A well fed Eurasian otter (Lutra lutra) on the bank of the river Usk in Wales. Photograph taken by Jeff Chard.

135x104mm (300 x 300 DPI)
Dietary complexity and hidden costs of prey switching in a generalist top predator

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Short title: Dietary complexity in a top predator
Summary

1. Variation in predator diet is a critical aspect of food web stability, health, and population dynamics of predator/prey communities. Quantifying diet, particularly among cryptic species, is extremely challenging however, and differentiation between demographic subsets of populations is often overlooked.

2. We used prey remains and data taken post mortem from otter *Lutra lutra* to determine the extent to which dietary variation in a top predator was associated with biotic, spatial and temporal factors.

3. Biotic data (e.g. sex, weight, length) and stomach contents were taken from 610 otters found dead across England and Wales between 1994-2010. Prey remains were identified to species where possible, using published keys and reference materials. Multi-model inference followed by model prediction were applied to test for and visualise the nature of associations.

4. Evidence for widespread decline in the consumption of eels (*Anguilla anguilla*) reflected known eel population declines. An association between eel consumption and otter body condition suggested negative consequences for otter nutrition. Consumption of *Cottus gobio* and stickleback spp. increased, but was unlikely to compensate (there was no association with body condition). More otters with empty stomachs were found over time. Otter sex, body length, and age class were important biotic predictors of the prey species found, and season, region, and distance from the coast were important abiotic predictors.

5. Our study is unique in its multivariate nature, broad spatial scale, and long-term dataset. Inclusion of biotic data allowed us to reveal important differences in costs and benefits of different prey types, and differences between demographic subsets of the
population, overlaid on spatial and temporal variation. Such complexities in otter diet are likely to be paralleled in other predators, and detailed characterisation of diet should not be overlooked in efforts to conserve wild populations.
Introduction

Dietary strategies are highly variable, on a broad spectrum between specialism and generalism (Futuyma & Moreno 1988; Bolnick et al. 2003). Generalist consumers often have the capacity to switch to alternative food sources when their preferred dietary items are unavailable (Kjellander & Nordstrom 2003; Fox 2005; Almeida et al. 2012). Such dietary plasticity decreases a species’ sensitivity to change and stabilises food webs (van Baalen et al. 2001; Clare 2014). Despite generalists being more robust to change, there may still be costs associated with dietary switching. For example, switching to suboptimal prey with a lower nutritional value or a higher contaminant load could reduce the fitness of a species in the short-term (Ruiz-Olmo & Jimenez 2009). In the longer term, consequences for population dynamics might threaten persistence of the species (Korpimaki 1992; Schweiger, Funfstuck & Beierkuhnlein 2015), with implications for food web stability and ecosystem functioning (Spitz & Jouma'a 2013).

Carnivore diet reflects both temporal and spatial variation in prey availability (Virgos, Llorente & Cortes 1999; Elmhagen et al. 2000; Prugh, Arthur & Ritland 2008). Availability of prey relates not only to abundance in the environment, but also to ease of capture, which varies with species (Sih & Christensen 2001) and time of year (Krawczyk et al. 2016). Variation in feeding behaviour may result from individual variation in morphology, health and competition, amongst other variables (e.g. Kitchener 1999; McDonald 2002; Bolnick 2004; Beck et al. 2007; Svanback & Bolnick 2007; Woo et al. 2008; Araujo et al. 2009; Murray et al. 2015; Broekhuis, Thuo & Hayward 2018). In addition, dietary requirements may vary between demographic subsets of a population including between age-classes and sexes (Houston et al. 2007; Navarro et al. 2009; Magnusdottir et al. 2012; Riccialdelli et al. 2013), which can lead to niche partitioning.
The consequences of dietary switching may therefore differ significantly between individuals and groups, which may result in exposure to differing selection pressures including contaminant and parasite loads.

A variety of methods are available for studying the diet of animals, each with associated strengths and weaknesses. Non-invasive analysis of faecal samples using morphological or molecular methods predominate (Pompanon *et al.* 2012; Valenzuela *et al.* 2013; Ripple *et al.* 2014). Using this strategy, it is difficult to collect information about the individual, unless the animal is captured or DNA analyses are employed (Prugh, Arthur & Ritland 2008, Dunn *et al.* 2018), which might provide valuable insight into dietary variation. Consequently, it is difficult to detect associations between diet and biotic variation. To achieve this, samples and data collected post mortem offer a unique opportunity to link the diet of individuals to a range of biotic variables (Lanszki *et al.* 2015).

The Eurasian otter (*Lutra lutra*, hereafter referred to as ‘otter’) is a semi-aquatic carnivore specialised to feed in aquatic ecosystems, mainly on fish (Kruuk 1995; Britton *et al.* 2006; Almeida *et al.* 2012; Krawczyk *et al.* 2016). Otter numbers declined dramatically across much of their European range during the last century. This decline was thought to be due to the bioaccumulation of pesticides and polychlorinated biphenyls (PCBs) and habitat modification (reviewed in Chanin 2003). Population distributions have since generally increased significantly across western Europe (Mason & Macdonald 2004; Roos *et al.* 2015) but those recoveries are occurring in an environment that has changed considerably in the intervening decades, with respect to habitat, prey availability (Hayhow *et al.* 2016) and freshwater pollution (Murray, Thomas & Bodour 2010). These
factors are likely to play significant roles in determining the rate of recovery and changing distribution of recovering species (Hayes & Harestad 2000).

In the current study we utilised a biobank of samples and data collected from otters found dead in England and Wales over 16 years, to test how diet varied between individuals with differing biotic characteristics (such as sex, age and condition), while controlling for temporal and spatial variation.

Methods

Sample collection

Otters found dead (mostly as a result of road traffic accident, RTA [92%]) were collected across England and Wales (see Fig. 5, results section) between 1994 and 2010, as part of a national scheme coordinated by Cardiff University. The entire stomach and intestine were taken during post mortem examination of 610 otters, and frozen at -20°C.

Abiotic variables

The year, month and location where each otter was found were recorded. Location data were provided as national grid references accurate to the nearest 100 m and were used to define region and distance to the coast. Distance to the coast via the nearest river (river distance) was measured using ArcMap GIS (V.9.2, ESRI 2006). Where otters were found more than 1000 m from a river, river distance was omitted. Each otter was assigned to one of eight regions, based on aggregations of adjacent river catchments (see Fig. 5, results section).

Biotic variables
Each otter was examined in detail at post mortem; sex, age class (adult, sub-adult, juvenile), reproductive status (females only), weight (kg, to the nearest 10 grams), length (mm, to the nearest 5 mm, measured nose to anus and anus to tail tip) and cause of death were determined. Morphometric and reproductive data were used to assign age class, such that males below 3 kg and females below 2.1 kg are recorded as juveniles. Above these weights, otters are considered adult if reproductively mature (males with baculum length ≥60 mm (van Bree et al. 1966), females with signs of reproductive activity such as placental scarring, prominent teats), and sub-adult if reproductive maturity is not apparent. Based on examination of the uterus and teats, female reproductive status was categorised as never reproduced, quiescent, pregnant, or lactating. Length and weight were used to calculate a condition index (\( K = \frac{W}{aL^n} \), where \( W \) = total body weight in kg, \( L \) – total length in m; for males \( a = 5.87 \) and \( n = 2.39 \); for females \( a = 5.02 \) and \( n = 2.33 \), Kruuk et al. 1987).

**Dietary analysis**

Stomach and intestine samples were defrosted and rinsed through a fine sieve. Recognisable dietary items (e.g. feathers, fur, etc) were recorded. Remaining solid material was transferred to a liquid detergent solution (water:detergent, 10:1) to aid removal of soft tissues. Samples were filtered repeatedly, and detergent solution replaced until only hard prey items remained. After air drying, prey items were examined using a binocular microscope (Leica 2000, x7-x30) and identified with the aid of published keys (Day 1966; Teerink 1991; Miranda & Escala 2002; Conroy et al. 2005; Cham 2007) and by comparison with reference material. Prey items were identified to species level whenever possible but to reliably differentiate salmon and trout, recovery of the atlas bone or jaw parts was required and these suffered poor recovery rates. Similarly,
cyprinids were not distinguishable to species from their vertebrae but where pharyngeal bones were found species identification was made. These data were reported as frequency of occurrence (\( FO = \frac{t}{n} \), where \( t \) = total number of occurrences of a particular prey type and \( n \) = total number of samples examined) and as relative frequency of occurrence (\( RFO = \frac{t}{p} \), where \( t \) = total number of occurrences of a particular prey type and \( p \) = total number of occurrences of all prey types) to enable comparison with earlier studies (Clavero, Prenda & Delibes 2004). RFO was calculated both relative to all prey types across taxa, and also (for fish) relative to total occurrences of all fish prey types. For statistical analyses, the response variable was the presence/absence of either a specified prey type, or an empty stomach.

Statistical analyses
To identify the importance of biotic and abiotic associations with otter diet, we used a series of generalized additive models (GAMs) in the R software environment (version 3.3.1, R Core Team 2016) utilizing the mgcv (Wood 2011) package, with binomial error distributions (see Table 1 for global model specifications, including all independent variables).

First, we examined whether or not otters had recently fed on vertebrate prey, using presence / absence of prey remains (of any type) in the gut as the binomial dependent variable, and tested for associations with a range of biotic and abiotic independent variables (as specified in Table 1, Model Groups 1 & 2). Model Group 1 used all individuals (n=610), and included sex as an independent variable so that we could test for sexual differentiation, while Model Group 2 (n=268) excluded males, and additionally included female reproductive status as an independent variable. Age class and the
majority of biotic interactions were excluded from Model Group 2 due to the reduced sample size (see Table 1).

Secondly, for those otters where identifiable prey remains were found, we used presence/absence of each of 11 individual prey types as the binomial dependent variable, and tested for associations with biotic and abiotic variables (as specified in Table 1, Model Groups 3 & 4). ‘Prey type’ was either species (European eel Anguilla anguilla, European bullhead Cottus gobio), or broader taxonomic/functional groupings where species identification was unreliable or where presence data for individual species were too few to permit robust modelling (cyprinid, salmonid, stickleback (family Gasterosteidae), crustacean, mammal, bird, insect, amphibian, marine fish). For these Model Groups we excluded juveniles due to small sample size (only 4 individuals with prey remains). Model Group 3 included all remaining individuals (n = 501) and included sex as an independent variable, while Model Group 4 (n=226) further excluded males, and included female reproductive status (as for Model Group 2).

In all Model Groups (1-4) interaction terms were included for biotic terms if there was an appropriate biological hypothesis and sufficient data to allow robust model predictions (as specified in Table 1). The most appropriate link function for each model was selected based on the lowest AIC (Akaike information criterion) values.

Interpretation of the most important variables was achieved using a multi-model inference approach, using the dredge function in MuMIn (Bartoń 2018) and applying model averaging where delta AICc (AIC corrected for small sample size) <2 (Symonds & Moussalli 2011). If the AICc of the second best model was >2, a model averaging
Rather than reliance on p-values alone, the most important relationships were described: those which either appeared in all top models (relative importance \( [RI] = 1 \)) regardless of probability, or where RI was > 0.5 and the relationship was statistically significant (\( p < 0.05 \)). Note that in some cases, variables were deemed important by inclusion in multiple (or all) top models, even where model averaging suggested non-significance (\( p < 0.05 \)) (Burnham & Anderson 2002). All global model residuals were visually assessed for temporal autocorrelation (using the autocorrelation function ‘acf’ in R, with a maximum lag of 12 months). There was no evidence for significant autocorrelation in the residuals from any global models so no further adjustments were made to model structures.

For model predictions (using the ‘predict’ function) we modelled the effect of each selected variable, while controlling all other important variables to either the most frequently observed level (Age = adult, Sex = male, cause of death = sudden, Year = 2008, Month = January and Region = Wales), or to their median Condition = 1, Length = 1050 mm, river distance = 30 km. Where predictions were calculated for different age-classes, body length was adjusted to the median specific to that group (juvenile: 663 mm, sub-adult: 1005 mm, adult: 1105 mm).

Results

Of the 610 otters examined, 268 were female (129 = never reproduced, 44 = pregnant or lactating, 90 = quiescent, 5 = not possible to assess) and 342 were male. Most were adult (343) or sub-adult (251) with very few juvenile (15), and it was not possible to determine the age class of one individual. Most died suddenly e.g. by road traffic accident (\( n = 560 \)),
some died of ill health (n = 40) while in other cases cause of death was unknown (n = 10).

Of all 610 otter gut samples examined, 505 (82.79%) contained identifiable vertebrate prey remains. Fish were the main component of otter diet (71.18% RFO). Amphibians also made a substantial contribution (14.86% RFO), while insect, mammal, bird and crustacean remains were relatively rare (≤5% RFO) (Table 2). Of the fish, the most common identified species were bullhead, (22.59% RFO) and eel (17.61% RFO). Cyprinids were commonly found (22.73% RFO) but note that this total potentially encompasses 16 species found in the UK, of which 9 were definitively identified (Table 2). Salmonids were commonly found (21.88% RFO) and where identification was considered reliable most remains were of trout (Table 2). Sticklebacks were also frequently found (11.36%) but in most cases it was not possible to discriminate between three-spined (Gasterosteus aculeatus) and nine-spined stickleback (Pungitius pungitius). Most species found were freshwater, with only 3.83% of samples including remains of marine fish. Fish remains identified as family Percidae, stone loach (Barbatula barbatula) and pike (Esox lucius) were also found occasionally but were not included in analyses due to low sample size (n = 18, 14, 3).

**Generalised additive models: presence / absence of prey remains**

The absence of vertebrate prey remains (i.e. the likelihood of having an empty stomach at death) was significantly associated with both biotic and abiotic variables. For Model Group 1 (analysis including both sexes), after applying the dredge function to our global model, there was only one top model (deviance explained = 22.7%, Appendix 1). Juveniles were approximately seven times more likely to have empty stomachs than adults (z = 3.01, p = 0.003) or sub-adults (z = 3.34, p = <0.001) (model predictions: 11
juvenile = 0.85 ± 0.08; sub-adult = 0.125 ± 0.026; adult = 0.118 ± 0.024). Males were
significantly more likely to have empty stomachs than females (z = 2.48, p = 0.013,
model predictions: females = 0.068 ± 0.014; males = 0.113 ± 0.025). Absence of prey
was associated with body condition, but the nature of the association differed with body
size (significant length: condition interaction, z = 2.49, p = 0.013). For larger otters, those
with empty stomachs tended to be in poorer condition, but this association was not
apparent for smaller otters. Feeding was not significantly associated with reproductive
status.

Between 1994 and 2010, the likelihood of having an empty stomach increased
significantly (z = 2.59, p = 0.01), with a probability of an empty stomach at 0.037 ± 0.01
in 1994, increasing to 0.215 ± 0.075 in 2010 (Fig. 1a). Otters that died following illness
were almost four times more likely to have empty stomachs than those that died suddenly
(z = -2.99, p = 0.003, model predictions: sudden = 0.113 ± 0.024; ill = 0.445 ± 0.248).
There was a small but significant effect of distance from the coast, with otters found in
coastal areas more likely to have empty stomachs (z = -2.43, p = 0.015), varying between
a probability of 0.145 ± 0.038 at the coast to 0.118 ± 0.026 30 km inland, and to 0.071 ±
0.017 135 km inland (note that 89% of otters for which it was possible to measure
distance from the coast [n = 506] were found within 135 km of the coast, with 50% <30
km from the coast).

Generalised additive models: stomachs containing prey remains
All 11 averaged models retained both abiotic and biotic variables, indicating that both are
important for understanding otter diet. Below we describe the most important
relationships (defined using RI (relative importance) and p (probability) as specified in Methods).

**Biotic variables**

Otter body condition, body length, age class and sex were all important predictors of otter diet (Appendix 2). Reproductive status was not an important predictor of diet, so Model Group 4 is not discussed further and all results described below are taken from Model Group 3 (including both sexes). The likelihood of consuming amphibians and mammals was negatively associated with body condition (amphibian: \( z = 1.96, \text{RI} = 0.85, p = 0.05 \); mammal: \( z = 2.05, \text{RI} = 1, p = 0.041 \)). For eels and salmonids the reverse was true (eel: \( z = 2.23, \text{RI} = 1, p = 0.026 \); salmonid: \( z = 2.12, \text{RI} = 1, p = 0.034 \)) (Fig. 2).

Larger otters (those with greater body length) were more likely to have consumed salmonids (\( z = 2.07, \text{RI} = 1, p = 0.039 \)), and bullhead (\( z = 2.043, \text{RI} = 1, p = 0.041 \)). For predation on amphibians, the association with body length was dependent on age: adult otters showed a negative association between length and consumption (i.e. large adults were less likely to eat amphibians), whereas sub-adult otters showed the reverse (large sub-adults were more likely to eat amphibians (RI = 1, \( p = 0.006 \)) (Fig. 3). The likelihood of eating crustaceans decreased with length but the effect size was very small and on average this term was not statistically significant (\( z = 1.34, \text{RI} = 1, p = 0.18 \)).

Sex proved to be an important (although statistically insignificant) variable in explaining the prevalence of some prey types. Female otters were 10% more likely than males to prey on bullhead (\( z = 0.44, \text{RI} = 1, p = 0.66 \), model predictions: females = 0.299 ± 0.063; males = 0.191 ± 0.047). The opposite trend was observed for cyprinid consumption, with...
males being >20% more likely to have consumed this group than females ($z = 0.97$, $RI = 1$, $p = 0.33$, model predictions: females $= 0.304 \pm 0.081$; males $= 0.513 \pm 0.117$).

Predation on mammals was rare, and sex differences varied with age (the $Sex: Age-class$ interaction was important, although not significant, $RI = 1$, $p = 0.22$). Adult males were more likely to prey on mammals than sub-adult males (predictions: adult males $= 0.084 \pm 0.093$; sub-adult males: $= 0.027 \pm 0.010$), whereas for females likelihood was low in both age groups (predictions: adult females $= 0.017 \pm 0.012$; sub-adult females $= 0.038 \pm 0.015$).

**Abiotic variables**

All abiotic variables tested (month, year, region and distance from the coast) were important predictors of otter diet (Appendix 2).

Seasonality (month nested within year) appeared in all top models for eel, bullhead, amphibian, cyprinid, and crustaceans ($RI = 1$). Eel consumption rose suddenly from near zero in March to a major peak in May followed by a steady fall through summer and autumn (Fig. 4a). Bullhead were predated throughout the year, but with a clear peak in autumn (Fig. 4b). Consumption of amphibians showed a clear trough in summer; the highest peak was in spring, but autumn and winter consumption was also high (Fig. 4c). Cyprinid predation was highly seasonally variable, with the largest peak in early summer and another high peak in December-January and smaller peak in autumn (although note larger error around autumn peak) (Fig. 4d).

Region proved to be an important variable for explaining the prevalence of amphibian, crustacean, cyprinid, and salmonid remains and appeared in all top models for these taxa.
Amphibians were prevalent primarily in the north and Wales, salmonids primarily in the north west, and cyprinids, although prevalent in all regions, show much higher prevalence in Anglian region than elsewhere. Crustacean consumption was rare overall, but was higher in the north west (Fig. 5).

Marine prey were less likely to occur with increased distance from the coast ($z = 2.56$, $RI = 1$, $p = 0.011$). Model predictions indicate a very sharp drop in probability of marine prey items to near zero by 50 km. The same relationship was found for eel remains ($z = 5.29$, $RI = 1$, $p < 0.001$). Model predictions suggest the probability of recovering eel remains was $0.17 \pm 0.066$ 10 km from the coast, decreasing to $0.073 \pm 0.036$ by 50 km inland. The reverse was true for amphibian ($z = 2.843$, $RI = 1$, $p = 0.005$) and bullhead ($z = 6.58$, $RI = 1$, $p < 0.001$) remains. Amphibian and bullhead remains were predicted at $0.33 (\pm 0.14)$ and $0.16 (\pm 0.041)$ 10 km from the coast and $0.44 (\pm 0.16)$ and $0.23 (\pm 0.055)$ 50 km inland, respectively.

Over time, the occurrence of eels in otter diet declined significantly ($z = 2.75$, $RI = 0.5$, $p = 0.006$). For example, for eels predicted probabilities were $0.35 (\pm 0.14)$ in 1995 but had dropped to $0.090 (\pm 0.044)$ by 2010 (Fig. 1b). For bullhead and stickleback remains, the converse was true (bullhead: $z = 2.23$, $RI = 0.5$, $p = 0.026$, stickleback: $z = 1.63$, $RI = 1$, $p = 0.1$), with predicted probabilities of $0.084 (\pm 0.036)$ in 1995 and $0.22 (\pm 0.055)$ in 2010 for bullhead (Fig. 1c), and $0.073 (\pm 0.026)$ in 1995 and $0.21 (\pm 0.061)$ in 2010 for stickleback (Fig. 1d).

In models run separately for females, reproductive condition was either not significantly associated with the prey prevalence (amphibian, bullhead, crustacean, cyprinid, eel, insect, salmonid or stickleback) or it was not possible to test for the importance of
reproductive condition due to low sample sizes when males were excluded (for avian, mammal, and marine prey).

Discussion

Otters are generalist predators that can opportunistically switch their diet according to the availability of prey (e.g. Britton et al. 2006; Remonti et al. 2010; Almeida et al. 2012; Krawczyk et al. 2016). Indeed, their generalist tendencies are likely to facilitate their wide global distribution (Clavero, Prenda & Delibes 2003; Roos et al. 2015) and have likely assisted their population recovery from widespread declines in 1960-70s. Today, otter populations in the UK are widely assumed to be stable or increasing (Mathews et al. 2018). However, by investigating both biotic and abiotic variables in a long-term study of otter diet, this study identifies costs associated with prey switching, and reveals potentially differing vulnerabilities between demographic groups, and regions of the UK. Such costs and vulnerabilities may impact the persistence of otter populations in the long-term and reduce their perceived resilience to the degradation of fish diversity and other aquatic prey due to factors such as climate change (Ficke, Myrick & Hansen 2007).

The prevalence of empty stomachs

Overall, evidence for recent feeding by otters (i.e. the presence of any prey remains in the gut) declined over time, suggesting that otters were more often going hungry in the latter years of the study. Empty guts were more often seen in individuals found nearer the coast, suggesting either lower prey availability in coastal habitats, or behavioural differences – for example, reduced cover, or increased anthropogenic disturbance in coastal areas may contribute to reduced feeding. Coastal areas of Wales and England were apparently some of the last to see otter populations return (Crawford 2010). Although prey type varied both seasonally and regionally, there was no evidence for
seasonal or regional variation in the overall occurrence of prey presence versus empty 
guts, suggesting that otters can be highly effective predators year round, across England 
and Wales. Juvenile otters were approximately seven times more likely to have empty 
stomachs than both adults and sub-adults. This is likely to be driven by a combination of 
factors including having been abandoned/orphaned prior to independence (a likely bias in 
our sample); being fed largely on milk or muscle tissue which would remain undetected 
in the morphological analysis of stomach contents; or an increased gut transit time. 
Model predictions based around the length:condition interaction term suggest that in 
larger otters, empty stomachs were associated with a long-term nutritional deficit 
resulting in loss of condition, whereas in smaller otters this was not the case.

Potential costs and benefits of prey switching

Selection of prey is presumed to reflect a balance between the energetic costs of prey 
capture, and nutritional benefits, following optimal foraging theory (Sih & Christensen 
2001). Eels are often cited as a highly favoured prey of otters (e.g. Jenkins & Harper 
1980; Britton et al. 2006; Miranda et al. 2008) due to their high calorific value compared 
to other prey species (Kruuk 1995). In recent years, eel population declines have been 
catastrophic (Westerberg et al. 2018), and reduced eel consumption by otters is reflected 
in the current study as well as previous, more localised studies (Copp & Roche 2003; 
Almeida et al. 2012; Kruuk 2014). Our study confirms a positive association between eel 
(and salmonid) consumption and otter body condition, which is not evident for other prey 
types. Our models can only provide evidence for association, and do not allow us to 
separate cause and effect. This association may therefore indicate that otters in better 
condition are able to catch more eels and salmonids, or that consumption of these fat-rich 
prey species contributes to improved body condition. Both are likely, and as eel
availability continues to decline, body condition is likely to suffer. Our evidence adds weight to previous concerns about food limitation causing localised otter population declines, which may go undetected in broad national distribution surveys (Kruuk 2014).

In our study, the only prey taxa to have increased in otter diet concurrently with eel declines were the bullhead and stickleback. Although these small species were not negatively associated with body condition, there were also no positive associations, suggesting that they are inadequate replacements for eel in nutritional terms. Conversely, this prey switch may reduce otter exposure to persistent, bioaccumulative, toxic chemicals (PBTs) including PCBs (polychlorinated biphenyls) and organochlorine pesticides linked to reproductive potential (Sonne et al. 2009; Jepson et al. 2016) and believed to have caused otter population declines (Chanin 2003). These chemicals are lipophilic, and consumption of fat-rich, long-lived eels is likely to have been a significant exposure route for otters. It is clear, however, that variation in diet must be carefully considered when evaluating apparent differences in pollutant exposure.

Mammals, crustaceans and amphibians were previously reported as ‘buffer prey’ taken by otters when seasonally abundant, or in the absence of more nutritious prey (Jedrzejewska et al. 2001; Clavero, Prenda & Delibes 2003; Remonti et al. 2010; Krawczyk et al. 2016). Both amphibians and crustaceans can form a very significant component of otter diet (Britton et al. 2006; Parry et al. 2011; Krawczyk et al. 2016) and it has previously been suggested that ease of capture of amphibians during their congregation for spawning or hibernation may compensate for lower nutritional value in comparison to fish (Nelson & Kruuk 1997; Krawczyk et al. 2016). The current study, however, suggests a negative association between amphibian consumption and body condition, indicating that reduced energy expenditure due to ease of capture is
insufficient to entirely compensate for reduced nutritional value. It should be noted, however, that this statistical association does not reveal whether lower quality prey leads to poorer body condition, or whether otters in poorer condition are less likely to compete for and catch higher quality prey types; both are likely.

Dietary variation across demographic groups

Although only eel and salmonid prey showed a positive association with body condition, this does not mean that other prey species are unimportant. Crustaceans were more likely to be preyed on by smaller otters, probably as a consequence of crustaceans being easier to catch by inexperienced individuals. For sub-adult otters, crustacean consumption was associated with an improved body condition. This prey type, despite being inferior in terms of nutrition to eel and salmonid is nonetheless particularly important for population subsets. Age-related dietary shifts such as these may arise as a consequence of body size or development (e.g. musculature) (Bolnick et al. 2003), behavioural changes such as learning (Estes et al. 2003), or exclusion by larger adults from territories where higher quality prey are abundant. This is in accordance with direct observations from the Scottish island of Mull where only sub-adults were seen foraging on crustaceans (Watt 1993). Although juvenile otters were excluded from our analyses, in the four cases where identifiable remains were found in juveniles, two contained mammalian and one, crustacean, remains. For amphibian consumption, associations with length and age-class suggest a non-linear association with age: consumption by sub-adults becomes more common as they increase in body length (perhaps as a result of learnt behaviour patterns) while in adult otters, consumption decreases with body length (perhaps as a result of switching to better quality prey in older individuals).
Dietary differences between the sexes are often attributed to sexual dimorphism, breeding behaviour (Begg et al. 2003) or differing energetic requirements associated with reproduction. Direct observations of otters on Shetland found that males took prey that was 22% larger than prey taken by females without cubs, but that mothers with cubs took prey similar in size to that of males (Kruuk, Conroy & Moorhouse 1987). The current study showed no associations between reproductive condition of females and either presence or type of prey, and showed limited evidence for sex differences (we showed sex differences in cyprinid consumption, but interpretation of this with respect to prey size is not feasible due to the lack of species resolution in this prey family).

Spatiotemporal variation in diet

Individual and demographic variation in prey selection inevitably occurs against a background of spatial and seasonal variation in availability, as well as long term changes over time. Complexity escalates when one considers not only absolute availability but also relative availability, across multiple potential prey species, each of which have differing costs and rewards (Ratcliffe et al. 2018). Several studies have compared otter diet with indices of prey availability and demonstrate clear associations (e.g. Remonti et al. 2010; Grant & Harrington 2015). In the current study, a lack of high-resolution spatio-temporally explicit records of fish (or other species) abundances across England and Wales, over the required fifteen year period, precludes such explicit comparisons. Broad patterns in both spatial and seasonal variation, however, do support presumed associations with availability. For example, the distinct trough in amphibian consumption in summer is at a time when amphibians are away from their aquatic breeding areas, and the largest peak coincides with the amphibian spring breeding migration (Beebee 2013). Similar seasonal trends in amphibian consumption have been shown previously in dietary
studies of limited geographic range (e.g. Clavero, Prenda & Delibes 2003; Britton et al. 2006; Parry et al. 2011). Secondary peaks (although predicted with less confidence) are indicated in autumn and winter, potentially reflecting an autumn sub-migration, and winter predation at a time when amphibians are vulnerable due to inactivity (Beebee 2013). Eel consumption was most common near the coast, and peaked in May followed by a gradual decline - presumably reflecting the mass arrival of elvers in UK estuaries in around April each year (White & Knights 1997). Bullhead were most frequently taken inland (perhaps reflecting their tendency to inhabit small, upland streams (Maitland & Campbell 1992)) and in autumn. An autumn peak in bullhead consumption is contrary to an earlier UK study where bullhead consumption peaked in summer (Grant & Harrington 2015). Grant and Harrington (2015) suggest that otters were switching between consuming bullhead in summer and cyprinids in winter, but their study was restricted to one river in southern England, whereas the current study indicates the reverse. Interpreting temporal trends for cyprinids should be treated with caution given the ambiguity in species identification, but a winter peak (December-February) is in accordance with other European studies based on the analysis of spraints (Chanin 1981; Breathnach & Fairley 1993; Taastrom & Jacobsen 1999; Grant & Harrington 2015) and is likely to reflect increased ease of capture with reduced fish swimming speeds in colder water temperatures. The summer peak evidenced in the current study may reflect ease of capture due to shoaling behaviour, which occurs variously from April to June (Maitland & Campbell 1992). Where regional variation was significant, cyprinid prey were particularly important in Anglian Region, whereas salmonids were important in the North West, and amphibians in the north and Wales.

Summary
The current study supports the theory that otters in Wales and England are generalist predators with the capacity to prey switch. Abiotic associations are largely consistent with previous studies and expectations, while the biotic data collected at post-mortem have allowed us to explore some of the potential costs and benefits of prey switching. These associations are important aspects of carnivore foraging strategies and population dynamics, and are a key consideration for conservation management in a changing world.

Acknowledgements

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Conflict of Interest

None Declared.

Author contributions

EC conceived the study, GP and SV undertook prey remains identification, RMG led statistical modelling and writing of the manuscript, EK contributed substantially to data
analysis and interpretation. All authors contributed critically to the drafts and gave final approval for publication.

**Data Availability Statement**

Dietary, biotic and abiotic data are archived on Dryad: doi: [10.5061/dryad.5dv41ns3k](https://doi.org/10.5061/dryad.5dv41ns3k)
References


Sonne, C., Gustavson, K., Rigét, F.F., Dietz, R., Birkved, M., Letcher, R.J., . . . Petersen, G. (2009) Reproductive performance in East Greenland polar bears (*Ursus maritimus*) may be affected by organohalogen contaminants as shown by...


Figure 1. Temporal trends in otter diet between 1994 and 2010. Plot (a) indicates the change in the probability of otters having empty stomachs with time. Plots (b), (c) and (d) indicate changes in the probability of finding eel, bullhead, and stickleback remains, respectively, in otter stomachs over time. Model predictions are plotted alongside the standard error surrounding those predictions. For the associations between year and other prey types, refer to Appendix 2.
Figure 2. Variation in otter diet with body condition. Associations between otter body condition index and different prey remains: (a) = eel, (b) = salmonid, (c) = amphibian. Model predictions are plotted alongside the standard error surrounding those predictions. For the associations between body condition and other prey types, refer to Appendix 2.
Figure 3. Dietary associations with otter body length. Associations between otter body length and different prey remains: (a) = salmonid, (b) = bullhead, (c) = amphibian (plotted separately for adults (black) and sub-adults (grey)). Model predictions are plotted alongside the standard error surrounding those predictions. For the associations between body length and other prey types, refer to Appendix 2.
Figure 4. **Seasonality in otter diet.** Seasonality of the prevalence of different prey remains: (a) = eel, (b) = bullhead, (c) = amphibian, (d) = cyprinid. Model predictions are plotted alongside the standard error surrounding those predictions. Details for crustacean predation not shown due to a low probability of occurrence and large standard errors. For the associations between month and other prey types, refer to Appendix 2.
Figure 5. **Spatial variation in otter diet.** Black circles indicate average model predicted probability of prey taxon occurring in otter diet (± standard error), for all models where significant associations with Region were indicated. Note that other prey types e.g. eel, bullhead were equally important across all regions (see frequency of occurrence, Table 1). Predictions by Region are made while other significant predictor variables are standardised (see methods). Too few data were available to reliably predict probabilities for Thames or Southern Regions; pairwise differences were not tested for significance due to high likelihood of error due to multiple testing. **[A]** Grey dots indicate locations where otter samples were sourced (note that the distribution of points is not homogenous within Regions, particularly NW and Midlands); white lines indicate Regional boundaries, which follow river catchments. Taxa are labelled as underlined: **Cyprinid**, **Salmonid**, **Amphibian** and **Crustacean**. **[B]** Standard compass point abbreviations are used for NW, NE and SW Regions, or as underlined for Wales, Midlands, and Anglian). Note adjusted scale on y axis for Crustacea. Details for mammal predation not shown due to a low probability of occurrence and large standard errors.
### Table 1. Independent variables included in global Model Groups 1-4.

Factors (categories) and continuous variables are denoted (f) and (c) respectively. Model Groups 1 & 2: dependent variable is presence/absence of an empty stomach. Model Groups 3 & 4: dependent variable is the presence of each of 11 different prey types. Prey types were: Eel, bullhead, cyprinid, salmonid, stickleback, crustacean, mammal, bird, insect, amphibian, marine fish. Cause of death was not included in Model Groups 3 and 4 due to the vast majority of deaths being 'sudden' in these reduced datasets (93.8% for Model Group 3, and 92.0% for Model Group 4). The link functions selected were as follows: probit for eel model group 3 and bullhead model group 4; cloglog for bullhead model group 3 and crustacean model group 4; logit for cyprinid model group 4; cauchit for all remaining models.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Categories / data range</th>
<th>Included in Model Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Biotic variables</strong></td>
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<td></td>
</tr>
<tr>
<td>Sex (f)</td>
<td>Female, Male.</td>
<td>y</td>
</tr>
<tr>
<td>Age class (f)</td>
<td>Adult, sub-adult, juvenile. NB. Juveniles excluded from Model Groups 3 &amp; 4</td>
<td>y</td>
</tr>
<tr>
<td>Body length (c)</td>
<td>490-1307 mm</td>
<td>y</td>
</tr>
<tr>
<td>Body condition (c)</td>
<td>0.5-2</td>
<td>y</td>
</tr>
<tr>
<td>Reproductive status (f)</td>
<td>Never reproduced, quiescent, pregnant or lactating, Term applicable to females only</td>
<td>-</td>
</tr>
<tr>
<td>Cause of death (f)</td>
<td>Sudden (n = 560), ill (n = 40), unknown (n = 10)</td>
<td>y</td>
</tr>
<tr>
<td><strong>Biotic interactions</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex:Age, Sex:Body length, Sex:Body condition, Age:Body length, Age:Body condition, Body length: Body condition, Reproductive status: Body condition, Reproductive status:Body length</td>
<td>y</td>
<td>-</td>
</tr>
<tr>
<td><strong>Abiotic variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year (c)</td>
<td>Month (Jan-Dec), fitted with circular spline, nested in Year</td>
<td>y</td>
</tr>
<tr>
<td>Year (c)</td>
<td>1994-2010</td>
<td>y</td>
</tr>
<tr>
<td>Region (f)</td>
<td>8 regions (see figure 5)</td>
<td>y</td>
</tr>
<tr>
<td>Distance from the coast (c)</td>
<td>Distance to coast, following river channel, 0-235 km.</td>
<td>y</td>
</tr>
</tbody>
</table>
Table 2. Prey remains identified from otter stomachs. The eleven prey types represent species, or higher taxonomic ranks, as used in statistical analyses. RFO = relative frequency of occurrence (total occurrences of a particular prey type/total number of occurrences for all prey types, calculated both relative to the total occurrence of fish prey (n=704,’/fish’), and to all prey (n=989,’/all’). FO = frequency of occurrence (total occurrences of a particular prey type/total number of samples (n=610)), number of individuals in which that prey type occurred is indicated in brackets (n).

<table>
<thead>
<tr>
<th>z</th>
<th>RFO/fish</th>
<th>RFO/all</th>
<th>FO (n)</th>
<th>Species names / other taxonomic sub-groupings identified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anguillidae</td>
<td>18</td>
<td>13</td>
<td>20 (124)</td>
<td>Eel Anguilla anguilla</td>
</tr>
<tr>
<td>Cottidae</td>
<td>23</td>
<td>16</td>
<td>26 (159)</td>
<td>Bullhead Cottus gobio</td>
</tr>
<tr>
<td>Cyprinid</td>
<td>23</td>
<td>16</td>
<td>26 (160)</td>
<td>Minnow Phoxinus phoxinus (54), chub Leuciscus cephalus (12), roach Rutilus rutilus (11), dace Leuciscus leuciscus (4), carp Carassius spp. (3), tench Tinca tinca (2), barbel Barbus barbus (2), common bream Abramis brama (2), rudd Scardinius erythrophthalmus (1)</td>
</tr>
<tr>
<td>Salmonid</td>
<td>22</td>
<td>16</td>
<td>25 (154)</td>
<td>Salmon Salmo salar (3), trout Salmo trutta (38)</td>
</tr>
<tr>
<td>Stickleback</td>
<td>11</td>
<td>8</td>
<td>13 (80)</td>
<td>3-spined stickleback Gasterosteus aculeatus (2)</td>
</tr>
<tr>
<td>Marine fish</td>
<td>4</td>
<td>3</td>
<td>4 (27)</td>
<td>Goby (15) (family Gobiidae), flatfish (17: including dab Limanda limanda [1], Flounder Platichthys flesus [2], plaice Pleuronectes platessa [5], brill Scophthalmus rhombus [1]), four-bearded rockling Enchelyopus cimbrius (5), mackerel (1), Family blennidae (4), wrasse (family Labridae, seven species found in UK waters) (3), sand eel (1)</td>
</tr>
<tr>
<td>Amphibian</td>
<td>NA</td>
<td>15</td>
<td>24 (147)</td>
<td>Frog Rana temporaria (60), Toad Bufo spp (1), Newt Lissotriton spp (11) (in UK only L. vulgaris or L. helveticus)</td>
</tr>
<tr>
<td>Crustacean</td>
<td>NA</td>
<td>3</td>
<td>5 (28)</td>
<td>Crayfish (16), crab (4), mollusc (9) (not identified to species)</td>
</tr>
<tr>
<td>Mammal</td>
<td>NA</td>
<td>3</td>
<td>5 (32)</td>
<td>Common shrew Sorex araneus (2), water shrew Neomys fodiens (1), Sorex spp (4), rabbit Oryctolagus cuniculus (3), wood mouse Apodemus sylvaticus (2)</td>
</tr>
<tr>
<td>Bird</td>
<td>NA</td>
<td>3</td>
<td>5 (31)</td>
<td>Railidae (includes water rail Rallus aquaticus, moorhen Gallinula chloropus) and coot Fulica atra (4), also Anseriforme spp (diverse family of waterfowl, including ducks, geese, swans) (3)</td>
</tr>
<tr>
<td>Insect</td>
<td>NA</td>
<td>5</td>
<td>8 (47)</td>
<td>Diptera (true flies) (1), Dytiscus (diving beetle) (5), Odonata (includes dragonflies and damselflies) (3)</td>
</tr>
<tr>
<td>Other Fish</td>
<td></td>
<td></td>
<td></td>
<td>Percidae (18), stone loach (Barbatula barbatula) (14) and pike (Esox lucius) (3)</td>
</tr>
</tbody>
</table>
Appendix 1. Results of generalised additive models from Model Groups 1 and 2, both modelling the prevalence of empty stomachs. For Model Group 1, there was only one top model so a model averaging approach was not applied and the results displayed are for the single top model. Model Group 2 (females only) revealed that reproductive status was not an important predictor of empty stomachs (shown) so the remainder of the results for Model Group 2 are not shown. ¥ To be interpreted in interaction term.

| Model Group | Variable                      | Estimate | SE    | Z value | Pr(>|z|)   | Relative Variable importance |
|-------------|-------------------------------|----------|-------|---------|------------|-----------------------------|
| 1           | Age Class = Juvenile          | 5.63E+00 | 1.87E+00 | 3.01 | 0.00261 ** |                            |
| 1           | Age Class = Sub-adult         | 4.01E-01 | 6.12E-01 | 0.654 | 0.51296 |                            |
| 1           | Cause of death = Sudden       | -2.53E+00 | 8.45E-01 | -2.987 | 0.00282 ** | -                          |
| 1           | Cause of death = Unknown      | 2.86E+00 | 3.47E+00 | 0.825 | 0.40918 | -                          |
| 1           | Body condition                | 2.18E+01 ¥ | 9.84E+00 | 2.217 | 0.02663 * | -                          |
| 1           | Body length                   | 2.65E-02 ¥ | 9.59E-03 | 2.767 | 0.00566 ** | -                          |
| 1           | Distance from the coast       | -1.75E-05 | 7.22E-06 | -2.426 | 0.01528 * | -                          |
| 1           | Sex = Male                    | 1.92E+00 | 7.77E-01 | 2.477 | 0.01326 * | -                          |
| 1           | Year                          | 4.53E-01 | 1.75E-01 | 2.59 | 0.0096 ** | -                          |
| 1           | Body condition:Body length    | -2.40E-02 | 9.64E-03 | -2.494 | 0.01265 * | -                          |
| 2           | Reproduction status           | -         | -      | -      | -          | 0.4                         |
Appendix 2. Results of averaged generalised additive models from Model Groups 3 and 4, each model modelling the prevalence of a single prey type. Relative variable importance (RI) is shown for each variable, for each modelled prey type, significance (p) is indicated as: * (<0.05), ** (<0.01), *** (<0.001). Model Group 4 (females only) revealed that reproductive status was not an important predictor of the prevalence of prey types (although note that for some prey types [marked NA] models were not run due to small sample sizes when males were removed). The remainder of the variables for Model Group 4 are therefore not shown (e.g. age class, sex, etc) as these were all incorporated in model group 3.

<table>
<thead>
<tr>
<th>Model Group</th>
<th>Variable</th>
<th>Amphibian</th>
<th>Avian</th>
<th>Bullhead</th>
<th>Crustacean</th>
<th>Cyprinid</th>
<th>Eel</th>
<th>Insecta</th>
<th>Mammal</th>
<th>Marine</th>
<th>Salmonid</th>
<th>Stickleback</th>
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<tbody>
<tr>
<td>3</td>
<td>Age class</td>
<td>1</td>
<td>0.46</td>
<td>0</td>
<td>1</td>
<td>0.37</td>
<td>0.44</td>
<td>0.58</td>
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<td>0.1</td>
<td>0.75</td>
<td>0.09</td>
</tr>
<tr>
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<td>Sex</td>
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<td>0.19</td>
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<td>0</td>
<td>1</td>
<td>0.13</td>
<td>0.42</td>
<td>1</td>
<td>0.11</td>
<td>0</td>
<td>0.38</td>
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<tr>
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<td>0.71</td>
<td>0</td>
<td>1</td>
<td>0.65</td>
<td>1 (*)</td>
<td>0.68</td>
<td>1 (*)</td>
<td>0.29</td>
<td>1 (*)</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>Body length</td>
<td>1 (*)</td>
<td>0.14</td>
<td>1 (*)</td>
<td>1</td>
<td>0.39</td>
<td>0.5</td>
<td>0.46</td>
<td>0.43</td>
<td>0.11</td>
<td>1 (*)</td>
<td>0.89 (.)</td>
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<tr>
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<td>Sex:Age class</td>
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<td>0.06</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.13</td>
<td>0.35</td>
<td>1</td>
<td>0</td>
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<tr>
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<td>Sex:Body condition</td>
<td>0</td>
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<tr>
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<td>0.11</td>
<td>0.5 (*)</td>
<td>0.5</td>
<td>0.5</td>
<td>(**)</td>
<td>0.32</td>
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<td>0.6 (.)</td>
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<td>0</td>
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<td>0</td>
<td>1</td>
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<tr>
<td>3</td>
<td>Distance from coast</td>
<td>1 (+,**)</td>
<td>1 (-)</td>
<td>1 (***)</td>
<td>1</td>
<td>0.89</td>
<td>1 (***)</td>
<td>0.33</td>
<td>0</td>
<td>1 (*)</td>
<td>0</td>
<td>0.23</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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