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The anthropic transformation of the landscape has brought the arrival of novel ecosystems. Since these ecosystems will likely become increasingly common in the future it is important to know if they can provide food for wildlife. Here we test whether European otters *Lutra lutra* can have high foraging success in human-made reservoirs. Rhythms of daily activity were studied in a small (365 ha) and shallow (6–15 m) reservoir in NW Spain in which otters show diurnal activity and can be observed directly when foraging. We studied time of permanence in the water and fish catch rate during the period in which water levels were kept artificially low (autumn–winter 2015, 2016 and 2017). Results indicate that otters had at least two peaks of diurnal activity (from 10:00 to 11:00 a.m. far from sunrise and from 06:00 to 07:00 p.m. immediately before sunset). Otters spent an average of 74 min (54–94, 95% CI) in the water foraging daily, and had a minimum fish catch rate of ca 600 g h^{-1} of small fish. According to a pre-existing theoretical model, otters eating at that rate can satisfy their daily energy requirements with just 1.5 h of daily foraging activity, what roughly coincides with the upper confidence limit of the parameter estimate. When considering as well the capture of large fish otters obtained ca 850 g of fish per day in only 1.2 h in the water. Otters in the reservoir satisfy their daily requirements in autumn–winter with the same time investment than Shetland Island otters foraging during the day on marine fish during the summer. This coincidence is most likely due to the fact that winter water temperature in our study site is similar to that in the Shetland Islands in summer.

Keywords: activity rhythms, diurnal activity, fish catch rate, *Lutra lutra*, time in the water

Eurasian otters were highly threatened in southern Europe a few decades ago due to direct human persecution and water pollution (Mason and Macdonald 1986, Delibes 1990, Jiménez and Delibes 1990, Ruiz-Olmo et al. 1998). However, they have shown a remarkable plasticity to withstand landscapes heavily modified by human activity typical of the Anthropocene (Steffen et al. 2011, Weinberger et al. 2016), as it has been the case of other mammal groups (Galán-Acevedo 2019). This plasticity is helping them to recover their population numbers and former geographical ranges (Jiménez et al. 2008, López-Martín and Jiménez 2008). In fact, they are not only recovering their past ranges, but also colonizing and/or recolonizing new habitats (see Silliman et al. 2018 for a similar case with sea otters). One of the novel ecosystems (sensu Hobbs et al. 2009) that otters are increasingly using nowadays is reservoirs, used either for irrigation, water supply to cities or production of

hydroelectric power. These novel ecosystems were colonized by otters soon after their creation (Basto et al. 2011), despite they were initially perceived as a potential threat for otter persistence worldwide (Palmeirim et al. 2014). Reservoirs act as a barrier preventing fish migration (decreasing otter prey abundance) and they also can disrupt otter dispersal (Ruiz-Olmo and Jiménez 2008). In addition they convert a lotic system into a lentic one. The latter was perceived initially as a negative factor because otters have been traditionally considered to be riverine species specialized in a life in the upper stretches of rivers (Ruiz-Olmo et al. 2005, Pedroso et al. 2013), where they simply had survived as refugees during decades or centuries of direct persecution and water pollution (Martínez-Abraín et al. 2019). Surprisingly, otters are now increasingly using reservoirs (and many other human-made habitats) eating mostly exotic invasive species in them, as reported by many Iberian studies (Pedroso and Santos-Reis 2006, Sales-Luis et al. 2007, Ruiz-Olmo and Jiménez 2008, Basto et al. 2011, Pedroso et al. 2013). Some authors have hypothesized that reservoirs are low-quality habitats for otters (Pedroso et al. 2013), that are mostly used when native fish become scarce in rivers or that otters only use reservoirs due to density-dependent dispersal from

saturated river populations (Pedroso and Santos-Reis 2006, Ruiz-Olmo and Jiménez 2008, Basto et al. 2011).

To find out whether otters can have high foraging success in human-made reservoirs, loaded with exotic prey species, we studied otter hunting efficiency in a reservoir where otters show much diurnal activity and hence can be observed directly when foraging, an infrequent opportunity. Specifically the rhythms of activity, time of permanence in the water during the day while foraging and fish catch rate during the low water period (autumn–winter) were studied. Our a priori expectation was that otters could have lower foraging efficiencies in reservoirs compared to natural lakes.

Material and methods

The study site

Spain is poor in lakes, except in the Pyrenean region, but during the 20th century ca 880 major reservoirs (functionally equivalent to lakes) were built throughout the country. Major reservoirs are used to produce hydroelectric power, supply tap or irrigation water or to cool down power plants. The study site was the Cecebre-Abegondo reservoir, formed by the confluence of the rivers Mero and Barcés. It is located in NW Spain within the province of A Coruña (Fig. 1) (central point coordinates: 43°16′56″N, 8°17′18″W). It is a core area of a Biosphere Reserve (Reserva da Biosfera Mariñas Coruñesas e Terras do Mandeo), a site of community importance (SCI) and a special area of conservation (SAC) under the Nature 2000 network. It was built in 1976 and covers some 365 ha when full, holding a maximum of 22 million m³ of water. The reservoir dam has a height on

foundations of 22.5 m. It presents a marked artificial seasonality, with water levels kept low during autumn–winter, to prevent flooding, and high during spring–summer, to guarantee the supply of tap water to approximately 400 000 people (Coruña city and its metropolitan area). The reservoir is located at ≈ 35 m a.s.l., and is relatively shallow (6–15 m depth). Recreational boating is forbidden. Water temperatures are mild (15.5 ± 3.33°C, mean ± SD annual temperature) and rain is frequent throughout the year, although more common in winter (1115 ± 188.6 mm, annual precipitation). The reservoir has a narrow fringe of riparian vegetation and a wider fringe of oak forest *Quercus robur* where otters find shelter during their resting and breeding periods (i.e. otters not only make use of the riparian vegetation belt but also use extensively the oak forest for shelter). During the study period a minimum of seven individuals (two adult females with two cubs each plus one adult male observed simultaneously) were present in the reservoir. The study individuals are known to make extensive use of the riverine system downstream from the dam (Martínez-Abraín et al. unpubl.). The usual crossing points from the reservoir to the river in the dam were detected by means of camera trapping and indirect evidences (spraints and footprints of otter passing). Some otters are frequently observed also in the Mero river mouth (Ría de O Burgo), but we cannot be sure that they are the same individuals that make use of the reservoir as they were not marked by means of tele-detection devices. Three females with cubs have been observed in the reservoir during the last four years and each of them had two grown-up dependent cubs. Females with offspring frequented territories in opposite shores of the reservoir, whereas the adult resident male was observed ranging freely across the territories of the two females.
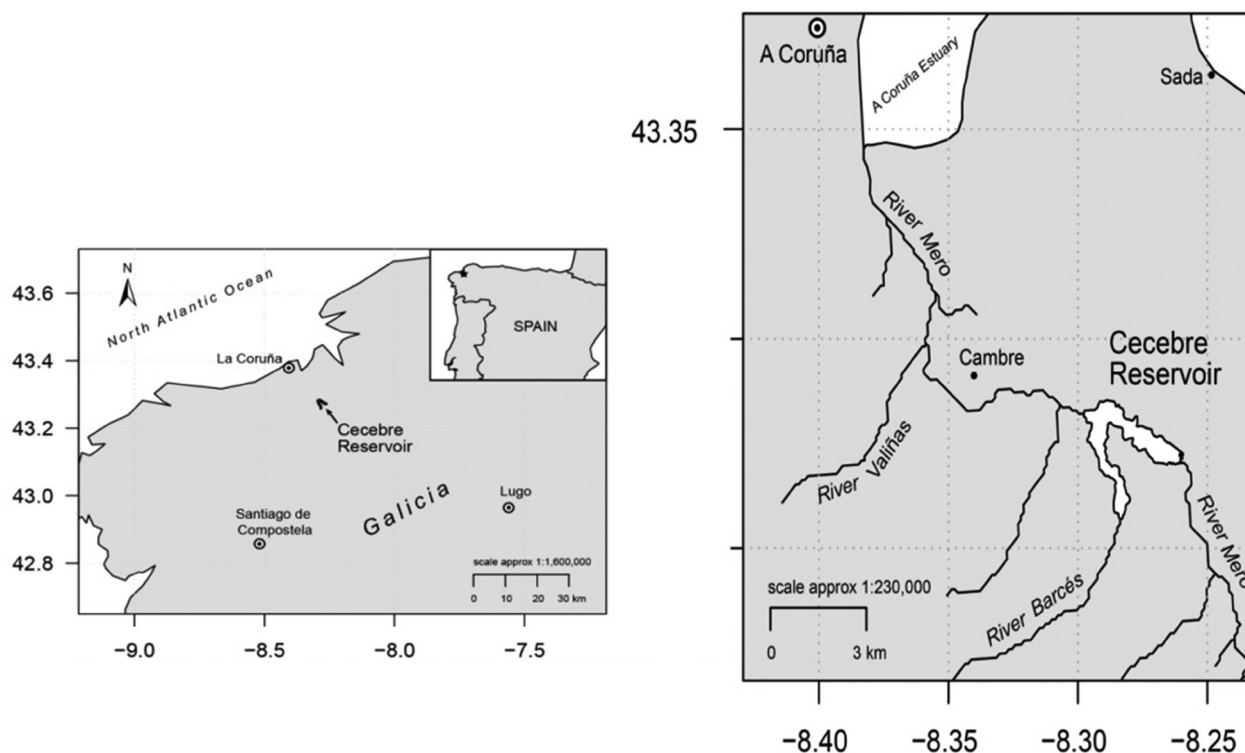

Figure 1. Location of the study reservoir within the context of Galicia and NW Spain.

Otter monitoring

Otters were observed during the day at the reservoir (one observer from approximately 08:00 a.m. to 02:00 p.m. and a second observer from approximately 05:00 p.m. to sunset). Otters were observed almost on a daily basis (Monday through Friday) during the autumn-winter seasons of 2015, 2016 and 2017. Observations were performed from vantage points with the aid of binoculars and terrestrial scopes. Otter observation from the distance was non-invasive and hence did not require any specific supervision or approval by the environmental authorities. Observation effort for the time period 02:00 to 05:00 p.m. was much lower than that for the rest of the day because previous pilot observations of the system in 2014 indicated that it was very unlikely to find otters active in the reservoir during those hours (i.e. precisely after one of the peaks of activity). As precautionary measure information available for that time period was not included in the final analysis of rhythms of activity. Nocturnal activity was not studied in a systematic way. Although study otters also showed diurnal activity in spring–summer at the reservoir they could not be monitored by direct observation during this part of the year. This is because otters abandon the use of relatively fixed and predictable hunting grounds in the open waters of the reservoir, shifting from a diet based on fish to a diet based on crayfish, foraging along the reservoir shores, coinciding with the period in which the stored water volume is artificially kept to a maximum. These relatively fixed hunting grounds could be linked to the presence of rock outcrops and/or to the existence of submerged human constructions where fish can gather.

A total of 655 hunting attempts, grouped in 85 hunting sessions were observed, representing a total of 51 h of active foraging. For each hunting attempt diving time and handling time were recorded. Time was recorded by means of a stop watch and foraging information was recorded with a digital voice recorder. Fish that were eaten by otters while floating vertically in the water were recorded as 'small' whereas fish taken ashore to be eaten were recorded as 'large'. Small fish typically were only a bit longer than otter mandible width, whereas large fish sticked out of the otter mouth sides clearly when observed from the distance. The number of hunting attempts (successful or failed) per fishing session and the total time span of a hunting session were also computed. A hunting session was considered to be over when a) an otter stopped its consecutive sequence of hunting dives on small fish and started traveling to a new hunting spot or b) when an otter captured a large fish and moved ashore to eat it. Hunting success was computed as the number of hunting attempts that resulted in a successful hunt in each hunting session.

Data analysis

Differences in mean time spent by otters in the water daily were analysed by means of a univariate ANOVA, together with post hoc Tukey HSD tests in R (<www.r-project.org>). In order to be as conservative as possible when estimating otter energetics we assumed that otters were foraging only on the less profitable fish prey (goldfish) during autumn–winter, although we know that otters consumed

straight-mouse nases *Pseudochondrostoma dueri* as an alternative fish prey during the second half of the autumn–winter period (Martínez-Abraín et al. unpubl.). Additionally, we did not take into account for our estimates of otter energetics the hunting attempts in which otters captured red-swamp crayfish *Procambarus clarkii* or large fish.

Results

Diurnal rhythms of activity

Otters presented at least two peaks of daily activity at the study site during the autumn–winter period (Fig. 2). A major first peak occurred in the morning (10:00–11:00 a.m.) far from sunrise, although some otters can be active since sunrise according to non-systematic observations obtained by means of camera trapping. A second peak took place in close after sunset (06:00–07:00 p.m.). Otters adjusted their evening activity in autumn–winter to variable sunset time.

Time of permanence in the water

We computed the average time spent by otters in the water while foraging during the morning (mean $\pm$ SD = 36.8 $\pm$ 11.2 min; n = 17), afternoon (19.2 $\pm$ 8.72 min; n = 6) and evening (18.4 $\pm$ 3.74 min; n = 32) hunting sessions (Fig. 3). We added the arithmetic means of the three periods in order to approximate the time spent by otters in the water during the day. Otters spent an average of 74 min (95% CI: 54–94 min) foraging in the water every day. Differences between the time spent in the water during the morning, afternoon and evening were found to be statistically significant (F = 7.85, df = 2, p-value = 0.001). More specifically the longest time of permanence in the water happened in the morning and the shortest in the evening. In fact, differences between morning and evening were found to be statistically significant (p-value = 0.001), whereas differences between morning and afternoon (p-value = 0.058) and afternoon and evening (p-value = 0.99) were not.

Fish catch rate

According to our data otters performed an average (median) of eight hunting attempts in each hunting session, when hunting for small fish. Considering that we estimated that average hunting success per hunting attempt was 63%, otters were successful in ca five hunting attempts per hunting session, as an average. According to DNA metabarcoding of otter spraints at the study site (Martínez-Abraín et al. unpubl.) the main otter fish prey in autumn–winter is goldfish *Carassius auratus*. Considering that the mean weight of the smaller goldfish size class at the study site was 27 g (Augas de Galicia 2009), otters gathered a minimum of 135 g of fish per hunting session. Given that the mean duration of each hunting session was 0.21 $\pm$ 0.16 h (mean $\pm$ SD) it turns out that study otters hunted at an approximate rate of 642 g h^{-1} (135 g/hunting session: 0.21 h/hunting session) as an average. Since otters also ate large fish (mainly straight-mouth nases according to our observations) in a proportion of one over four compared to small fish (goldfish), and the mean weight of a
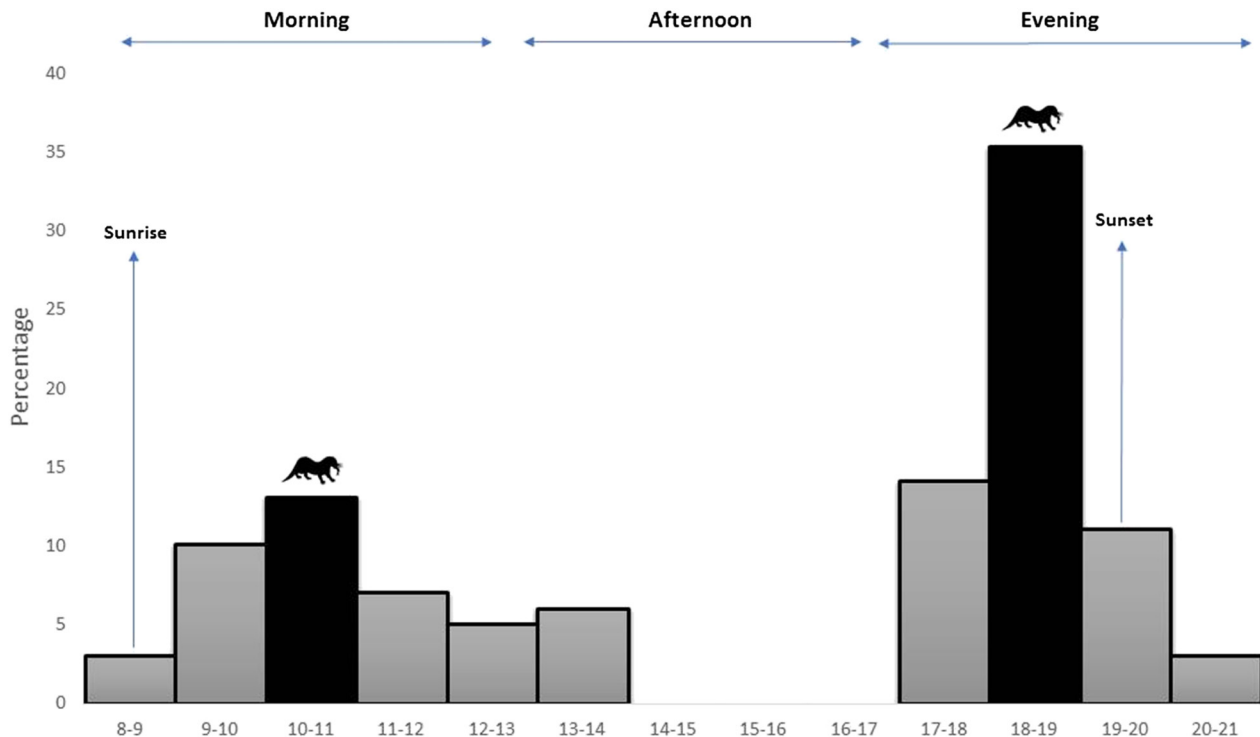
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Figure 2. Diurnal rhythms of otter activity at Cecebre-Abegondo reservoir. Black solid bars represent peaks of otter activity during the morning (08:00–12:00 a.m.) (n = 32) and evening (05:00–09:00 p.m.) (n = 64). Sample size for the afternoon period (02:00–05:00 p.m.) was small (n = 13). Vertical arrows indicate mean sunrise and mean sunset time during the autumn–winter period.

mean size nase in the reservoir (231 mm) was 164 g (Augas de Galicia 2009), we can estimate that otters gathered a total of 781 g h^{-1} of fish per hunting session.

Discussion

Diurnal rhythms of activity

Otters need 800–1800 g of fish every day (depending on water temperature) to satisfy their energy requirements, according to Kruuk (2006). The three periods of diurnal
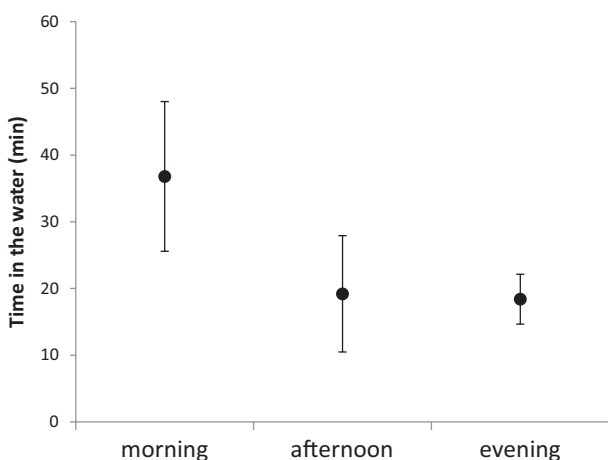

Figure 3. Average time (min) spent by otters foraging in the water at the study reservoir divided in three periods of the day (n = 17; n = 6; n = 32 hunting sessions respectively). Vertical error bars are 95% confidence intervals.

activity at the study site (with a high hunting success rate) could mean that otters had no need for much nocturnal activity to satisfy their energy requirements at the study site. However we cannot be conclusive on this matter because nocturnal activity was not studied systematically. Future radio-tracking studies would be necessary as a complement of our study based on direct diurnal observations to be more conclusive, and to account for inter-individual variations in activity patterns (Quaglietta et al. 2018). Diurnal otter activity is typically linked to nocturnal activity of their main prey (Kruuk 2006), as they are captured while resting. However, goldfish are active during the day in the reservoir (own observations of large banks of young goldfish in autumn). Large densities of slow-moving fish from lentic waters (i.e. easy to catch) could explain in part diurnal activity. Otter habituation to harmless people might also influence diurnal behaviour, as otters seem not to care much about close presence of harmless people at the study site (Martínez-Abraín et al. 2019).

Time in the water and fish catch rate

Average time spent in the water by otters (average 74 min, maximum of 94 min) was very low compared to north-east Scotland (5.2 h day^{-1}) or the Shetland Islands (2.6–3.4 h), where otters were also studied by direct observation (Kruuk 2006). The rate of hunting for small fish estimated in the reservoir was approximately 642 g h^{-1}. According to a theoretical model developed by Kruuk (2006) when it is feasible to hunt at rate of 600 g of fish per hour, otters would not have the need to be active more than 90 min day^{-1}. In that time they would be hunting 800 g of fish. If our study

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otters hunt during 74 min they would get 791 g of fish per day. If we consider the upper limit of the 95% confidence interval of the parameter estimate (94 min), otters would be getting ca 1000 g of fish per day (1 kg). When considering jointly the capture of both small and large fish study otters would get 854 g per day in only 74 min (1.2 h day^{-1}). Additionally, it is to be considered that energy requirements for southern European otters are likely in the lower extreme of the range for the species, because winter water temperatures are not as energetically demanding as those in central and northern Europe for which the theoretical model was developed (i.e. average winter water temperature at Cecebre = 11.5°C ± 1.65 compared to temperatures close to freezing in Scotland). In fact otters at Shetland Islands only need to fish 1.2 h day^{-1} during the summer, when water temperature is higher (T = 10°C), and the availability of marine fish is highest (Kruuk and Cars 1996). On the contrary, otters foraging on eels in the Dinnet freshwater lochs of Scotland (an ecosystem resembling more our artificial lake of study) need to be fishing during 2.3 h day^{-1} (Conroy and Jenkins 1986). In summary, our study otters need to be active in autumn–winter the same amount of time than Shetland otters foraging on marine fish in summer, suggesting a similar productivity of both ecosystems, coinciding with similar water temperatures in opposite seasons. On the contrary the productivity of natural Scottish lakes (comparing eels to goldfish + nases) could be much lower than that in our reservoir, because eels are easy prey to catch as they move slowly (op. cit) but much more time was needed to hunt for them on a daily basis.

Another relevant factor is that the study reservoir is relatively shallow (6–15 m) so that otters can make use of a large part of it, especially in autumn–winter when water level is kept artificially low. Reservoirs with steeper slopes (i.e. most reservoirs) likely only have otter foraging activity around the tributary inlet areas, where depths are shallower (<6 m). Kruuk et al (1985) also found this maximum of 6 m for successful hunting. In Spanish Mediterranean rivers otters are known to have a fish catch rate of only 274 g h^{-1} (Ruiz-Olmo 1995). This is two times lower than in our study reservoir what provides support for the idea that shallow reservoir waters can be suitable for otters at least part of the year (Pedroso and Santos-Reis 2006, Weinberger et al. 2016), acting as good substitution habitats (sensu Martínez-Abraín and Jiménez 2016). This conclusion is reinforced also by the fact that the design of our analysis has been as conservative as possible as we have only dealt with fish and have not included the crayfish captured. Adding this biomass would make even higher the quality of reservoirs as alternative habitats for otters, but we cannot apply Kruuk's theoretical model to crayfish capture.

Implications for otter population dynamics

Our results show that human-made reservoirs can provide large amounts of food for otters. Hence it is to be expected that otters will do an increasing use of reservoirs in the future as their formerly depressed populations recover and expand. We think that otters do not select reservoirs just because their river territories may be saturated now but because of active preference for these habitat types.

Evidence for that comes from the Mediterranean river basins in Spain where otters had a 32% occurrence in sampled reservoirs to 77% in 2014–2016, for a similar sampling effort, being now higher than in rivers (53–59%) (Martínez-Abraín et al. 2019). The respectful attitudes of current urban people allow otters to be active during the day and that provides otters with the possibility of being active more hours a day instead of restricting their activity to the night hours. Reservoirs could also act as insurance in cases of extreme droughts affecting rivers although more so in the Mediterranean river basins.

References

Augas de Galicia 2009. Asistencia técnica para la toma de datos del indicador biológico peces en las redes de monitorización de aguas superficiales en el ámbito de la demarcación hidrográfica Galicia-costa (Expte. OH.688.244.SV). – Consellería de Medio Ambiente, Territorio e Infraestructuras. Xunta de Galicia, Spain.

Basto, M. P. et al. 2011. Use of small and medium-sized water dams by otters in a Mediterranean ecosystem. – Anim. Biol. 61: 75–94.

Conroy, J. W. H. and Jenkins, D. 1986. Ecology of otters in northern Scotland. IV. Diving times and hunting success at Dinnet Lochs, Aberdeenshire and in Yell Sound, Shetland. – J. Zool. 209: 341–346.

Delibes M. (ed.) 1990. La nutria (*L. lutra*) en España. – ICONA Serie Técnica, Madrid.

Galán-Acevedo, C. et al. 2019. The conservation value of human-modified lanscapes for the world's primates. – Nat. Commun. 10, 152.

Hobbs, R. J. et al. 2009. Novel ecosystems: implications for conservation and restoration. – Trends Ecol. Evol. 24: 599–605.

Jiménez, J. and Delibes, M. 1990. Causas de la rarificación. – In: Delibes, M. (ed.), La nutria (*L. lutra*) en España. ICONA Serie Técnica, Madrid, Spain, pp. 169–177.

Jiménez, J. et al. 2008. ¿Por qué se está recuperando la nutria en España? – In: López-Martín, J. M. and Jiménez, J. (eds), La nutria en España: veinte años de seguimiento de un mamífero amenazado. SECEM, Málaga, Spain, pp. 273–304.

Kruuk, H. 2006. Otters: ecology, behaviour and conservation. – Oxford Univ. Press.

Kruuk, H. and Carss, D. N. 1996. Costs and benefits of fishing by a semi-aquatic carnivore, the otter *Lutra lutra*. – In: Greenstreet, S. P. R. and Tasker, M. N. (eds), Aquatic predators and their prey. Blackwell Scientific, pp. 10–16.

Kruuk, H. et al. 1985. The effects of depth on otter foraging in the sea. – Inst. Terrestrial Ecol. Annu. Rep. 1984: 112–115.

López-Martín, J. M. and Jiménez, J. 2008. Resultados del muestreo y diagnosis de la distribución de las poblaciones de nutria en España. – In: López-Martín J. M. and Jiménez, J. (eds), La nutria en España: veinte años de seguimiento de un mamífero amenazado. SECEM, Málaga, pp. 245–270.

Martínez-Abraín, A. and Jiménez, J. 2016. Anthropogenic areas as incidental substitutes for original habitat. – Conserv. Biol. 30: 593–598.

Martínez-Abraín, A. et al. 2019. Pax Romana: 'refuge abandonment' and spread of fearless behaviour in a reconciling world. – Anim. Conserv. 22: 3–13.

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Mason, C. F. and Macdonal, S. M. 1986. Otters, ecology and conservation. – Cambridge Univ. Press.

Palmeirim, A. F. et al. 2014. Giant otter population responses to habitat expansion and degradation by a mega hydroelectric dam. – Biol. Conserv. 174: 30–38.

Pedroso, N. M. and Santos-Reis, M. 2006. Summer diet of Eurasian otters in large dams of south Portugal. – Hystrix Ital. J. Mamm. 17: 117–128.

Pedroso, N. M. et al. 2013. The response of otters to environmental changes imposed by the construction of large dams. – Aquat. Conserv. 24: 66–80.

Quaglietta, L. et al. 2018. Extrinsic and intrinsic factors affecting the daily rhythms of a semiaquatic carnivore in a Mediterranean environment. – Hystrix Ital. J. Mamm. 29: 128–136.

Ruiz-Olmo, J. 1995. Observations on the predation behavior of the otter *Lutra lutra* in NE Spain. – Acta Theriol. 40: 175–180.

Ruiz-Olmo, J. and Jiménez, J. 2008. Ecología de la nutria en los ambientes mediterráneos de la Península Ibérica. – In: López-Martín, J. M. and Jiménez, J. (eds), La nutria en España, veinte años de seguimiento de un mamífero amenazado. SECEM, Málaga, Spain, pp. 305–343.

Ruiz-Olmo, J. et al. 1998. Factores que han determinado la situación actual de las poblaciones de nutria y propuestas de gestión. – In: Ruiz-Olmo, J. and Delibes, M. (eds), La nutria en España ante el horizonte del año 2000. SECEM, Málaga, Spain, pp. 223–242.

Ruiz-Olmo, J. et al. 2005. Habitat selection by female otters with small cubs in freshwater habitats in northeast Spain. – Lutra 48: 45–56.

Sales-Luis, T. et al. 2007. Prey availability and diet of the Eurasian otter (*Lutra lutra*) on a large dam and associated tributaries. – Can. J. Zool. 85: 1125–1135.

Silliman, B. R. et al. 2018. Are the ghosts of nature's past haunting ecology today? – Curr. Biol. 28: R527–R548.

Steffen, W. et al. 2011. The Anthropocene: conceptual and historical perspectives. – Phil. Trans. R. Soc. A 369: 842–867.

Weinberger, I. C. et al. 2016. Flexible habitat selection paves the way for a recovery of otter populations in the European Alps. – Biol. Conserv. 199: 88–95.