands that are several kilometers offshore. Sánchez and Ayala (2006) reported *L. felina* on Isla Pescadores (11°46′S), which is over 6 km away from the mainland but connected by several islets about 2 km away from each other.

Fig. 3. Rocky shore, habitat of the marine otter. (Photo: IDEAWILD / Elisa Ruiz.)

Rocky shore patches (Fig. 3) are preferred as they provide protected dens within caves with reproduction and resting places. Caves are above water at high tide and may be exposed to heavy seas (Cabello 1983; Ostfeld et al. 1989; Villegas et al. 2006) and present a variety of architecture (Medina-Vogel et al. 2006). Entrances, which may be several, are often well defined and do not have a submarine access, as they do have in other otter species (Sielfeld and Castilla 1999). If sandy ground is present in the inside, nest-shaped cavities may be built (10 cm deep and 50 cm in diameter) (pers. obs. by the author in 2009–2010). Human constructions like wharfs, ship wrecks, boats and artificial caves are used as part of their habitat (Medina-Vogel et al. 2007; Valqui 2004).

Diet and interactions

Diet studies are commonly based on scat samples, which can be found relatively frequent at the littoral, while foraging behavior is difficult to monitor (Valqui 2004). These studies may be biased, under-representing soft-bodied prey and over-representing prey with spines and carapaces (Larivière 1998), which often remain in scat (pers. obs. by the author in 2008–2011). *L. felina* feeds on invertebrates (decapods, shrimps, crabs and mollusks) and vertebrates (mostly fish, but also birds and even small mammals) (Sielfeld 1990a; Larivière 1998) in very variable compositions (see Ostfeld et al. 1989; Sielfeld 1990a; Medina-Vogel et al. 2004, 2008; Valqui 2004; Ruiz 2009 for numbers and percentages). According to research done by Sielfeld (1990a) south of 48°50′S, fish represents the main diet item (84.8%), followed by crustaceans (41.9%) and echinoderms (19.1%), which are preyed on seasonally, in the urchins' reproductive status. In contrast, urchins were found in 95% of the scat samples of the sea otter *Enhydra lutris* (Kenyon 1969). Gasteropods where found in only 2.9% of the scat samples, but represented over half of the prey rests found in dens and therefore seem to be an important part of the diet (Sielfeld 1990a). According to a study by Mangel et al. (2010), in which scat samples from nine study sites between 17°42′S and 39°40′S were analyzed, fish represents higher percentage of prey in the north, while it becomes less in more southern populations. In the south, crustaceans represent higher percentages of the diet (Mangel et al. 2010). Individuals preying on octopuses were observed in Pucusana (12°28′), Peru (Valqui 2004) and in Puñihuil (41°55′S), Chile, where in January 2010 an adult individual caught an octopus and fed its pup with it (Kevin Schafer, pers. comm.). Birds are only preyed on occasionally and opportunistically. Sielfeld (1990a) found ten bird species contained in 2.9% of 105 scat samples and in 11.5% of 68 prey rests associated to dens. More than half of them (66.6%), where from a cormorant *Phalacrocorax* sp. (Sielfeld 1990a). On Isla La Vieja (14°16′S), Peru, marine otters are presumed to prey regularly on a colony of the Peruvian Diving Petrel (*Pelecanoides garnotii*) (Mattern et al. 2002). In January 2009 one individual was observed capturing a chick of a Magellanic flightless steamer duck (*Tachyeres pteneres*) in Puñihuil, Chile (Kevin Schafer, pers. comm.). *L. felina* may even feed on small mammals (Sielfeld 1990a) and fruits (*Greigia sphacelata*, *Fascicularia bicolor*) (Brownell 1978; Cabello 1983), thus showing an overall opportunistic feeding behavior (Medina-Vogel et al. 2004).

L. felina may compete with gulls (*Larus* sp.) and the South American sea lion (*Otaria flavescens*) for prey (Cabello 1983). The latter was even shown to attack *L. felina* (Ruiz 2009). Allegedly, Orcas (*Orcinus orca*) and sharks represent predators (Cabello 1983; Parera 1996 in Larivière 1998), but no direct observations of attacks have ever been reported. Notably, Orcas do prey regularly on another otter species, the sea otter (*E. lutris*) in western Alaska (Estes et al. 1998).

Very little is known on parasites of *L. felina*. Nematodes and acantocephalans were identified as endoparasites (Cabello 1978). Villegas and Huamán (1989) detected undetermined hematophagous ectoparasites (acari).

Physiology

Marine otters are well adapted aquatic conditions due to their powerful tail and webbed feet (Larivière 1998). Due to a relatively small size and reduced body fat, heat loss is reduced by avoiding long-time periods in the water. They may swim 2 km in about 20 min (pers. obs. by the author in 2009), forage in shores with strong waves (Cabello 1983; Ostfeld et al. 1989; Villegas et al. 2006) and dive up to 77 s (Valqui 2004). They may even spend time swimming and feeding in the short period of time between two breaking waves (pers. obs. by the author in 2002, 2004, 2008, 2010 and 2011). Marine otters can move 50 m under water (Cabello 1978). As marine mammals are hypotonic, they regulate their salt balance by hormonal regulation of urine concentration and/or the by the rate of urine concentration (Ortiz 2001). Costa (1982) showed that sea otters (*E. lutris*) create urine in elevated concentrations. This osmotic ability allows them to excrete excessive Na^+ and Cl^-. Thus, sea otters can actively consume sea water and gain free water (Ortiz 2001). Individuals of *L. felina* living close to rivers might directly drink freshwater, while those living far away from rivers and in areas with absence of rainfall – something common in the coastal desert of Peru and Chile – may further compensate loss of water by a osmoregulatory mechanism similar to the sea otter.

Behavior

Behavior studies of *L. felina* are problematic due to difficulties to follow them in the field: they spend more than 80% of their time hidden in caves. It is furthermore impossible to recognize individuals (Medina-Vogel et al. 2006 and references therein) as neither characteristic individual pigmentation nor sexual dimorphism exist. Several studies describe behavioral aspects, but there are a lot of contradictions concerning reproduction, social behavior, migration and territoriality. Several observational studies stated that the marine otter displays activity peaks at specific hours during the day (e.g. in the morning, in the afternoon or between 3 and 5 pm) (Ostfeld et al. 1989; Sánchez 1992; Valqui 2004; Ruiz 2009). On the contrary, a radio-tracking study showed no significant preferences by the species for activity during the day, night, or any other period of time (Medina-Vogel et al. 2007). *L. felina* spends over 80% of its time on land, preferably resting in or nearby their dens (Medina-Vogel et al. 2007 and references therein). Nests are built and rebuilt repeatedly after high tide washed them away (pers. obs. by the author in 2009–2010). During long-distance swimming between rocky patches (pers. obs. by the author in 2002 and 2009) sandy beaches are eventually used for resting (Ebensperger 1992). To forage, they start to search for their prey once arrived at the bottom. Thus, dive length is correlated to water depth (Medina 1995). Foraging success ranges from 18% to 32% of the dives (Ostfeld et al. 1989; Medina 1995; Valqui 2004). Captured prey is carried in the mouth and may be put on belly while swimming on their back. Prey is then consumed with the help of the forepaws (pers. obs. by the author).

Although *L. felina* is reported as solitary and seldom to be found in groups (Castilla 1981; Cabello 1983; Larivière 1998; Sielfeld and Castilla 1999) there are several records of groups of five to eight individuals (Apaza et al. 2002; Valqui 2004; Ruiz 2009; Mangel and Alfaro-Shigueto 2004; pers. obs. by the author in 2009). In a radio-tracking study in Quintay (33°11′S) Chile, a group of individuals shared an area less than 100 m^2 in several occasions. Moreover, the study revealed a home range of <5 km for *L. felina*, with home-range overlap and no avoidances between individuals (Medina-Vogel et al. 2007).

Marine otters were formerly assumed to reproduce in austral summer (December–February) (Larivière 1998) but in recent years records of pups all year round have been made (Valqui 2004; Medina-Vogel et al. 2006; Ruiz 2009). Presumably, low seasonal variation of the cold waters of the HCS creates conditions that allow a continuous reproduction throughout the year. Parturition occurs after 60 days of gestation (Larivière 1998 and references therein). The litter of two to four pups stays with the mother for ten to twelve months (Cabello 1983; Parera 1996; Larivière 1998; Valqui 2004). During this time, adults carry pups in their mouths to move between dens (Valqui 2004) or let them rest on their bellies as they swim on their back (Castilla and Bahamondes 1979). Nursing and feeding may overlap: in Puñihuil (41°55′S), Chile, a mother was observed breastfeeding a young individual while simultaneously feeding it with prey (pers. obs. by the author in 2010). Marine otters are presumed to be monogamous (Larivière 1998) but difficulties in assessing territoriality and spatial behavior impede to confirm patterns of reproductive behavior (Medina-Vogel et al. 2007).

Play behavior is observed in many taxons of mammals and interestingly the advantages of such behavior do not appear to carry an immediate biological benefit, such as access to mate or food or maintenance of a territory. Thus, the significance of this behavior is not yet clear (Pellis 1988). Individuals of *L. felina* have been observed displaying play behavior in several studies (Castilla and Bahamondes 1979; Ebensperger and Castilla 1991). Play behavior turning over into mating, fighting or separation has also been observed (Valqui 2004). High pitched vocalizations have been reported during fighting (Ostfeld et al. 1989). In Pucusana, Peru, several different vocalizations were registered during swims and while playing or foraging (Valqui 2004).

For scent marking, marine otters defecate in latrines or singular places at cave entrances (Valqui et al. 2010). Feces are regularly washed by high tides or high spring tides (Castilla and Bahamondes 1979). They may also defecate directly into the water while swimming (pers. obs. by the author in 2010).

Population genetics

Since non-invasive molecular techniques have improved in the last decades, genetic analysis no longer relies on tissue samples that imply the capture of individuals. Genetic analysis can for example be based on scat samples (Kohn and Wayne 1997). This is especially relevant concerning species, that are elusive or on which ethical issues may arise due to animal handling (e.g. setting traps, supplying anesthesia).

In the first study along the entire distribution of *L. felina* at the Peruvian coast by Valqui et al. (2010), 87 scat samples were collected. 41 of those samples were sequenced at 265 bp of the control region of mtDNA, yielding 24 individuals with 11 haplotypes and 13 polymorphic sites. Considering a 5 km home range, pseudoreplication was avoided by excluding samples that came from within a distance of 5 km or less. No population substructure (based on *F*-statistics) and no isolation by distance (based on a Mantel-test) could be detected. Considering the low population numbers reported, this study yielded surprisingly high values of haplotype diversity (h) = 0.86 and nucleotide diversity (π) = 0.0017, compared to variability values of the Eurasian otter (*Lutra lutra*), h = 0.16 and π = 0.0006 (Ferrando et al. 2004), which has considerably higher population numbers. h (varies between 0 and 1) is a measure of the uniqueness of a particular haplotype in a given population and is related to the relative haplotype frequency. A high value of h represents a high number of haplotypes. π (varies between 0 and 1) is a measure of the degree of polymorphism (diversity) in a given population (Nei and Tajima 1981). π represents the average number of nucleotide differences per site between two randomly chosen DNA sequences from the sample population. A high value of π represents a high number of differences within a sample (Nei and Li 1979). Based on geographic criteria the Peruvian groups can be separated into four groups (Fig. 2, Table 1). This separation has to be inspected by further genetic analysis. The second study was carried out in Chile and Peru by Vianna et al. (2010), sequencing the control region of mtDNA in 168 out of 419 collected samples of blood (16), tissue (46) and scat (357). Analysis of 2261 bp of mtDNA (control region, ND5 and Cyt-b sequences) yielded 26 haplotypes. Combining mtDNA haplotypes and microsatellite genotyping, 89 individuals were identified within the 126 scat samples processed. A significant population sub-structuring was detected (F_{ST} = 0.86–0.77, P < 0.0001) and the overall variability values were h = 0.93 and π = 0.0047. This is in the range of the study done in Peru (Valqui et al. 2010). Vianna et al. (2010) determined six groups (based on a spatial analysis of molecular variance, SAMOVA), with the Peruvian group separating from Chilean groups, while the two southernmost groups showed reduced genetic diversity (Chile Central-South: h = 0 and π = 0; Chile South: h = 0.39 and π = 0.00069) as it is often recorded in peripheral populations (Wisely et al. 2004; Vianna et al. 2010).

In an analysis covering data of about 3000 animal species Bazin et al. (2006) note that high levels of diversity are not always proportionally related to large population numbers. In fact, maintenance of high levels of allelic variation in spite of a severe bottleneck in population size has been observed in some mammal populations, like the brown bear *(Ursus arctos)* in the Western Carpathians (Hartl and Hell 1994), the greater one-horned rhinoceros (*Rhinoceros unicornis*) (Dinerstein and McCracken 1990) and several gazelle species (Zachos et al. 2010 and references therein). According to Dinerstein and McCracken (1990) the erosion of genetic diversity attributed to bottlenecks may be overemphasized and Bazin et al. (2006) suggest data on nuclear markers to be more fitting in describing the relation between population size and genetic diversity. Although both genetic studies on *L. felina* have not yet detected if the population has actually gone through a bottleneck, thousands of otter pelts exported from Chile between 1910 and 1954 (Iriarte and Jaksic 1986) suggest a significant decrease in population numbers in the 20th century. The results obtained in the genetic studies of Valqui et al. (2010) and Vianna et al. (2010) suggest that gene flow occurs despite habitat fragmentation along the Peruvian and Chilean coast, which is in contradiction to the low dispersion capacity reported by Medina-Vogel et al. (2007). Young individuals of another otter (*Lutra lutra*) move several kilometers in search of new habitat (Kruuk and Moorehouse 1991; Koelewijn et al. 2010) and tracked Giant otters (*Pteronura brasiliensis*) have been recorded moving up to 160 km along a river in a period of 6 months (Staib 2002). A somehow similar behavior might cause remixing of genetic material in the marine otter population, neutralizing the effect of isolation by great distances between patches of rocky shore. Further studies on migration behavior of the species are needed to confirm this hypothesis.

Threats – past and present

Natural factors

Land refuges are decisive on the distribution of *L. felina* (Medina-Vogel et al. 2007) and due to natural fragmentation of the coastal habitat in Peru and Chile the population is disjunct (Redford and Eisenberg 1992; Valqui et al. 2010). Small habitat patches isolated from each other – a frequent scenario for *L. felina* – impede gene flow and present unfavorable conditions to support a marine otter population (Peltonen and Hanski 1991).

The El Niño Southern Oscillation (ENSO) is a periodic phenomenon causing more or less drastic climatic and oceanographic changes. Rise of temperature and reduction of nutrient supply of superficial waters considerably reduce the primary production, causing the mortality of several marine communities from fish to mammals (Apaza and Figari 1999; Wang and Fiedler 2006). Although very little information exists about concrete mortality events – 5 dead individuals were reported in a period of three months during a study on the mortality effects of the ENSO on marine fauna in Marcona, Peru (Apaza and Figari 1999) – ENSO events are considered to cause a decrease in population sizes of *L. felina* (Vianna et al. 2010).

Anthropogenic factors

In the last decades, heavy migrations from the Andes to the coast of western South America caused an intensive urbanization of the littoral. In Peru, the human population has increased from 7 million in 1940 to 28 million in 2007, with now 54% of the population living at the coast (INEI 2007). In Chile, the human population has increased from 5 million in 1940 to 15 million in 2005, with four of the five biggest Chilean cities at present located directly at the coast (INE 2002).

The pressure put on the coastal ecosystem by the increasing number of human settlements has accelerated habitat degradation and increased habitat fragmentation (Brownell 1978; Eisenberg and Redford 1989; Sielfeld and Castilla 1999; Medina-Vogel et al. 2008; Vianna et al. 2010).

Industrial and artisan fishing ports have been established along the Pacific coast, affecting structure and productivity of marine life communities. Fishing has intensified natural declines in the abundance of many forage fishes, leading to reduced reproductive success and reduced abundance of birds and marine mammals (Majluf et al. 2002). Mariculture has increased dramatically in number and extraction volume in Peru (Apaza et al. 2004). Furthermore building of docks, dredges, dams, breakwaters, canalizations and sanding also produces enormous disturbances of coastal ecosystems (INRENA 2003).

L. felina may adapt to the fragmented habitat (Valqui 2004; Mangel and Alfaro-Shigueto 2004; Valqui et al. 2010) and shows certain capacity to coexist with humans, even in a severely modified environment. In Pucusana, Peru, a group of marine otters is present in a bay (400 m in diameter) where fishing, swimming, diving and jet skiing are regular human activities all year round (Valqui 2004; Ruiz 2009). In Chile, *L. felina* has been reported to live in fishing boats, ship wrecks and near highly populated areas (Medina-Vogel et al. 2007). Still, this coexistence implies competition for resources, that humans exploit for food, commerce and housing (Moreno et al. 1984; Ostfeld et al. 1989; Moreno 2001; Medina-Vogel et al. 2004, 2007, 2008).

Another threat for marine otters is accidental death by entanglement in fishing nets (Mangel and Alfaro-Shigueto 2004). 15 cases of bycatch or intoxication by rat poison were reported between February 2006 and October 2008 (Pizarro 2008), accidental death in crab pots occured in Chile (Medina-Vogel et al. 2004). Dynamite fishing is a frequent problem in several localities of the Peruvian coast, such as Huarmey (Luis Rios, pers. comm.) and Paracas (Apaza et al. 2004; pers. obs. by the author in 2010). Additionally, individuals that live close to mariculture areas are threatened to be killed by armed guards (Apaza et al. 2004).

Human presence has a side effect, whose consequences seem not to be directly harmful to the marine environment, but is definitely affecting the marine otter population. In and around human settlements, big dens with broad terrestrial entrances may be occupied or at least frequently visited by dogs, cats and rats. Several places with evidence of rats and cats inhabiting potential otter caves (and where otters have been spotted nearby) have been sighted in northern Peru (Apaza et al. 2003; pers. obs. by the author in 2008, 2010 and 2011). Dog attacks were increasingly reported in several locations of the distribution (Medina-Vogel et al. 2008; Mangel et al. 2010; Vianna et al. 2010).

Dozens of beach resorts have been built, especially in the vicinity of big cities like Lima (Ludeña 2004), where it is common to observe jet skis and motor boats affecting the local fauna with oil spillage and extreme noise (Valqui 2004). Furthermore, several centers of industrial fishing activity spill their waste directly or indirectly into the ocean (Apaza et al. 2004). This is especially the case of Chimbote, probably the most important fishing port at the Peruvian coast corresponding to the northern distribution limit of the marine otter. In the mining cities Ite, Ilo and Marcona in Peru, tailings have been spilled directly into the ocean for over 40 years, altering several kilometers of the littoral (Apaza et al. 2004). Additionally, spills of domestic effluents reach the ocean directly or through rivers (Hinrichsen 1998; Thorne-Miller 1999). Thus, heavy metals and other toxic substances can be diffused through currents and progressively transmitted through the food chain (Valqui 2004; Apaza et al. 2004).

Hunting was the major threat on the marine otter in the 20th century (Red List of Threatened Species Version 2011.1; Sielfeld and Castilla 1999). However, there is a lack of specific numbers. In a report on Chilean fur trade it is documented that 38,000 otter pelts were exported from Chile between 1910 and 1954 (Iriarte and Jaksic 1986). Due to the fact that two otter species (*L. provocax* and *L. felina*) were subsumed as "otters", no certain population estimate of each species can be inferred from this data. Indeed, it shows the magnitude of the pelt industry in the 20th century. Today, the lack of demand in the pelt market and fur trade prohibitions have diminished the hunting threat considerably. Nonetheless, illegal hunting for fur and trophies still occurs in Samanco (Sánchez and Ayala 2006), La Libertad (15°29′S) and Morro Sama (18°00′S) (Apaza et al. 2004), Peru and south of 39°S latitude in Chile. Killings do not implicate consequences for the hunters as law enforcement is not comprehensive (Red List of Threatened Species Version 2011.1).

A scenario of increasing human impact on the Pacific coast of South America is given for the next decades. In this context, Medina-Vogel et al. (2008) hypothesized that habitat fragmentation due to human impact might turn isolation into a cause of local extinction events. A level of interruption between habitat patches too big to be compensated by migration could be arrived, blocking gene flow. Considering the adaptability of the species, this hypothesis certainly remains under discussion.

Current rates of decline indicate that the population of *L. felina* will be reduced by at least 50% over the next three generations (30 years) (Red List of Threatened Species Version 2011.1). Although methods to obtain this estimate are not mentioned and recent results do not correspond to this prediction, the uncertainty about total population numbers, effective population size and population trends support its classification as "Endangered" based on the precautionary principle. Further studies and monitoring have to clarify the reasons for the distribution reduction of the last decades to avoid further reduction or increased levels of threats.

From the early 1900s, Peruvian governmental agencies protected the terrestrial part of a system of islands and headlands along the Peruvian coast to secure the accumulation of guano in bird colonies, mainly of the Guano Cormorant (*Phalacrocorax bouganvilii*), the Peruvian Booby (*Sula variegata*) and the Pelican (*Pelecanus thagus*) (Muck and Pauly 1987). Although the marine otter was no subject of the plan, the species obviously benefited from the protection status of parts of its habitat. The Guano Administration Agency of Peru from the Ministry of Agriculture was focused in extracting the fertilizer from those areas. In December 2009, this production system was converted into a system of protected areas (Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras, RNSIIPG) of the Peruvian Natural Resources Agency (Dirección General Forestal y de Fauna Silvestre) and the surrounding oceanic waters were included. This increase of the protected area (1120 km^2 in total) presents a potential improvement of the protection of the coastal ecosystem. But certainly, several conflicts with the artisan and industrial fisheries were inherited from the former system (Apaza et al. 2004) and more will yet rise. The new prohibition to fish in the nearby waters of those areas is in conflict with the ever growing pressure put on the marine ecosystem by more intensive fisheries. The ever increasing threat of displacement demands permanent solutions that allow the marine otter to evade introduced species occupying their habitat.

Although the marine otter is protected by law it has not been involved in any concrete conservation program by the Peruvian government. Environmental education work is a task of independent non-governmental organizations, both in Peru and Chile. Pro Delphinus (www.prodelphinus.org), an organization working at the Peruvian coast since 1995, focuses on the conservation of *L. felina* (especially in Pucusana, Ilo, Puerto Grau and Vila Vila), providing workshops for both schoolchildren and fishermen. A better understanding of the ecological interactions of the marine environment and ideas to support conservation of marine otters and other threatened species are generated. The author has collaborated with Pro Delphinus for the last three years and with the support of Yaqu Pacha created "Proyecto *Lontra felina*" (see facebook group under the same name) to unite the efforts regarding environmental education work as well as to promote scientific research. In Chile, the NGO "OBC Chinchimen" has established an environmental network in the region of Valparaíso in central Chile, since 2001. A marine otter rehabilitation and reintroduction program is accompanied by non-invasive behavioral studies (especially in Acantilados de la Quirilluca) assessing conservation priority areas (Ricardo Correa, pers. comm.).

Recommendations

In Peru, the reasons for the retrieval of *L. felina* from the regions north of Chimbote (9°00′S) have to be clarified and solutions to revert these conditions have to be proposed. Occasional events of occupation in those regions have to be monitored and conservation measures (bycatch reduction, total prohibition of dynamite fishing and hunting) have to ensure conditions for the species to return to its historical distribution. Given a favorable scenario, translocation and re-stocking programs should be taken into consideration. Another region to which special attention should be paid is the area around Morro Sama and Quebdrada de los Burros (17°59′S to 18°02′S) in southern Peru, where conspicuous groups of *L. felina* have been reported (Mangel and Alfaro-Shigueto 2004) in an area with a low density of human population (pers. obs. by the author). This area has never been protected nor is it comprised in the RNSIIPG. A proposal of an establishment of a regional conservation area exists (Ulloa et al. 2010) and has to be supported (Valqui et al. 2010). The area represents the southernmost group of otters in Peru which could act as a source to adjacent marine otter groups, especially to those over 300 km further south, in northern Chile. Mangel et al. (2010) suggest that habitat modified by humans and artificial habitats (shipwrecks, docks, etc.) can be used as stepping stones between rocky seashore patches widely separated from each other and that their management should be included in a strategy for marine otter conservation. The new system (RNSIIPG) in Peru, at least theoretically, points in that direction. Understanding population structures and dynamics as well as the species' migration and territorial behavior will allow compensation measures against the fragmenting effect of geographical barriers.

In Chile, to hinder the consequences of fragmenting forces acting upon *L. felina*, Medina-Vogel et al. (2008) suggested that conservation management should consider the need of establishing reserve networks including the protection of rocky seashore patches that would allow migration (gene flow) and secure the species survival. Domestic animals should be controlled within these areas (Medina-Vogel et al. 2008). Considering political and logistical implications, this idea seems very difficult to put into practice and will have to be supported by the protection of other species. Studies in the southern part of Chile have to test the hypothesis of southern population extinction (Vianna et al. 2010). In Argentina a monitoring program should be established for Isla de los Estados and Mitre Peninsula to update the information on the species (Cassini 2008).

Further studies have to assess regional and total population numbers by molecular techniques (Kohn et al. 1999; Xu and Fu 2004) as well as by improvement of field techniques (Medina-Vogel et al. 2006), resulting in better estimates of the real population size. The effective population size has to be determined by genetic, behavioral and ecological studies describing reproduction ratios. Nuclear markers (microsatellites) should be used to deepen the knowledge on population history and demography (Bazin et al. 2006). Studies on parasites, diseases, as well as the impact of pollutants on marine otters living in highly contaminated waters (Apaza et al. 2002), have to be continued. Physiological issues concerning the performance of the marine otter in its environment (e.g. osmoregulation) have to be addressed. Relevant information on reproductive ecology was found in studies of captive Giant otters (*P. brasiliensis*) (Redford and Eisenberg 1992). Captive marine otters (at least 3 otters captive in Peruvian Zoos) could be used as reference or study subjects.

L. felina possesses a special status as flagship and umbrella species, which should be exploited to support educational campaigns along its distribution range. Sensitization of local people (especially fishermen) towards *L. felina* might lead to conservation programs potentially contributing to the conservation of marine ecosystems in Peru, Chile and Argentina. It is strongly recommended to coordinate efforts between research and environmental working groups, between and within these three countries.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2011.08.004.

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