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Diet of the European otter (*Lutra lutra*) in the Massif central (Auvergne, France): spatial and seasonal variations between two study sites

Charles Lemarchand[1], Yves Boulade[2], Noël Gouilloux[3] & Roland Libois[4 †]

[1]Muséum Henri-Lecoq, Clermont Auvergne Métropole, 15 rue Bardoux, 63000 Clermont-Ferrand, France - clemarchand@clermontmetropole.eu (corresponding author)
[2] yves.boulade@orange.fr
[3]noel.gouilloux@orange.fr
[4]Laboratoire de Zoogéographie, Université de Liège, Belgium

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Abstract

In order to evaluate predation strategy and variations during an active population dynamic, diet of European otter (*Lutra lutra*) was studied during a year-round cycle in two different aquatic systems in Auvergne (France). First were tributaries of Allier River in Haute-Loire and second were marshes, creeks, rivers and ponds in Puy-de-Dôme. Preys were identified and quantified (occurrences, abundances and biomasses) from otter spraints sampling. Diet was mainly consisted by little- and medium-sized fish (74% to 89% of consumed biomass, size generally less than 17.5 cm). Dominant prey in otter's diet were the most numerous species in studied rivers and marshes, which corresponds to the most efficient predation strategy. Crayfish, amphibians, reptiles and small mammals constituted most of time secondary prey, but sometimes dominated diet. Spatial and temporal differences in prey diversity, abundances and biomasses were recorded. Data illustrating species diversity in rivers and marshes recently recolonized by European otter were not modified by its predation impact. The study of a top-predator diet can therefore be considered as an additional way in habitats studying and biodiversity and management conservation strategies, in natural or anthropogenic alteration contexts.

Keywords
European otter
Diet
Auvergne

Résumé

Afin d'évaluer la stratégie de prédation et ses variations au cours d'une dynamique de population active, le régime alimentaire de la loutre d'Europe (*Lutra lutra*) a été étudié au cours d'un cycle annuel dans deux sites d'études, respectivement dans le bassin de la rivière Allier en Haute-Loire et dans des marais, ruisseaux, rivières et étangs des Combrailles dans le Puy-de-Dôme. L'étude a consisté à identifier des restes de proies contenus dans les déjections de l'animal (épreintes), collectées selon un protocole adapté. L'essentiel (74 % à 89 %) de la biomasse capturée a concerné les poissons de taille modeste (moins de 17,5 cm). Pour chaque site les proies les plus abondamment consommées ont été les espèces dominant les peuplements ichtyologiques, dans les spectres de taille où les individus étaient les plus nombreux et les plus accessibles, ce qui correspond au mode de prédation le plus efficace sur le plan énergétique. Les écrevisses, les amphibiens et dans une moindre mesure les reptiles et les mammifères semi-aquatiques ont constitué des proies complémentaires, parfois abondantes à certaines périodes. Des variations spatiales et saisonnières de la diversité des espèces capturées et de leur contribution à la biomasse totale ingérée ont été observées entre les sites et au cours de l'année d'étude, respectivement. L'antériorité des données piscicoles, augmentée de l'étude de paramètres complémentaires (suivi des populations d'écrevisses à pattes blanches par exemple) a montré que le retour ou le rétablissement des populations de loutres n'a pas entrainé de régression des peuplements des espèces leur servant de proies. Au-delà du suivi de la dynamique de population, l'étude du régime alimentaire d'un super-prédateur comme la loutre est donc un élément supplémentaire de la connaissance de la diversité, du fonctionnement et de la gestion d'un habitat aquatique et humide donné, mais aussi de son évolution face à des perturbations d'origine naturelle ou anthropique.

Mots-clés
Loutre d'Europe
Régime alimentaire
Auvergne

Introduction

Within the Massif central, the Auvergne territory is one of those from which the European otter *Lutra lutra* (Linnaeus, 1758) has never disappeared, even at the height of the destruction campaign once carried out against it (Fig. 1).

Figure 1 – European otter (*Lutra lutra*) © C. Lemarchand.

It is also in this same territory that the natural recolonization of the species, following its legal protection, has been observed and followed step by step, since the mid-1980s and up to the present day. At the end of 2019 - date of the last update of the distribution data -, the species was almost continuously present along of the Auvergne hydrographic web (Rosoux & Lemarchand 2019).

The Ministry in charge of the Environment has integrated the conservation of the European otter through a National Action Plan strategy, declined in the Auvergne-Rhône-Alpes region under the management of the local authority (DREAL) and local NGOs or companies (Kuhn *et al.* 2019; Lemarchand *et al.* 2011a, b, c, 2012a, b; Lemarchand & Bouchardy 2010, 2011; Teyssier & Lemarchand 2018).

The European otter is one of the top predators of aquatic food webs. Diet study is a major approach among the actions to improve general knowledge about otter ecology and conservation, associated to a better management of its natural habitats. The estimate of its daily food consumption varies from 600 to 1200 g, depending on the season, the activity or the reproductive status of the animal. This food is taken from within the home range of each individual, which can reach 10 to more than 30 km of linear waterways depending on the conformation and the resource of the local habitat (Rosoux 1998; Rosoux & Lemarchand 2019).

Based on the analysis and identification of prey remains contained in otter spraints (droppings, Fig. 2) or stomach content, diet constitutes one of the most studied aspects of the species' ecology, over practically all of its range (Clavero *et al.* 2003; Kruuk 2006; Libois *et al.* 2015; Rosoux & Lemarchand 2019). Studies of otter feeding behavior remained rare in the regional territory (Bouchardy 1986; Libois 1997; Lemarchand 2007). However, work of this type are necessary at the local level, in the context of the natural recolonization of the species on one hand, but also considering the rapid evolution of the populations of certain species used as food resource (fish, amphibians, crayfish) on the other hand.

Almost all otter predation occurs in aquatic environments, with local exceptions. All aquatic environments are potentially exploited, from source sectors to estuaries and seafronts, including watercourses and all of their hydraulic margins, but also artificial aquatic environments or aquaculture production such as ponds, reservoirs, ditches, canals or fish farms (Clavero *et al.* 2003; Kruuk 2006; Libois *et al.* 2015; Rosoux & Lemarchand 2019).

The species, characterized by a great ecological plasticity, is opportunistic and adapted to a wide spectrum of prey and to their spatial or temporal variations (Kruuk 2006; Rosoux & Lemarchand 2019). Population density is highly variable and very difficult to evaluate. The most represented prey are fish, caught near the banks or the river bottom rather than in open water. Taxa such as amphibians, crustaceans, reptiles and birds complete the diet with variable, but sometimes high proportions depending on the location or the season. Overall, the prey are rather small (15 to 20 cm for fish) and correspond to the most abundant species in the habitat (Clavero *et al.* 2003; Kruuk 2006; Rosoux & Lemarchand 2019).

Diet studies were recently conducted within habitats recently and naturally recolonized by the otter, with a view to compare them with the available data from ancient populations, or to assess the impact of changes in the local fauna complex (species regression or disappearance, alien species introduction) on the predation behavior of the otter. A synthesis of studies conducted in France was published by Rosoux & Lemarchand (2019).

In this context and in order to complete the available knowledge about local diet of the otter, the NGO Conservatoire d'Espaces Naturels d'Auvergne and Catiche Productions Co. carried out a sample collection within two representative sites about local issues of knowledge, conservation, restoration or management of aquatic and wetland environments. One was a set of creeks, rivers, wetlands and ponds in Combrailles (Puy-de-Dôme), recently recolonized by the otter, other one were rivers located in Margeride (Haute-Loire), from where the species has never disappeared. Main objectives of the study were to evaluate and compare otter's predation behavior, prey diversity contribution to the diet and spatial and/or temporal variations of prey in diet in a current recolonization area and a historical stronghold.

Figure 2 – An otter spraint © C. Lemarchand.

Materials and methods

Sampling areas

Two separate spraints (droppings) collect campaigns were conducted in the two different areas, respectively streams, ponds and wetlands near the town of Pulvérières (Puy-de-Dôme), and rivers of Margeride, near the towns of Saugues and Desges (Haute-Loire).

Reference points were summarized in Table 1. Their choice was motivated by various criteria, which had to reflect the diversity of the aquatic environments of the region - restricted for this study to the top of basins and ponds - and where the dynamics of the species was well known, but also characterized by availability of fish data or specific management issues for wildlife.

Table 1 – Sampling sites of otter spraints in Auvergne.

Department	Town	Site	Coordinates
Haute-Loire	Desges	Desges river	45.015382/3.454812
Haute-Loire	Esplantas-Vazeilles	Seuge river	44.923695/3.542023
Puy-de-Dôme	Pulvérières	Pulvérières pond	45.890727/2.912889
Puy-de-Dôme	Chapdes-Beaufort	Pommier marsh	45.876442/2.879492
Puy-de-Dôme	Pulvérières	A89 fauna crossing	45.887172/2.928167

Margeride (Haute-Loire) is one of the habitats where the otter has always remained, while the Combrailles (Puy-de-Dôme) were deserted by the species during the 1980's, following its hunt and its destruction, then was naturally recolonized during the 1995-2000 period, about twenty years after legal protection. Otter predation on prey can therefore be globally considered as a constant factor in Haute-Loire, and relatively new in Puy-de-Dôme. All sites benefit from fish, amphibians or crayfish population studies, habitat management and conservation operations. This leads to the availability of data about species diversity, abundance or local biomass, which can be compared to those measured in otter's diet.

Spraint sampling

Combrailles (Puy-de-Dôme) and Margeride (Haute-Loire) sampling sites were about 160 km far one to another. Each sampling site was constituted by about 500 m of river or pond banks, and all otter spraints discovered during the same sampling date were systematically gathered, constituting a spraint sample for a given station and a given date. Spraints were therefore new ones each sampling date. Spraint sampling time was close to 2 hours for each site. Within the different sampling sites, otter spraints (Fig. 2) were systematically collected twice a month, for a full year from autumn 2014 to autumn 2015, so as to locally integrate all the potential feeding behaviors of the European otter. All discovered spraints were systematically collected and stored in listed bottles, then stored in deep cold to avoid any degradation.

It should also be noted that the studied period was characterized by particular hydrological and weather conditions: the winter period was not characterized by major episodes of flooding or frost, spring and summer turned out to be hot and very dry, leading to an early, severe and lasting low water level in the rivers and study sites, with a return of significant rainfall during fall, however without flooding.

Considered as terms of food availability for a generalist predator like the otter, these characteristics of the year could explain part of the seasonal results observed.

Spraint analysis

Spraints were washed and filtered with clear water on a fine-mesh sieve. The bone fragments were then dried and sorted, then counted (total number and left and right numbers). The identification of the remains of undigested prey found in the spraints was then carried out. It has indeed been proven that almost the entire skeleton of the fish eaten by the otter is found as bone remains in spraints: the bones do not undergo any chemical attack during intestine transit (Erlinge 1968; Libois *et al.* 1991; Libois 1995). A standardized method for handling spraints was followed (Libois *et al.* 1987a). Teleosts, decapod crustaceans, ophidians and amphibians were determined by identifying characteristic bone pieces, based on reference collections and previous work: Doucet (1969); Hallet (1977); Libois *et al.* (1987a et b); Libois & Hallet-Libois (1988); Delooz (1990); Libois *et al.* (2015). The determination keys of Day (1966) and Debrot *et al.* (1982) have been used for the identification of birds and mammals.

For estimation of fish size and biomass, bone pieces were measured according to Wise (1980) for vertebrae, Hallet-Libois (1985), Libois *et al.* (1987b), Libois & Hallet-Libois (1988) and Hajkova *et al.* (2003) for head skeleton pieces. For certain species for which the direct correspondence between the size of the fragments and the biomass was more difficult, standardized values have been assigned: 25 g for crayfish, 5 to 20 g for amphibians according to size assessment, 20 g for small mammals, 50 g for birds (except additional data) and 100 g for reptiles.

Fish diversity and abundance in otter's diet were compared to fish population studies and management carried out by French biodiversity office (OFB), using electrofishing and fish population reinforcement along Haute-Loire and Puy-de-Dôme rivers and ponds concerned by study.

Results were expressed according to 3 ways: the *relative occurrence* corresponded to the frequency of the events of discovery of a taxon in the samples, and therefore leaded to assess the regularity of the capture of this taxon by the predator. The *relative abundance* let know the frequency of the abundance of a taxon in relation to the total number of prey identified, and therefore expressed the number of captured individuals. Finally, the *relative biomass* allowed to finely express the contribution of each taxon to the total quantity of food absorbed, based on the number of individuals captured and their calculated or estimated mass (Libois *et al.* 1987a, 1991; Libois & Rosoux 1989, 1991; Libois 1995, 1997).

Results were compared using *G* independence Test (Sokal & Rohlf 1981).

Table 2 – Identified taxa, relative occurrences, abundances and biomasses of otter prey in Desges river.

Taxa and species	Relative occurrences (%)	Relative abondances (%)	Relative biomasses (%)
Fish			
Brown trout (*Salmo trutta fario*)	31.5	64.1	85.8
Bullhead (*Cottus gobio*)	15.7	13.3	2.5
Common rudd (*Scardinius erythrophthalmus*)	1.1	0.4	0.4
Cyprinids (*Cyprinidae sp.*)	3.4	1.2	0.3
Crustaceans			
White-clawed crayfish (*Austropotamobius pallipes*)	6.7	2.3	1.05
Reptiles	7.9	2.7	4.9
Barred grass snake/Viperine snake (*Natrix helvetica/maura*)			
Amphibians	21.3	8.9	3.9
Toads (*Bufo sp.*)			
Frogs (*Rana sp.*)			
Mammals	2.3	0.8	0.4
Voles (*Microtus sp.*)			
Birds	2.2	0.8	0.7
Aves			
Insects	7.9	5.5	0.1

Spatial and temporal variations

Given the proximity between the three Combrailles (Puy-de-Dôme) sampling sites, which are also connected to each other by local rivers or wetlands and susceptible to belong to the same otter's territory, associated results were integrated into a single dataset and compared to Margeride (Haute-Loire) ones. For seasonal approach of prey relative abundances, winter data corresponded to December – February sampling period, spring by March – May sampling period, summer by June – August sampling period, and autumn by September – November sampling period.

Results and discussion

Sampling

Spraint collect allowed to obtain useful samples at almost each sampling date, both in time and in space.

All of the material collected was then analyzed. 120 spraint samples were constituted, gathering 307 spraints. Sampling allowed the identification of 1.100 prey belonging to 38 different taxa, including 23 species of fish.

Sites of Haute-Loire

Desges river

28 samples were collected on the Desges river during the studied period, representing a total of 76 spraints. All the taxa identified in the Desges river and their respective relative occurrences, abundances and biomasses were summarized in table 2 and figure 3 (biomasses only), with a view to appreciate the diet diversity.

The presence and numerous occurrences of brown trout and bullhead in the diet of the otter were quite logical, as both species are typical of the local aquatic habitat: their presence and their abundance have been underlined by recent inventories in Desges river (densities recorded as 2.550 brown trouts/ha and 374 bullheads/ha in July 2014, OFB *pers. comm.*). These two species thus constituted almost half (48%) of the total occurrences.

Occurrences of the white-clawed crayfish, of semi-aquatic or aquatic reptiles such as snakes of the genus *Natrix* (barred grass snake or viperine snake), or amphibians (toads and frogs, not determinable to the species) in the spraints reflected their relatively regular predation by otter, with an overall occurrence reaching more than a third (36%) of the total (Tab. 2).

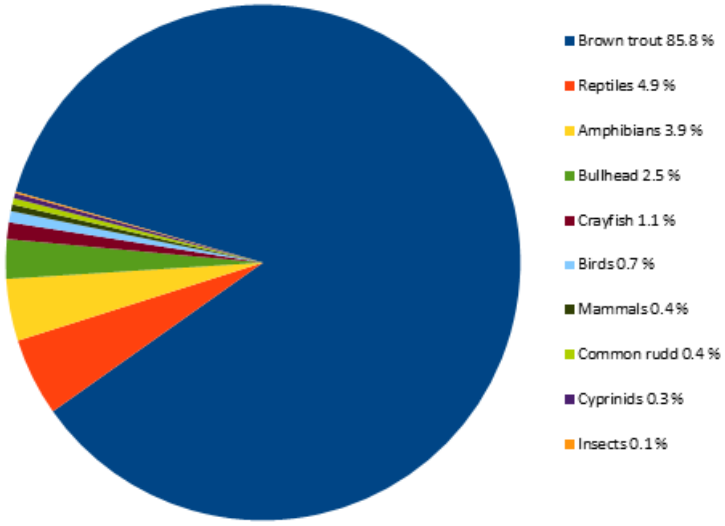

Figure 3 – Relative biomasses of otter prey in Desges river.

Birds, mammals and insects appeared with low occurrences. Birds could not be determined to genus or species, and the few mammals identified were "small" voles (Microtidae type *Microtus*, *e.g.* field vole *M. agrestis*). The occurrence of insects was relatively high, which may be related to deliberate consumption by the otter in its hunting activity (insects caught under stones in search of fish such as bullhead), or to the stomach contents of the fish caught. Three cyprinids, including a rudd, were also identified in the otter spraints on the Desges river. The finding of cyprinid species in the Desges river may appear surprising, insofar as the studied site of the river does not correspond to the habitat of many cyprinids, in particular the rudd. However, this fish could have been captured by an otter in its nearby hunting territory, in a pond or a local ornamental basin, a movement of the order of 5 km being possible between the place of capture and the place of emission of the corresponding spraint (Libois 1995).

The expression of the results using relative abundances, and especially relative biomasses allowed a better comprehension of the contribution of a given taxon in the diet (Tab. 2, Fig. 3). Thus, if fish constituted 52% of the occurrences identified in diet, they represented 78% of the abundance and 89% of the biomass of the prey captured by the otter within the study site.

Brown trout, the most abundant species in the river by number of individuals and biomass per hectare, was also the most abundant species in otter's diet, which clearly confirms the opportunism of the predator. The contribution of the bullhead, a species of small size and low mass quite often encountered in the river, was lower in the diet, that of the other fish species being negligible. The contribution of birds and insects to the diet were very low (Tab. 2, Fig. 3). The white-clawed crayfish represented only a very small part of the otter diet (1.05% of the captured biomass, Tab. 2) suggesting that predation was not an important factor in the local regression of this threatened crustacean. Reptiles and amphibians represented nearly 10% of the annual biomass captured by otters, which is comparable to available references (Clavero *et al.* 2003; Fig. 3) and therefore constituted resource inputs for the otter, significantly improving diet at certain times (see below).

Table 3 – Identified taxa, relative occurrences, abundances and biomasses of otter prey in Seuge river.

Taxa and species	Relative occurrences (%)	Relative abondances (%)	Relative biomasses (%)
Fish			
Brown trout (*Salmo trutta fario*)	22.2	40.6	77.9
Bullhead (*Cottus gobio*)	2.38	1.22	0.43
Stone loach (*Barbatula barbatula*)	4.76	2.87	0.16
European perch (*Perca fluviatilis*)	0.79	0.41	0.14
Sunbleak (*Leucaspius delineatus*)	0.79	0.41	0.01
Chub (*Squalius cephalus*)	0,79	0,82	0,31
Roach (*Rutilus rutilus*)	2.38	1.23	0.53
Gudgeon (*Gobio gobio*)	0.79	0.4	0.04
Minnow (*Phoxinus phoxinus*)	1.58	2.05	0.13
Cyprinids (Cyprinidae sp.)	0.79	0.41	0.73
Crustaceans	22.2	26.6	12.14
White-clawed crayfish (*Austropotamobius pallipes*)			
Crayfish sp.			
Reptiles	0.79	0.41	0.19
Barred grass snake/Viperine snake (*Natrix helvetica/maura*)			
Amphibians	23.8	12.3	3.1
Toads (*Bufo sp.*)			
Frogs (*Rana sp.*)			
Mammals	7.14	3.7	3.3
Voles (*Microtus sp.*)			
Southwestern water vole (*Arvicola sapidus*)			
Garden dormouse (*Eliomys quercinus*)			
Edible dormouse (*Glis glis*)			
Water shrew (*Neomys sp.*)			
Birds	1.59	0.82	0.75
Aves			
Insects	7.14	5.7	0.1

Seuge river

31 samples were collected on the Seuge river during the studied period, representing a total of 108 spraints. All the taxa identified in the Seuge river and their respective relative occurrences, abundances and biomasses were summarized in table 3 and figure 4 (biomasses only), with a view to appreciate the diet diversity.

Significant differences compared to those observed for the Desges river were noted. The number of taxa identified in otter's diet was twice as high in the Seuge river (22 *vs.* 11 for the Desges river, Tab. 3). The occurrences were also different between the two rivers, with comparable proportions in Seuge river for brown trout, crayfish and amphibians (between 22 and 24%, see Tab. 3), the latter representing the majority of occurrences. Bullhead and reptiles were much less represented in the occurrences observed on the Seuge river (2 and 1% respectively) than in those of the Desges river (16 and 8% respectively), while crayfish were more so (22% for the Seuge river and 7% for the Desges river), all these differences were significant between the two rivers ($p<0.05$).

Concerning crayfish, if the white-clawed crayfish was identified in the spraints, other remains were also observed, not showing the characteristics of the autochthonous species. The presence of the spiny-cheek crayfish (*Orconectes limosus*) having been reported in the Saugues lake and on the Seuge river situated downstream (Duperray 2010), located at short distance from the study site, it is likely that the otter indifferently captures the two species of crustaceans in all of these aquatic environments. Given the local ecological continuity, it is also to be feared an expansion of the exotic species upstream of the Seuge river basin, which constitutes a risk of rapid disappearance of the white-clawed crayfish through ecological competition and pathology transmission.

The captured birds could not be identified to genus or species. The two species of aquatic snakes were observed in the area during our surveys (a viperine snake in the Seuge river near Esplantas, and a barred grass snake in the Saugues lake), and both are probably part of the otter's local diet.

The presence and proximity of the Saugues lake, as well as those of nearby ponds, can probably explain, on the one hand, the presence in the diet of fish species not recorded during electrofishing carried out on the Seuge river, and on the other hand the fairly high representation of amphibians, some species of which being well adapted to ponds (Tab. 3). Thus, perch, roach, sunbleak and chub may have been captured by the otter in these ponds, while brown trout, bullhead, loach, minnow or gudgeon have been inventoried by electrofishing in the stream near the study site; the trout seemed to display a high density there (8.405 ind./ha, 2015 data, FDAAPPMA 43, *pers. comm.*) and fairly active reproduction.

Finally, it should be noted that there was a fairly strong representation of mammals in the local diet of the predator (Tab. 3): 5 species were identified, this figure constituting a minimum given the uncertainty of the determination of Microtidae (small voles). For the other identified mammals, the presence of the southwestern water vole (observed *in situ* during our surveys), at least one species of aquatic shrew (*Neomys sp.*), and two species of the family of Gliridae (garden dormouse and edible dormouse) should be underlined. If these last two species are only exceptionally identified in the diet of the otter (Kruuk 2006; Rosoux & Lemarchand 2019), on the other hand the presence of semi-aquatic mammals such as the water vole or aquatic shrew was more logical and underlined here again the opportunistic character of the animal.

As observed for the Desges river, the expression of the results according to relative abundances and especially relative biomasses provided additional results (Tab. 3, Fig. 4). Thus, the proportion of fish, which represented only 22% of the relative occurrences (Tab. 3), reached 49% of the relative abundance and 80% of the relative biomass captured by the otter, the brown trout being once again by far the most abundant species in the predator's diet, as it is in the study site. The contribution of other fish (such as bullhead or loach, the latter being only rarely noted in the diet) to the total biomass captured by otter was very low, but these species can still constitute prey of interest for the predator, under certain conditions like a major flood or a period of intense freezing of the river. Given these diet study results, and according to the data from electrofishing, the otter predation on the diversity and abundance of fish caught seemed weak.

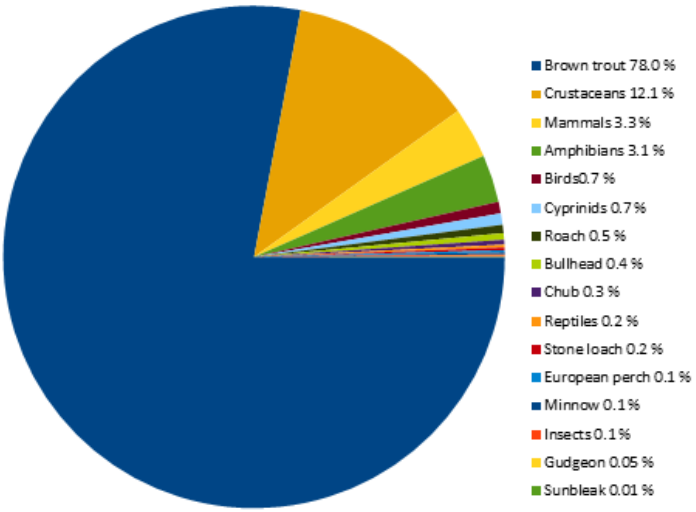

Figure 4 – Relative biomasses of otter prey in Seuge river.

Since the local otter populations have been stable and homogeneous for several years (Lemarchand & Bouchardy 2010, 2011; Rosoux & Lemarchand 2019), with a typical population dynamic (large individual home ranges and low densities), this predation parameter is not expected to change significantly in the future.

The representation of the other identified taxa also differed from the results concerning Desges river. The respective proportions of amphibians (3% of the biomass captured in the Seuge river, Tab. 3, Fig. 4), and above all of reptiles (close to 0% in biomass), were clearly lower, while those of mammals and crayfish (respectively 3% and 12% of the biomass captured in the Seuge river) were clearly higher than those observed in the Desges river (respectively 0% and 1% in biomass), all these differences being significant ($p<0,05$).

Crayfish thus constituted a relatively important element of the diet of otters on the Seuge river. However, the impact of predation on the native species (white-clawed crayfish) is difficult to quantify, particularly insofar as this predation (here expressed globally for the "crustacean" taxon) was also exerted on the invasive spiny-cheek crayfish noted downstream of the study station (Duperray 2010). Moreover, the presence of homogeneous and reproductive populations of otters and crayfish for many decades along this river, despite past otter destruction campaigns and very active crayfish fishing activity, seems rather to indicate henceforth the existence of a certain balance between the predator and one of its complementary prey. The possible expansion of invasive crayfish is probably a greater and more immediate threat to the conservation of the native crustacean than the evolution of otter predation.

Finally, and as in the case of Desges river, the contribution of birds and insects to the total biomass captured by the otter was very low (Fig. 4).

Size of consumed fish

The preservation of the fish remains in the spraints allowed to accurately estimate the size of the latter, and therefore their mass, *i.e.* the biomass consumed by the otter. The size distribution of fish eaten by otters along Desges river and Seuge river is shown on figure 5.

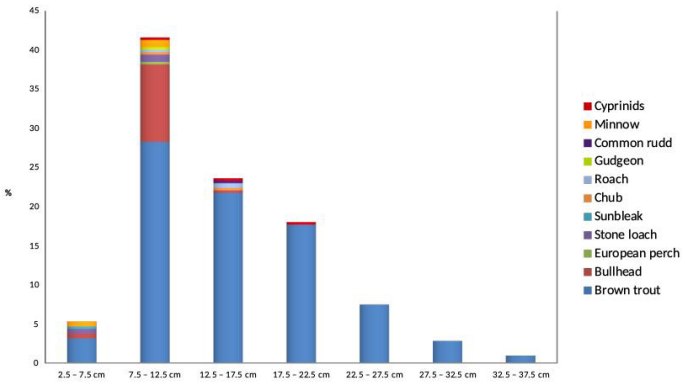

Figure 5 – Size (cm) of fish consumed by otters along Haute-Loire sites.

As shown, most (70.8%) of the fish caught by the otter were less than 17.5 cm in size, this spectrum corresponding to the highest densities of fish (particularly concerning brown trout) in the Seuge river, for which we have local electrofishing data (2015, FDAAPPMA 43, *pers. comm.*, Fig. 5).

Very small fish (less than 7.5 cm) were little consumed (5.3% of catches), due to the low amount of energy provided by their consumption compared to that needed to catch them. On the same principle, large brown trout (greater than 27 cm) were poorly represented (3.7% of catches), due to their rarity and catching difficulty, which are not very energy-efficient.

These results illustrated the opportunistic behavior of the otter, focusing not on the largest fish, but the most numerous, having the greatest probability of capture.

Spatial and temporal variations

The availability of homogeneous data, collected at regular and comparable time intervals for both rivers, allowed their statistical comparison. Thus, significant differences in the diversity of otter's diet between the Desges river and Seuge river were observed (see above), especially for abundance data and therefore biomass (Tab. 2 & 3). Trout, bullhead and reptiles were more represented in the diet on the Desges river than on the Seuge river, while crayfish were much more abundant in the diet on the Seuge river (Gtest=125.1, p<0.001). No statistical differences were observed between the two rivers regarding amphibians. As significant differences can be observed between two close study sites, the study of the diet must therefore remain localized to be really precise (Clavero *et al.* 2003; Rosoux & Lemarchand 2019).

Seasonal variations in prey relative abundance in Margeride (Haute-Loire) were represented in table 4. Significant variations of prey relative abundances (and therefore biomass) were observed, depending on the season (Tab. 4). Brown trout was thus less represented during summer and spring compared to autumn and winter, bullhead were more caught during spring, and crayfish were mainly caught in summer (Tab. 4). These observations are consistent with the phenology of these species, depending on the water temperature or breeding periods.

However, it is more surprising that no significant seasonal variations were observed in the abundance of reptiles or anuran amphibians in the otter diet during the study.

Concerning reptiles, these results can be weighted by a low number of captures (8 individuals for both rivers during the study), and therefore a lack of statistical robustness, but it is not the same for anurans. Catches were indeed recorded all year round, including in winter, where they were however rarer. If the

Table 4 – Seasonal variations in prey relative abundance in Margeride (Haute-Loire). *Marks show significant differences (Gtest=69.5, p<0.001).

Taxa and species	Spring (%)	Summer (%)	Autumn (%)	Winter (%)
Brown trout (*Salmo trutta fario*)	53	38*	62**	65**
Bullhead (*Cottus gobio*)	13	3*	4*	1
Anurans	10	13	6	14
Reptiles	2	3	–	1
Crustaceans	9	27**	11	4*
Insects	6	9	4	1
Other prey	7	7	13	5

altitude of the sites is moderate (about 670 m for both sites), the winters are often cold and snowy, greatly slowing down the activity of ectotherms. The otter is certainly able to find prey buried in sand or sediment during winter (Clavero *et al.* 2003; Kruuk 2006; Rosoux & Lemarchand 2019), but it can also be assumed that the mild winter during study allowed the predator to access amphibians without seasonal discontinuity.

Sites of Puy-de-Dôme

61 samples were collected from all sites (Pulvérières, Pommier and Ambène, see Tab. 1) during the period of study, representing a total of 123 otter spraints.

All taxa identified on Puy-de-Dôme site and their respective relative occurrences, abundances and biomasses were

Table 5 – Identified taxa, relative occurrences, abundances and biomasses of otter prey in Puy-de-Dôme..

Taxa and species	Relative occurrences (%)	Relative abondances (%)	Relative biomasses (%)
Fish			
Brown trout (*Salmo trutta fario*)	6.2	3.7	20.6
European eel (*Anguilla anguilla*)	0.4	0.1	0.29
Pike (*Esox Lucius*)	1.2	0.7	6.2
Bullhead (*Cottus gobio*)	1.2	1	0.4
European perch (*Perca fluviatilis*)	9.9	11.5	12.8
Pikeperch (*Sander lucioperca*)	0.4	0.2	0.01
Largemouth bass (*Micropterus salmoides*)	0.4	0.2	0.1
Sunbleak (*Leucaspius delineatus*)	0.4	0.2	0.01
Bleak (*Alburnus alburnus*)	0.8	0.5	0.06
Common barbel (*Barbus fluviatilis*)	0.4	0.2	0.02
Common bream (*Abramis brama*)	3.7	6.8	1.05
Crucian carp (*Carassius sp.*)	0.4	0.2	0.1
Common carp (*Cyprinus capio*)	0.4	0.2	0.2
Chub (*Squalius cephalus*)	0.8	0.3	0.8
Roach (*Rutilus rutilus*)	9.5	27.8	7.7
Gudgeon (*Gobio gobio*)	4.9	4.3	2.1
Common naze (*Chondrostoma nasus*)	0.4	0.2	0.2
Rudd (*Scardinius erythrophthalmus*)	5.8	4.2	2.8
Tench (*Tinca tinca*)	3.7	2.8	7.3
Minnow (*Phoxinus phoxinus*)	1.2	0.8	0.1
Common dace (*Leuciscus leuciscus*)	0.8	1	0.3
Cyprinids (*Cyprinidae sp.*)	9.1	7.3	11.7
Crustaceans	9.9	10.2	10.6
Spiny-cheek crayfish (*Orconectes limosus*)			
Signal crayfish (*Pacifastacus leniusculus*)			
Reptiles	0.4	0.2	0.7
Barred grass snake/Viperine snake (*Natrix helvetica/N. maura*)			
Amphibians	19.8	11.8	9.6
Toads (*Bufo sp.*)			
Frogs (*Rana sp.*)			
Mammals	2.5	1	2.9
Voles (*Microtus sp.*)			
Southwestern water vole (*Arvicola sapidus*)			
Montane water vole (*Arvicola scherman*)			
Birds	1.2	0.5	1.03
Aves			
Insects	3.7	2.2	0.9

summarized in table 5 and figure 5 (biomasses only), with a view to appreciate the diet diversity.

A large diversity of prey species in otter's diet was underlined: a minimum of 32 taxa was thus observed, including both river and wetlands or ponds species (Tab. 5). Calculated according to the list of identified taxa, the Shannon diversity index was high (H'=3.91).

Relative occurrences were dominated by cyprinids (over 42%, Tab. 5), with a minimum of 14 cyprinids species appearing in the diet; roach was the most frequent species among fish (10% of occurrences).

Predatory fish (perch, pike, pikeperch and black-bass, the occurrences of the last three being very low) were noted, as well as species constituting their prey (roach, rudd, bleak and other small cyprinids), these latter appearing in much higher proportions. Trout and bullhead (respectively 6% and 1% of occurrences, Tab. 5) were fairly poorly represented in the diet of otters in this complex of habitats mainly composed of ponds and wetlands.

Amphibians (toads and frogs) were the most occurred taxa for this sites (Tab. 5). According to inventories carried out by local naturalists as part of monitoring operations, several species were know to be abundant in the study area. This diversity of species with variable seasonal behavior can thus constitute an important resource for a predator like the otter.

The remains of crustaceans found in the spraints, compared with data on the presence of the various known species in the area, made possible to identify spiny-cheek crayfish and signal crayfish, their relative occurrences being relatively high (Tab. 5).

No data about presence of the white-clawed crayfish were reported for theses sites, in the diet of the otter or during additional inventory surveys. These results suggested an immediate integration of invasive alien species to otter's diet, and therefore opportunistic hunting behavior during an active population dynamic (Rosoux & Lemarchand 2019).

Reptiles, mammals, birds and insects only appeared with low occurrences. Identified reptiles were, as observed for Haute-Loire sites, aquatic snakes of the genus *Natrix*, but their occurrences in the local diet of the otter were lower here than on the Desges river or the Seuge river (see Tab. 2 & 3).

Identified mammals were voles, with occurrences of small voles of the genus *Microtus* and of southwestern water vole and montane water vole (Tab. 5). This latter species, which is infrequent in the diet of the otter (Kruuk 2006; Rosoux & Lemarchand 2019), was however abundant (proliferation zone) in the fields bordering the linear areas of the study sites and the tributaries of the Pulvérières pond, where it may have been captured. Furthermore, the absence of the identification of muskrats (*Ondatra zibethicus*) or coypu (*Myocastor coypus*) remains on this site of Puy-de-Dôme (as moreover on the sites of Haute-Loire) can be underlined, whereas these two invasive rodents are present on the site and may occasionally appear on the otter's diet, especially during harsh winters, when the ice disrupts fishing activity (Bouchardy 1986). Birds and insects could not be identified to species (Tab. 5).

Fish remained the dominant taxa in the diet, both in relative abundance and in relative biomass (74%, Fig. 6). Among the fish, if the roach was by far the most abundant species caught by otters (28% of the relative abundance), it represented only 8% of the total ingested biomass.

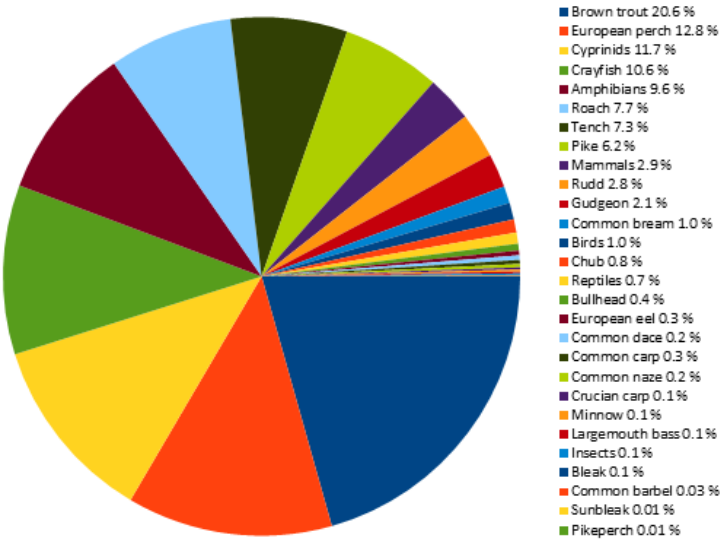

Figure 6 – Relative biomasses of otter prey in Puy-de-Dôme sites.

More generally, cyprinids were the major prey in terms of occurrences, abundance (56%) and relative biomass (35%). On the other hand, brown trout, which represented only 4% of the abundance of fish caught, constituted 21% of the total ingested biomass. The other predatory fish, and in particular perch and pike, represented almost 20% of the total ingested biomass (Fig. 6).

The diversity noted in the occurrences was also found in the relative biomasses, where no fish species clearly dominated the diet. Shannon's diversity index, applied to biomass data, reached H'=3.52, which also confirmed this broad food spectrum of the otter on theses sites. These results confirm the overall diversity and richness of this study site, also frequented by other fish-eating species (grey heron *Ardea cinerea*, great cormorant *Phalacrocorax carbo*, osprey *Pandion haliaetus* for example).

Anurans and crustaceans (crayfish), which constituted a very important part of the occurrences, also ensured remarkable abundances and relative biomasses (10% and 11% respectively, Fig. 6) in the diet of the otter, especially during spring concerning anurans, summer and autumn concerning crustaceans.

The opportunistic nature of the predator, which has significantly integrated the invasive alien crayfish species into its diet as its own natural recolonization was going on was well illustrated. The proportion ensured by amphibians was by far the highest in this study, which highlighted the importance of this taxon, and therefore its conservation (and that of its habitats) in maintaining of the natural prey-predator balance.

Size of consumed fish

The size distribution of fish eaten by otters along Puy-de-

Dôme sites is shown on figure 7. As noted for the Haute-Loire sites, most of the consumed fish were small. Indeed, 84% of them measured less than 12.5 cm, and almost 92% less than 17.5 cm. The large number of roaches consumed in this size spectrum largely explained this result, but it can also be noted that a large proportion of bream and percomorph fish (European perch and pikeperch) were also small in size.

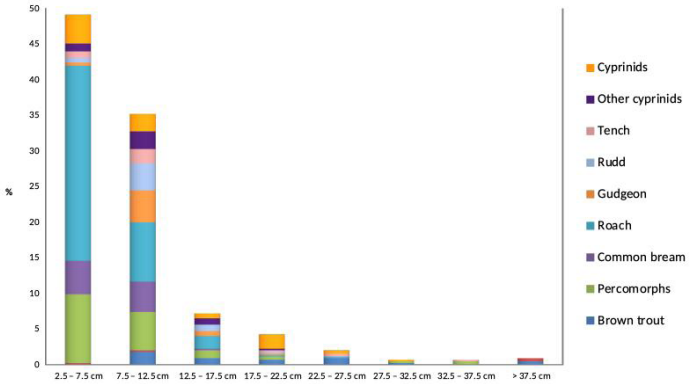

Figure 7 – Size (cm) of fish caught by otter in the Puy-de-Dôme sites.

The few larger fish consumed turned out to be brown trout (7 individuals over 22.5 cm), percomorphs (pikeperch and European perch: 3 individuals between 27.5 and 37.5 cm), pike (2 individuals more than 37.5 cm) and a tench (between 32.5 and 37.5 cm).

The total annual proportion of these "large" species (all species over 22.5 cm) reached 4.3% of the ingested biomass (Fig. 7). Here again, the opportunistic nature of otter predation, directed towards the most numerous species and individuals and therefore the easiest to capture for better energy efficiency, was confirmed.

Spatial and temporal variations

As the diet data from Puy-de-Dôme sites were merged, spatial variations were studied by comparison with Haute-Loire sites. Prey diversity was higher in Puy-de-Dôme rather than in Haute-Loire (Tab. 5, 2 and 3, respectively), as underlined by the observed Shannon's diversity indexes (H'=3.91 and H'=3.11 for occurrences, respectively). This could be related to habitats and species diversity, higher in Puy-de-Dôme sites. Respective proportions of prey biomasses underlined a generalist diet in Puy-de-Dôme, much more dominated by brown trout in Haute-Loire (Shannon's diversity indexes reached H'=3.52 and H'=1.17 for biomasses, respectively). Comparison between sites underlined the opportunistic predation behavior of the otter, even in a recolonization and low population density context, as noted elsewhere in France or in Europe (Kruuk 2006; Rosoux & Lemarchand 2019).

Seasonal variations in prey relative abundance in Combrailles (Puy-de-Dôme) were represented in table 6. Significant variations of prey relative abundances (and therefore biomass) in the diet of otters were observed, depending on the season (Tab. 6). These variations turned out to be quite low with regard to the relative occurrences of prey (Gtest=42.2, p<0.005, data not shown), for which only crayfish and certain cyprinids (*e.g.* bleak, bream, crucian carp, carp, tench) were characterized by significant seasonal variations.

Crayfish were caught more regularly in summer and autumn than in spring and winter (Tab. 6), which corresponded well to the overall activity of crustaceans. The contribution of crayfish (particularly numerous near Pulvérières or Ambène for example) to the total ingested biomass was thus much greater in summer (during which they represent the bulk of the otter's diet) and in autumn compared to winter and spring. Some cyprinids (roach, rudd, Tab. 6) were much less frequently found in summer in the spraints and thus represented only a small part of the biomass consumed in summer. Since these species may tend to stay at greater depths in summer, the otter probably captures them in smaller quantities, as its fishing activity is mainly carried out in shallow areas. On the other hand, pond cyprinids were much more consumed during winter (Tab. 6).

Regarding river fish (brown trout, bullhead, some cyprinids) and predatory fish in relatively calm waters (perch, pike, black bass or pikeperch), seasonal variations were small and insignificant, which can be also linked to the behavior of fish in these different environments and the type of fishing activity of the otter.

Finally, and as we observed in Haute-Loire (see above), amphibians were captured all year round, including winter, without significant seasonal variations. The winter of the study period having been generally mild without long cold periods, the otter was probably able to access this resource throughout the year.

Although these observations have already been made in areas with an oceanic or Mediterranean climate (Clavero *et al.* 2003; Kruuk 2006), these results are not very common for more continental areas and differ from comparable studies conducted several decades ago (Bouchardy 1986).

As mild winters, associated with potentially hotter and drier summers, are expected to increase in probability and severity due to climate change, it is likely that the relative proportions of certain taxa consumed by otters, and more generally by predators, evolve in the future, depending on their availability, but also on their own reaction to these habitat changes.

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