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Seasonal use of ponds as foraging habitat by Eurasian otter with description of an alternative handling technique for common toad predation

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Abstract. Research in freshwater ecology has traditionally focused on water courses or large still waters. However, ponds support proportionately high levels of biodiversity relative to other inland waters in Europe, and foraging by Eurasian otter *Lutra lutra* (L., 1758) could have considerable impacts on species composition in these small water bodies. The aim of the present study was to analyse otter spraints around ponds during two contrasting seasons (winter and spring) in north Norfolk (eastern England), where both otter and ponds are of particular conservation concern. Spraint density, prey diversity and the consumption of river-associated species were higher in spring than winter. In both seasons, birds were the most important prey category as ingested biomass. European eel *Anguilla anguilla* (L., 1758) and amphibians, specifically common frog *Rana temporaria* L., 1758 and common toad *Bufo bufo* (L., 1758), were more consumed in spring, whereas northern pike *Esox lucius* L., 1758 and tench *Tinca tinca* (L., 1758) were taken in winter. Non-native common carp *Cyprinus carpio* L., 1758 was important in both seasons, whereas threatened native crucian carp *Carassius carassius* (L., 1758) was a minor prey item. Massive kills of common toad, which involved a new handling technique for predation on this species, were observed mainly in spring. The study demonstrated otters to display great plasticity in foraging behaviour and contributes to the understanding of otter predatory pressure on pond biodiversity, with implications for landscape management.

Key words: amphibians, *Bufo bufo*, feeding behaviour, pond biodiversity, spraint analysis

Introduction

Diet is an essential element for understanding how Eurasian otter *Lutra lutra* (L., 1758) is re-colonising its former range (Roche et al. 1995, Romanowski 2006) following the population declines observed during the 1950s-1970s in Europe (e.g. Mason & Macdonald 1993). An apex predator in aquatic environments, the otter is essentially an opportunistic forager based on fish (e.g. Roche 2001, Copp & Roche 2003) and its diet normally reflects the most abundant prey items available in its foraging area (e.g. Kruuk et al. 1993, Copp & Roche 2003). This makes the otter a useful surrogate for assessing changes in the abundance or availability of prey species (Almeida et al. 2012a), which may come as a result of phenology, ecosystem succession or alteration. However, otters may feed preferentially on secondary prey (e.g. amphibians) at sites where fish densities are low (Remonti et al. 2009). Thus, otters have morphological and physiological adaptations that favour predation on fishes, their preferred prey type. When fish availability decreases, otters can opportunistically switch to alternative aquatic or terrestrial prey, and this can include massive kills of amphibians (e.g. Weber 1990, Sidorovich & Pikulik 1997, Slater 2002, Ayres & García 2009, Cogalniceanu et al. 2010, Ayres & García 2011). In the case of common

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toad *Bufo bufo* (L., 1758), otters have been found to employ a particular feeding behaviour to avoid the toad's poisonous skin, especially the paratoid glands. Using the so-called "progressive skinning" technique (Slater 2002), otters skin and then eat the hind legs of toads, with the front half of the toad discarded. At one toad breeding site, Slater (2002) also reported otters to have eaten the entire toad body by making a vertical incision to remove the whole skin in one piece. For toads, there is no known published description of an alternative handling technique to this "progressive skinning" behaviour.

Research in freshwater ecology has traditionally focused on water courses or large still waters, but interest in smaller water bodies (i.e. ponds) is increasing (Williams et al. 2003, Copp et al. 2008, 2010). Effectively small "islands" of biodiversity, ponds are known to sustain a disproportionately high number of different aquatic taxonomic groups (e.g. Oertli et al. 2002, Williams et al. 2003), and they are the subject of investigations by members of the European Pond Conservation Network (www.europeanponds.org) and related initiatives such as the UK "Million Ponds Project" (www.pondconservation.org.uk). Regarding otter diet, much research has focused on water courses, but interest in ponds is increasing due to the potential effect of otter predation on the commercial and endangered pond fishes (e.g. Kortan et al. 2007, Poledník et al. 2007, Almeida et al. 2012a). Moreover, information on the seasonal role of ponds in otter foraging is essential for the comprehensive conservation management of this carnivore, such as has been demonstrated for otters during the characteristic summer droughts of Mediterranean Europe (Ruiz-Olmo et al. 2007). In England, the otter is a Biodiversity Action Priority (BAP) species (Biodiversity Action Reporting System, accessed February 2013), and in the county of Norfolk, ponds are of particular concern, as they are important for ecosystem function at the landscape scale and provide several endangered aquatic species with suitable habitat and food resources (e.g. Sayer et al. 2011, 2012, Almeida et al. 2012a). Thus, otters may exert a considerable impact on species composition in the small water bodies of Norfolk.

The aim of the present study was to assess temporal differences in marking intensity and feeding habits of the otter in ponds from north Norfolk during winter and spring. Specifically, spraint density, diet composition and prey diversity were compared between these two contrasting seasons, as well as common toad kills. Furthermore, a particular handling technique associated with predation on common toads is described for the first time. The hypotheses of the present study were that otters mark and forage, in terms of ingested biomass, around ponds more intensely in winter because these environments may provide a more reliable food supply during cold seasons (Kortan et al. 2007, Poledník et al. 2007). Whereas otters consume a higher amount of species from flowing waters in spring, where and when they can find more active prey. Consequently, the marking activity will be lower at ponds during spring, although the overall diet will be more diverse, i.e. including prey from both ponds and rivers (Almeida et al. 2012a).

Material and Methods

Spraint surveys were carried out in February (i.e. winter) and May (i.e. spring) 2011 at 59 small, shallow (< 0.1 ha surface; < 2 m deep) and isolated ponds located to the northern county of Norfolk (eastern England). This region is characterized by arable and pasture lands, meadow and woodland settings, with small patches of mixed deciduous and coniferous woodland associated with fluvio-glacial sand and gravel deposits. There are a few small water courses (< 18 km length, < 50 m a.s.l.) in this area, in particular Kelling Stream, Spring Beck and the rivers Glaven and Stiffkey. The vicinity around each pond was carefully searched, with particular attention paid to well known types of marking locations and with descriptions of common toad kills annotated. Camera trapping is an appropriate method to record direct evidence and thus to consider the otter as the responsible predator for the massive toad kills. However, this technique was not used in the present study because of the lack of funds and landowner permission (most of the ponds were private). Nevertheless, the kills were attributed to otters because: 1) a high number of dead toads (601 individuals) were found at the margins of the ponds (Cogalniceanu et al. 2010), mostly accumulated in piles, with only a few toads observed out of the water and widely spread; 2) the toad remains were fresh, which indicates that the predator was most likely aquatic (i.e. no kites *Milvus* sp., no buzzards *Buteo* sp., no corvids *Corvus* sp.), and some toad remains were demonstrative of "progressive skinning", a handling technique previously described for otters (Slater 2002); 3) fresh otter spraints were observed next to the toad kills, as well as solitary individuals of otters at dusk or dawn (see Cogalniceanu et al. 2010 for another example); and 4) although other predators (grey heron *Ardea cinerea* L., 1758; European polecat

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Mustela putorius L., 1758; American mink *Neovison vison* (Schreber, 1777); European badger *Meles meles* (L., 1758)) are able to catch and manipulate toads – badgers, specifically, have been reported to prey on great quantities of amphibians (Balestrieri et al. 2009, Roper 2010) –, "progressive skinning" has not been described in these predatory species. The fresh otter spraints were stored in individual plastic bags, labelled with the date and pond location. In the laboratory, the spraints (n = 133) were soaked in soapy water for 24 hours and dried in the oven at 60 °C for 1 h. Food items were identified to the lowest possible taxonomic level using a dedicated reference collection of fishes and other vertebrates as well as published literature (Conroy et al. 1993, Miranda & Escala 2007, Masson et al. 2011). Food items were also counted (minimum number for each food category per spraint). Diagnostic structures of fish (vertebrae, pharyngeal arches, etc.) and crayfish (exopodites, telson) were measured with a digital calliper to the nearest 0.01 mm.

Regression equations between the size of hard structures (fish bones and crayfish appendages) and the wet weights were used to estimate the ingested biomass of consumed fish and crayfish (e.g. Conroy et al. 1993, Copp & Kováč 2003, Masson et al. 2011). Ingested biomasses for other categories were estimated using their mean weights in the environment or the mean weights of specimens from collections. Three dietary indices were calculated and expressed as a percentage for each prey category: frequencies of occurrence (*Fq*, number of spraints containing a particular prey category relative to the total number of spraints), number (*n*, number of individuals of a particular prey category relative to the total number of individuals) and weight (*Wt*, mass of a particular prey category relative to the total ingested mass). Prey diversity was measured using the Shannon index (*H'*). To estimate spraint density as a measure of otter activity (Guter et al. 2008), the number of spraints per 100 m of bank was calculated (Prenda & Granado-Lorencio 1996).

For statistical analyses, pond site was the elementary unit to avoid pseudo-replication (i.e. the average of data from spraint at each pond). Students' *t*-tests were



Fig. 1. Photograph of four predated common toads (*Bufo bufo*) found at the margins of a pond. The dorsal and lateral incisions from where otters feed on internal organs are shown. The coin is one British pound. © C.D. Sayer.

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Table 1. Diet composition of the Eurasian otter *Lutra lutra* in north Norfolk, England (*n* = 53 spraints in winter and *n* = 80 in spring). Frequencies of occurrence (*Fq*), number (*n*) and weight (*Wt*) for each prey category are indicated in every season. Significant higher ingested biomasses between seasons for the main prey (> 10 % of *Wt*) are in bold, after Mann-Whitney *U*-tests with Bonferroni corrections.

Season	Winter			Spring		
Prey category	*Fq* (%)	*n* (%)	*Wt* (%)	*Fq* (%)	*n* (%)	*Wt* (%)
terrestrial invertebrates	7.55	4.39	0.36	12.50	6.55	0.98
aquatic invertebrates	11.32	6.14	0.20	27.50	10.48	0.63
roach *Rutilus rutilus* (L., 1758)	18.87	9.65	2.16	10.00	3.93	1.81
rudd *Scardinius erythrophthalmus* (L., 1758)	9.43	5.26	1.33	8.75	3.49	1.51
[a] water vole *Arvicola amphibius* (L., 1758)	5.66	2.63	4.30	2.50	0.87	2.61
[a] white-clawed crayfish *Austropotamobius pallipes* (Lereboullet, 1858)	-	-	-	7.50	2.62	2.97
[a] European eel *Anguilla anguilla* (L., 1758)	3.77	1.75	2.92	15.00	5.68	**19.35**
[a] brown trout *Salmo trutta* L., 1758	3.77	1.75	1.05	6.25	2.62	2.65
[a] gudgeon *Gobio gobio* (L., 1758)	-	-	-	11.25	5.24	0.93
[a] stone loach *Barbatula barbatula* (L., 1758)	-	-	-	3.75	1.31	0.32
[a] European bullhead *Cottus gobio* L., 1758	-	-	-	23.75	11.36	1.34
[b] northern pike *Esox lucius* L., 1758	5.66	2.63	**11.68**	-	-	-
[b] tench *Tinca tinca* (L., 1758)	9.43	4.39	**10.06**	1.25	0.44	2.00
[b] crucian carp *Carassius carassius* (L., 1758)	7.55	3.51	4.67	3.75	1.31	2.90
[b] common carp *Cyprinus carpio* L., 1758	16.98	7.89	12.26	13.75	4.80	9.97
[b] threespine stickleback *Gasterosteus aculeatus* L., 1758	16.98	11.41	0.51	22.50	8.73	0.83
[b] Eurasian perch *Perca fluviatilis* L., 1758	5.66	3.51	7.26	2.50	0.87	3.54
[b] Birds	45.28	21.93	35.86	30.00	10.49	31.30
[b] Amphibia	22.64	13.16	5.38	41.25	19.21	**14.36**

[a] River-associated species, [b] Pond-associated species.

performed to reveal seasonal differences in spraint density (paired-sample comparison) and prey diversity (only for ponds with presence of spraints, i.e. $n = 33$ ponds in winter and $n = 42$ ponds in spring). Mann-Whitney *U*-tests were used to compare the ingested biomass for prey categories between seasons. Prey categories < 10 % of ingested biomass were not tested because they cannot be considered as key resources for otters (Barrientos & Virgos 2006, Almeida et al. 2012b). To assess the seasonal use of ponds as foraging habitat, prey were designated as river- or pond-associated species according to the distribution and abundances from previous surveys in the study area (Zambrano et al. 2006, Sayer et al. 2011, Almeida et al. 2012a), either by direct observation (amphibians and birds) or by electrofishing and netting (fish and crayfish). Only species that could be clearly classified into a group, either river- or pond-associated, were used for the comparison between seasons (see Table 1). Thus, a species was allocated to a habitat type when its frequency of survey occurrence was higher than 90 % in that particular habitat. Chi-square (χ^2) tests with Yates' corrections were used to compare the proportions of toad kills. Data on spraint density were transformed by using ln (x + 1). Assumptions of normality of distributions and homogeneity of variance were verified using Shapiro-Wilk and Levene tests, respectively. All statistical analyses were performed with SPSS v17 (SYSTAT Software Inc., Chicago, USA). The significance level was set at $\alpha = 0.05$. Sequential Bonferroni corrections were performed for every set of multiple tests.

Results

Spraint density was significantly lower in winter (mean = 0.90 spraints 100^{-1} m, SE = 0.16) than it was in spring (mean = 1.36 spraints 100^{-1} m, SE = 0.20) ($t = 3.56$, $P < 0.001$). Terrestrial invertebrates found in the spraints consisted of snails (Gastropoda Helicidae), beetles (Coleoptera Geotrupidae and Tenebrionidae) and wolf spiders (Licosidae). Aquatic invertebrates included dragonfly nymphs (Odonata Anisoptera), adults of water skaters (Heteroptera Gerridae), adults of water boatmen (Heteroptera Notonectidae) and adults of diving beetles (Coleoptera Dytiscidae). Both categories of invertebrates were relatively frequent in the diet, but not important in terms of biomass (Table 1). European eel *Anguilla anguilla* (L., 1758) was consumed significantly more in spring than in winter ($z = 3.04$, $P = 0.002$) and the opposite was observed for northern pike *Esox lucius* L., 1758 ($z = 3.36$, $P < 0.001$) and tench *Tinca tinca* (L., 1758) ($z = 2.54$, $P = 0.008$). Non-native common carp *Cyprinus carpio* L., 1758 was similarly consumed in both seasons ($z = 0.43$, $P = 0.669$). Remains of amphibians found in the spraints consisted mainly of common frog *Rana*

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temporaria L., 1758 (i.e. > 90 % of frequency) and also common toads. Amphibians were consumed more in spring than in winter ($z = 2.53$, $P = 0.011$). Birds taken as prey were mainly rallidae, such as common moorhen *Gallinula chloropus* (L., 1758) and Eurasian coot *Fulica atra* L., 1758, with a few individuals of little grebe *Tachybaptus ruficollis* (Pallas, 1764) and mallard duck *Anas platyrhynchos* L., 1758. Birds were the most important prey in terms of ingested biomass, and they were taken equally ($z = 0.38$, $P = 0.787$) in both seasons (Table 1). Although the remaining prey categories were not statistically tested (i.e. < 10 % of ingested biomass), many of them were more abundant in the diet during spring (e.g. > 2× more for brown trout *Salmo trutta* L., 1758) or did not even appear in the spraints during winter (i.e. white-clawed crayfish *Austropotamobius pallipes* (Lereboullet, 1858), gudgeon *Gobio gobio* (L., 1758), stone loach *Barbatula barbatula* (L., 1758) and European bullhead *Cottus gobio* (L., 1758). Also, some other prey categories were more consumed in winter (i.e. crucian carp *Carassius carassius* (L., 1758), Eurasian perch *Perca fluviatilis* L., 1758 and mammals). The only mammal remains observed in spraints were from water vole *Arvicola amphibius* (L., 1758). Roach *Rutilus rutilus* (L., 1758), rudd *Scardinius erythrophthalmus* (L., 1758) and threespine stickleback *Gasterosteus aculeatus* L., 1758 were of very low importance and similarly taken in both seasons (Table 1). River-associated prey were consumed significantly more often in spring (28.39 %) than winter (4.48 %) ($z = 2.18$, $P = 0.029$), whereas no seasonal difference was observed for pond-associated prey, with a value of 64.07 % in spring and 87.17 % in winter ($z = 1.46$, $P = 0.145$). Prey diversity was significantly lower in winter ($H' = 0.54$, SE = 0.10) than it was in spring ($H' = 0.95$, SE = 0.11) ($t = 2.59$, $P = 0.012$).

The proportion of ponds with evidence of toad kills was significantly higher ($\chi^2 = 4.91$, $P = 0.027$) in spring (54.76 %) than in winter (15.15 %). Dead toads were found from 6 to 55 individuals per pond site. At ponds with toad kills, most carcases were fresh and found in piles. At these sites, 25.00 % of ponds had < 10 carcases, 53.57 % had 10-30 carcases and 21.43 % had > 30 carcases. Most of toad carcase remains (78.37 % of 601 dead toads) consisted of nearly complete bodies that possessed a characteristic, slightly lateral incision along the back and behind the paratoid glands (Fig. 1). In most of these cases, the internal organs (e.g. heart, lung, liver, guts, eggs of female toads) had been removed. The remaining dead toads showed either "progressive skinning" (7.82 %) or they were completely smashed (13.81 %).

Discussion

Otters generally have broad (e.g. > 10 km^2) home ranges (see Erlinge 1967) and a high capacity of ambulation to mark different habitats within the territory equally (i.e. ponds and rivers). Nonetheless, otters have been shown to use one habitat type more often than others for feeding and marking in particular seasons (Remonti et al. 2011, Almeida et al. 2012a). Otter foraging (and thus marking intensity) around ponds was expected to be high during winter, but this expectation was not met in the present study and this may be due to a lower degree of territorial behaviour during this cold (non-breeding) season. Thus, the peak in the marking activity during spring was probably due to a more intensive territorial behaviour associated with juvenile dispersal (Macdonald & Mason 1987).

Otters made greater use of river-associated species in spring, probably due to easier detection (e.g. crayfish out of burrows, fish more active at swimming, Barbaresi & Gherardi 2001, Nunn et al. 2010), resulting in a more diverse diet for this season. In winter, ponds may provide otters with a reliable food supply during the cold period (Kortan et al. 2007, Poledník et al. 2007) because of the increased likelihood of encountering prey more confined and more active than in rivers. However, a general greater use of pond-associated prey during winter was not observed in the present study. This pattern was only observed for pike and tench, which were important prey in terms of ingested biomass (see present results). Moreover, these two fish species can reach relatively high abundances in some ponds (Zambrano et al. 2006), which may explain a greater use by otters during winter.

The Eurasian otter is an opportunistic species, switching from fish, their preferred prey type, when fish availability decreases to consume non-fish prey such as amphibians (Remonti et al. 2009) and birds (as observed in the study ponds), which may be hunted and ambushed more easily within the confines of small ponds (Almeida et al. 2012a). Amphibians are consumed more frequently in late winter and spring, when these animals are more active for reproductive purposes (Griffiths 1997). Eel, pike, tench and common carp were fish species playing a key role as food resources at each particular habitat (i.e. river or pond), probably because these prey supply with high amount of biomass in a single catch (Copp & Roche 2003, Miranda et al. 2008, Almeida et al. 2012a). The case of crucian carp is of particular concern from

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a conservation point of view because the species is in decline in the U.K. (Sayer et al. 2011) and as a consequence has been granted BAP conservation status in Norfolk. The results of the present study provide no evidence to suggest that otters are playing an active role in the decline of this fish species, as crucian carp was an infrequent prey item. To ensure that otter predation pressure does not focus on crucian carp, fish populations in water courses should be maintained. For instance, eel is a favoured prey of otters (Copp & Roche 2003, Miranda et al. 2008), but the decline in eels throughout Europe (Dekker 2003) is apparent in the diet of Norfolk otters (Almeida et al. 2012a). Thus, current initiatives to promote eel conservation in Europe would, if successful, also help divert otter predation pressure away from species of conservation interest (e.g. crucian carp) and those of angling interest (common carp and other cyprinids). Regarding the use of non-native species, results showed that otters take common carp relatively frequently in both winter and spring, which is a source of consternation amongst anglers and provokes conflicts between conservationists, fishery owners and recreational anglers (Miranda et al. 2008, Crawford 2010, Václavíková et al. 2011). In relation to this, the otter's habit of taking only a small portion of each fish and abandoning the remainder (Kortan et al. 2007) can attract disproportionately more attention, despite its rare occurrence.

Amphibians may be significant in the diet of otters in ponds (Poledník et al. 2007, Cogalniceanu et al. 2010, also Table 1). In particular, toads are usually avoided by otters because of the venomous glands in the skin, although this prey can be important in the diet when unfavourable feeding conditions occur, for instance when their preferred prey (fish) are in low abundance (Sidorovich & Pikulik 1997). In north Norfolk, common toad is very abundant during spring, when this species congregates in high numbers in ponds where suitable breeding conditions (e.g. underwater vegetation, no current) are present (Griffiths 1997). Moreover, the small size of some ponds can result in high densities of highly-active amphibians, rendering them easier to detect and capture by predators. This seasonal pattern of toad exploitation has been also described for other temperate regions of Europe (e.g. Weber 1990), when the toads congregate for breeding (even in winter, see García-Díaz & Ayres 2010) and fish abundances are reduced.

Otters showed a selective consumption of the toad's internal organs, which means a small amount of ingested biomass. A similar phenomenon has been described for the Iberian ribbed newt (*Pleurodeles waltl* Michahelles, 1830) in southern Spain (Cogalniceanu et al. 2010). The relatively low biomass return per prey item probably explains the high number of toads taken per pond, and the predominate consumption of soft tissues (without bones) suggests that the predatory pressure of otters on toads is probably underestimated when based on spraint analysis (Carss 1995, Cogalniceanu et al. 2010). The handling technique by otters to feed on amphibians appears to be species-dependent, with newts being subjected to abdominal opening (Cogalniceanu et al. 2010) and toads with the skin progressive pulled back to the legs (Slater 2002, García-Díaz & Ayres 2010, Ayres & García 2011). In the present study, some toads were subjected to the "progressive skinning" technique described here above, but mostly the otter used a dorsal incision to reach the toad's internal organs. This reveals a wide plasticity in consumption technique when handling the same and different prey species that suggests a learning component of foraging behaviour (Watt 1993, Slater 2002).

In conclusion, this paper provides insights into the habitat use and feeding tactics of the Eurasian otter, highlighting the ecological importance of ponds for this carnivore during critical periods of the year (e.g. Ruiz-Olmo et al. 2007) and expanding our understanding of seasonal variations in otter predation pressure on pond-dwelling animals. This information is of particular relevance to the conservation and management of pond biodiversity and Eurasian otters at the landscape scale.

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