The diet of spotted-necked otters foraging in trout-stocked waters in Mpumalanga, South Africa

Authors: Rowan K. Jordaan[1] (rowanjor@gmail.com) (Corresponding author)
Michael J. Somers[1, 2]
Grant Hall[1]
Trevor McIntyre[1, 3]

Affiliations: [1]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[2]Eugène Marais Chair of Wildlife Management, Centre for Invasion Biology, University of Pretoria, Pretoria, South Africa
[3]Department of Life and Consumer Sciences, University of South Africa, South Africa

Abstract

Human-wildlife conflict is likely to increase as urbanisation increases. African clawless otters, *Aonyx capensis*, and spotted-necked otters, *Hydrictis maculicollis*, are illegally persecuted for their perceived role in reducing trout in artificially stocked habitats in South Africa. The diet of African clawless otters has been investigated, but little is known about the diet of spotted-necked otters in these habitats. Using stable isotope techniques, we investigated the diet of spotted-necked otters occupying habitats artificially stocked with trout. Stable isotope analyses revealed that the diet of spotted-necked otters included equal proportions of crab and trout followed by frog. Diet was found to vary between, as well as within, individuals suggesting individual dietary plasticity. Temporal variation in foraging areas was evident for some otters. These results suggest that individual animals specialise on trout when available. However, this was not consistent between individuals. The resulting conflict with freshwater fisheries may, therefore, be primarily due to individual animals adapting to diets consisting largely of farmed trout. The extent of spotted-necked otter influence on stocked trout, however, needs further investigation.

Key words: Damages, fishery management, human-wildlife conflict, stable isotopes, trout

Introduction

As urbanisation increases and natural areas diminish in quantity and quality, human-wildlife conflict is likely to become more prevalent (Luck and Smallbone 2010). Human-wildlife conflict results in a variety of costs to humans. Some typical conflicts include the loss of livestock to various carnivores (Thirgood et al. 2005; Wang and Macdonald 2006; Holmern et al. 2007), crops and stored food to rodents and elephants, *Loxodonta africana* (Thouless 1994; Perez and Pacheco 2006) and the threat of predation by lions, *Panthera leo* (Packer et al. 2005). Lethal control is a common response by humans to conflict, but it can pose a threat to populations of the targeted species (Frank et al. 2006).

Conflict between fishermen and fish predators is prevalent worldwide. In particular, otters are considered to be one of the main fish predators and conflict has been recorded between fisherman and the Eurasian otter, *Lutra lutra*, at fish ponds in the Czech Republic, Poland and Portugal (Kloskowski 2011; Poledníková et al. 2013; Santos-Reis et al. 2013), and giant otters*, Pteronura brasiliensis* in Brazil (Rosas-Ribeiro et al. 2012). Similarly, in Africa, conflict between spotted-necked otters, *Hydrictis maculicollis*, and fishermen has been documented in Benin (Akpona et al. 2015). In South Africa, conflict exists between otters (both spotted-necked and African clawless otters, *Aonyx capensis*) and the fly-fishing tourism industry (de Vos 2018), and the presence of these otters in urban and peri-urban areas (Ponsonby and Schwaibold 2018) suggest likely continued conflict in the future. The fly-fishing tourism industry in South Africa developed following the introduction of Brown, *Salmo trutta*, and rainbow trout, *Oncorhynchus mykiss*, in 1890 and 1897, respectively (Cambray 2003). The growth of this industry lead to the establishment of numerous trout farms and has contributed significantly to the economic development of remote areas of South Africa (Hoogendoorn 2014). However, trout farms often exist at the expense of otters and other fish predators, which are illegally persecuted for foraging on trout (de Vos 2018).

The persecution of otters in South Africa takes place despite early evidence suggesting that invasive trout is a relatively unimportant prey species in the diets of both otter species (Butler and du Toit 1994; Rowe-Rowe 1977a). While more recent work suggests that African clawless otters do predate on trout in stocked waters, considerable inter-individual variation is evident in their diet, and not all otters in, and around, stocked waters predate trout (Jordaan et al. 2019).

African clawless otters occupy a wide range of coastal and freshwater habitats and are more abundant in waters that have few or no fish, but where crabs and frogs are abundant (Rowe-Rowe 1990; van Niekerk et al. 1998).

Spotted-necked otters are absent from coastal habitats typically occupying permanent freshwater bodies that support large populations of freshwater fish (Rowe-Rowe 1990; Lejeune and Frank 1990). Despite occupying fish abundant habitats, little is known about the diet of spotted-necked otters, particularly the prevalence of trout in their diet. Studies based on scat (spraint) analysis, suggest that spotted-necked otters include fish, crabs, frogs, birds, insects and molluscs in their diet (Rowe-Rowe 1977a; Kruuk and Goudswaard 1990; Lejeune 1990; Somers and Purves 1996). It has been suggested that spotted-necked otters are better adapted for fish capture when compared to the African clawless otter (Rowe-Rowe 1977a) and the diet of spotted-necked otters in areas that support large freshwater fish populations mostly comprises of fish (Kruuk and Goudswaard 1990). However, in areas where fish populations are low, their diet appears to be supplemented by crabs and frogs (Rowe-Rowe 1977a; Somers and Purves 1996). One study has suggested that trout are an unimportant prey species for spotted-necked otters in South Africa where otters feed primarily on crab in trout stocked waters (Rowe-Rowe 1977a). This same study suggested that temporal variation in diet was present for spotted-necked otters with more trout prevalent in the diet at the end of winter and crabs during spring, summer and autumn.

Many techniques have been used to infer the diets of predators, including the use of fatty acid signature analysis (e.g. Iverson et al. 1997; Hooker et al. 2001), gut content analysis (e.g. Norbury and Sanson 1992; Ford et al. 1998), direct observations (e.g. Ford et al. 1998; Somers 2000), and by bio-logging approaches (e.g. Tinker et al. 2007). Scat analysis is also commonly used (Angerbjörn et al. 1994; Gorgadze 2013; Day et al. 2015) and has been the most frequently used technique in African clawless (e.g. Somers and Nel 2003; Jordaan et al. 2015) and spotted-necked otter diet studies (e.g. Rowe-Rowe 1977a; Kruuk and Goudswaard 1990; Lejeune 1990; Somers and Purves 1996), despite its numerous shortcomings (Englund 1965; Jenkins et al. 1979; Carss and Parkinson 1996; Somers 2000; Emmerson and Philip 2004). Limitations aside, scat analysis remains a comparatively cost effective, simple and important means of determining carnivore diets when results are interpreted with suitable caution (Klare et al. 2011).

The analyses of stable isotope ratios (SIA) is a technique that overcomes many of the limitations associated with spraint analysis and has been used to investigate the diets and isotopic niches of various otter species (Angerbjörn et al. 1994; Grey 2001; Newsome et al. 2009; Carrasco et al. 2019; Jordaan et al. 2019). This method makes use of various animal tissues including bone collagen (Angerbjörn et al. 1994), red blood cells and blood plasma (Hilderbrand et al. 1996), muscle tissue (Grey 2001), teeth (Carrasco et al. 2019) and vibrissae (Lübcker et al. 2016; Lerner et al. 2018). The use of vibrissae is often favourable as they provide multiple data points providing a temporal component due to the slow growth rate of vibrissae and their constant nutrient assimilation (Lübcker et al. 2016).

We, therefore, applied SIA on sequentially sectioned vibrissae to determine the diet, as well as inter-individual and temporal variation in the diet of spotted-necked otters occupying an area of intensive trout farming. Since spotted-necked otters rely more on fish as a primary dietary component (Rowe-Rowe 1977a), the proportion of trout in the diet is of interest. Associated with their fish specialisation, we expected to find limited evidence for intra- or inter-individual differences in their diet.

Materials and Methods

Study Sites

Highlands Meander

The Highlands Meander region (Fig. 1) lies in the higher reaches of the South African escarpment and is comprised of numerous rivers that have been dammed at intervals to provide year-round recreational fishing as part of the fly-fishing tourism industry. This area includes the towns of Belfast, Dullstroom, Machadodorp, Lydenburg and Waterval-Bovan and has the largest concentration of stocked trout dams and rivers in South Africa (approximately 1200) (KPMG 1999). Conflict between farmers/anglers and otters (amongst other trout predators) are evident (Jordaan pers. obs.).

Millstream Farm (25.4520° S, 30.0919° E) is a fly-fishing farm near Dullstroom and consists of numerous weirs along the Witpoort River, runoff filled dams, and a large lake filled by the river and dam overflow. Fly-fishing is the main activity of holidaymakers that frequent the area, and the dams and weirs are stocked year-round with rainbow trout of varying weights (minimum = ±250g) (de Vos 2018). Natural vegetation including large reed beds (*Phragmites spp.*) surrounds the lake, dams and weirs. *Escherichia coli* bacteria levels are high in the lake and river as a result of pollution by upstream sewage works, while dams have lower levels of *E. coli* as they are fed by ground- and rainwater (Millstream staff pers. comm.).

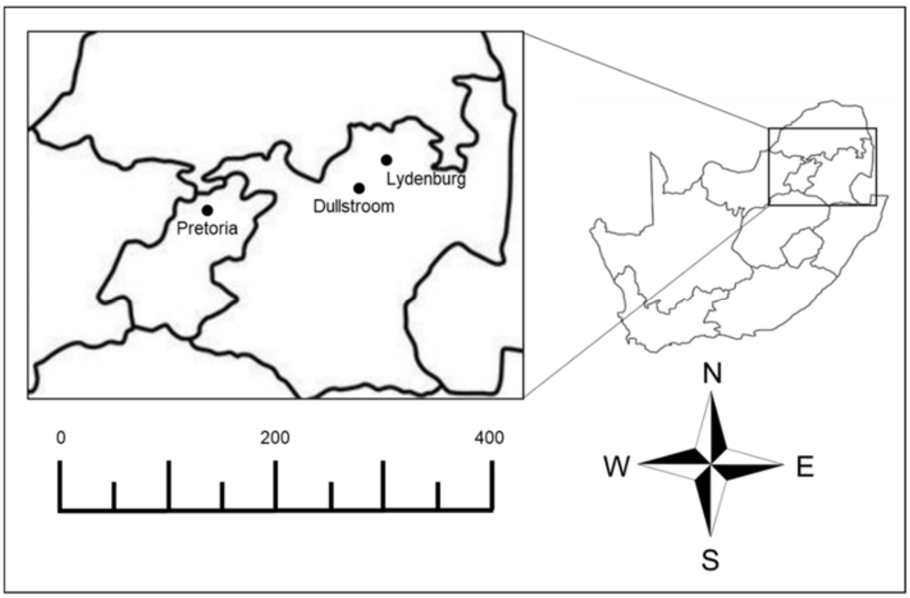

Figure 1. The study area (Highlands Meander) located in the Mpumalanga province of South Africa. The insert represents the location of the study area in relation to the rest of South Africa (dark shading) and southern Africa.

Sampling Procedure

We collected three vibrissae at Millstream Farm after spotted-necked otters were captured in baited carnivore cage traps intended for African clawless otters (see Jordaan et al. 2019 for details). These traps (1.5m x 0.7m x 0.8m) were baited with fresh African clawless otter spraints and trout and placed at suitable locations within Millstream Farm (e.g. latrine sites, holts, well used pathways, etc.). Traps were set overnight and checked at sunrise. Captured spotted-necked otters were coaxed from the trap into a custom designed funnel made from expanded metal. This funnel was attached to the cage after capture and reduced the space available to the otter. Once in the funnel and mobility was limited, a single vibrissa was plucked using a pair of long-nosed pliers, the sex of the otter was determined, and the otter was released. An additional vibrissae sample from a male otter at a trout farm outside Lydenburg (approx. 55km from Millstream Farm) was obtained from local parks board officials (Mpumalanga Tourism and Parks Authority (MTPA)). All samples are summarised in Table 1. All field research was done with permission from the University of Pretoria Animal Ethics Committee (project number: EC034-15).

At Millstream Farm, potential dietary items identified from previous studies (Rowe-Rowe 1997a; Somers and Purves 1996) were sampled and frozen. Prey items were collected using different techniques, including angling (fly fishing) for trout capture, rock flipping for crab and frog capture and stick baiting for crab capture. .

Crabs collected were separated into two groups namely "crab1", originating from waters connected to the river system (i.e. weirs); and "crab2" originating from waters separated from the river system (i.e. dams). Crabs were separated into these two sub-populations per source since pollution levels are known to differ between the two systems (Millstream management team pers. comm.). The differences in pollution levels have resulted in notable variation in the $\delta^{13}C$ and $\delta^{15}N$ ratios of these crabs due to the effect pollution has on basal isotopic ratios (Table 2). The remaining prey items did not show any variation between the two systems and were therefore not separated in the analyses.

Isotope analysis

All samples were processed and analysed for $\delta^{13}C$ and $\delta^{15}N$ at the Stable Isotope Laboratory located in the Mammal Research Institute, University of Pretoria, South Africa. Vibrissae were rinsed with a 2:1 chloroform: methanol solution to remove any surface contaminants (as described by Newsome et al. 2009), placed in an Ultrasonic Bath (Branson 1200, Branson Ultrasonics, Danbury, U.S.A.) for 5 min before being dried at 70^{o}C for 48 hours. To obtain sequential isotopic ratios, cleaned vibrissae were subsampled, with the use of a scalpel, into approximately 0.4 mg segments and sealed into toluene cleaned tin capsules for analysis.

Prey items were prepared for analysis by removing their soft and edible muscle tissue and drying this in an oven (Labotec Oven Dryer Model 323, Labotec, Midrand, South Africa). Once dried, this tissue was homogenised with a mortar and pestle. Lipids in the homogenised samples were removed by rinsing the samples in a 2:1 chloroform: methanol solution. Lipids were removed since they are depleted in $\delta^{13}C$ when compared to other compounds and therefore yield inaccurate results (O'Leary 1981). Approximately 0.5 mg of rinsed sample was weighed into tin capsules. The samples were combusted at 1020°C in an elemental analyser (Flash EA, 1112 Series, Thermo™, Thermo Fisher Scientific) and $\delta^{13}C$ and $\delta^{15}N$ isotope values were determined with the use of a continuous-flow isotope ratio mass spectrometer (Delta V Plus, Thermo Finnigan). Results are presented using standard delta notation in parts per thousand (‰) relative to an international standard: Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 (Air) for $\delta^{15}N$ (Coplen 1994).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios were used in this study because measures of $\delta^{13}C$ ratios can be used to understand the foraging zones and habitat preferences of study animals (Kelly 2000). This is possible due to differences in photosynthetic pathways (i.e. C3, C4, CAM) of the vegetation within those habitats (Farquhar et al. 1989). Nitrogen isotope ratios were used as they provide insight into the trophic position and diet composition of the consumer due to the enrichment of ^{15}N relative to ^{14}N at each step in the trophic level (De Niro and Epstein 1981; Minagawa and Wada 1984; Hobson and Welch 1992).

Data analyses

To infer the diet of spotted-necked otters, SIMMR (Stable Isotope Mixing Model in R), a stable isotope mixing model (Parnell 2016) was used in the R environment (R Core Team 2018). SIMMR uses a Bayesian framework and discrimination factors to solve mixing models for stable isotope data and estimate the source (prey) proportions that make up the diet. Vibrissae trophic discrimination factors for spotted-necked otters have not been determined, so 'standard' discrimination factors commonly used for carnivores and southern sea otters were used instead (Newsome et al. 2009; Newsome et al. 2010). The trophic discrimination factors used were 2.2‰ for carbon and 3.5‰ for nitrogen, along with standard deviations of 0.7‰ and 0.6‰ for carbon and nitrogen, respectively (Newsome et al. 2010). The mean $\delta^{13}C$, $\delta^{15}N$ and C/N ratios for all vibrissae and potential prey samples collected are summarised in Tables 1 and 2.

Table 1. Overall vibrissae length, mean δ13C, δ15N and C/N ratios and sex of spotted-necked otters (SE in parenthesis) from the Highlands Meander. Sample size (n) refers to the number of segments that were sampled from each vibrissa.

Individual	n	Length (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C/N	Sex	Location
SN1	7	3.8	-16.87 (0.10)	13.81 (0.44)	3.68 (0.06)	M	Millstream Farm
SN2	5	3.2	-19.78 (0.31)	11.40 (0.26)	3.60 (0.03)	M	Lydenburg
SN3	7	3.7	-16.15 (0.06)	10.31 (0.28)	3.75 (0.03)	F	Millstream Farm
SN4	4	3.7	-15.26 (0.21)	12.77 (0.53)	3.75 (0.02)	F	Millstream Farm
Mean (SE)	5.75	3.6	-17.01 (1.95)	12.07 (1.53)	3.70 (0.07)		

Table 2. Mean δ13C, δ15N and C/N ratio values of likely prey species collected at Millstream Farm (SE in parenthesis) in the Highlands Meander. Some groups comprise of several species. Additional parentheses indicate the location prey was collected (R = River and D = Dams).

Group name	Common name	Species name	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C/N	Location
Crab1 (R)	River Crab	*Potamonautes spp.*	11	-17.67 (0.22)	21.28 (0.98)	4.02 (0.04)	Millstream Farm
Crab1 (D)	River Crab	*Potamonautes spp.*	10	-20.84 (0.47)	7.23 (0.36)	4.28 (0.09)	Lydenburg
Trout	Rainbow Trout	*Oncorhynchus mykiss*	24	-17.56 (0.19)	7.05 (0.16)	4.11 (0.06)	Millstream Farm
Frog	Common River Frog	*Amietia angolensis*	3	-20.51 (1.13)	5.50 (0.83)	4.29 (0.04)	Millstream Farm
Fish	Various	*Barbus spp.*	6	-15.32 (0.75)	18.90 (0.15)	4.10 (0.03)	

Prey categories were grouped for analyses due to the similarity of taxa and their economic importance (i.e. trout was separated from other fish before samples were taken. Separation was based on distinctive morphological characteristic differences between species). More detail on these groups and the prey species within them are reported in Table 2. Time series line-graphs were drawn up in Microsoft Excel (2013) where both the carbon and nitrogen isotope values of each vibrissa were plotted to visualise individual isotopic variation over time and variation between individuals.

Results

In total, four spotted-necked otter vibrissae and 54 prey samples from four taxa were collected between April 2015 and May 2016. The details of the vibrissae and prey species collected are summarised in Table 1 and 2, respectively.

The sequential plotting of $\delta^{13}C$ and $\delta^{15}N$ values for each segmented vibrissa showed variation between individuals as well as variation within individuals (Fig. 2). When moving from the tip to the base of the vibrissa for SN1, $\delta^{13}C$ values remained stable while $\delta^{15}N$ values were initially stable before they increased (Fig. 2A). SN2 had $\delta^{13}C$ values that gradually increased while $\delta^{15}N$ values were stable before they dip fractionally (Fig. 2B). The $\delta^{13}C$ values of SN3 remained stable while the $\delta^{15}N$ values gradually decreased (Fig. 2C). Lastly, SN4 had $\delta^{13}C$ values that remained stable and $\delta^{15}N$ values that were also stable before decreasing gradually (Fig. 2D).

Overall, mean percentages of prey that make up the diet of spotted-necked otters are modelled to be: crab = 34.68% ± 19.55% (Crab1 = 8.75% ± 4.65%, Crab2 = 25.93% ± 14.9%), Trout = 34.95% ± 14.6%, Fish = 8.83% ± 5.2% and Frog = 21.5% ± 14.85%. Figure 3 shows that the highest mean proportions of trout are found in the diet of SN3 (58.3% ± 14.5%) and SN4 (47.6% ± 19.5%). The highest mean proportions of crab from dams (Crab2) are found in SN2 (49.3% ± 26.2%) and SN1 (28.2% ± 13%) and the highest proportion of crab from the river (Crab1) is found in the diet of SN1 (16.5% ± 6.6%). Frog appears in the diet of all otters with mean proportions between 15.7% and 26.2% while fish appears greatest in the diets of SN4 (13.8% ± 8.0%) and SN1 (12.5% ± 6.7%) and less prominently in the diets of SN2 (5.4% ± 3.3%) and SN3 (3.6% ± 2.9%). All vibrissae have isotopic values that fall into the isotopic space created by the freshwater prey species in the bivariate plot with SN1, SN3 and SN4 clustered close to one another while SN2 is clustered away from the rest (Fig. 4).

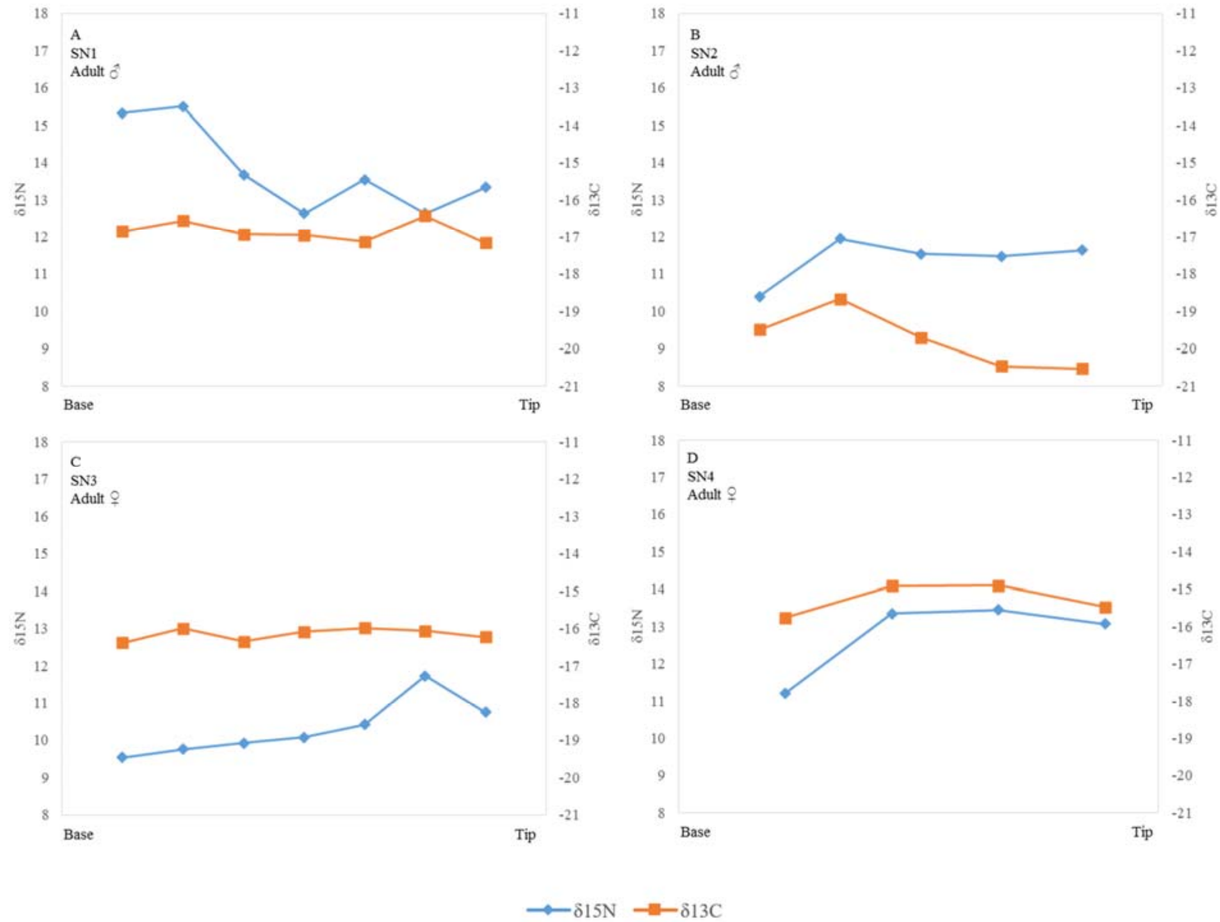

Figure 2. The $\delta^{13}C$ and $\delta^{15}N$ ratios in sequential vibrissae segments obtained from four spotted-necked otters in the Highlands Meander. Otters reflected here are SN1-SN4 (A-D respectively), and additional information such as sex and age class is displayed in each plot. Base and tip denote the orientation of the vibrissae. The tip of the vibrissae represents the oldest growth while the base represents more recent growth.

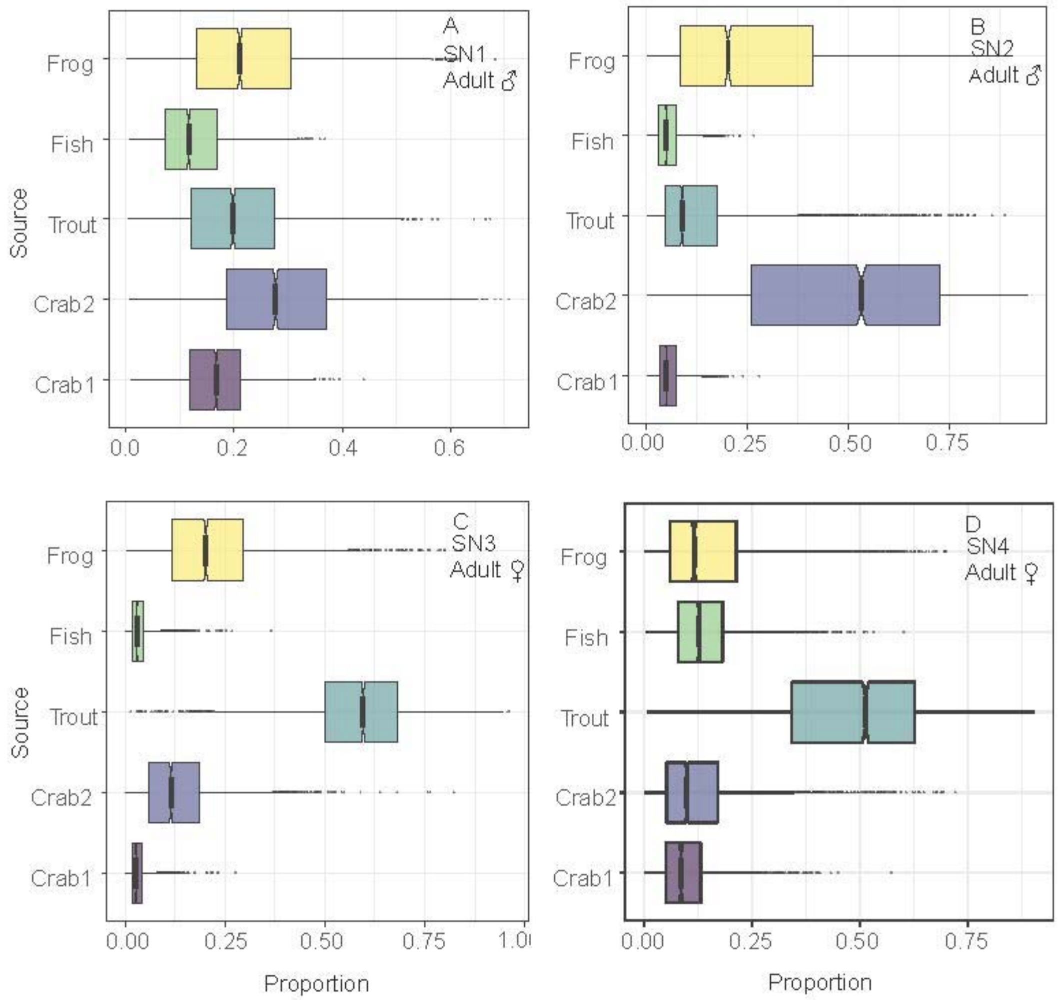

Figure 3. The proposed dietary contribution of potential prey species for four spotted-necked otters from the Highlands Meander. Details on otter ID, sex and age class are displayed in each plot. Otters reflected here are SN1-SN4 (A-D respectively). Contributions were obtained through the analysis of otter and potential prey isotopic values in SIMMR. Box lines represent the 25th, 50th (median), and 75th percentiles.

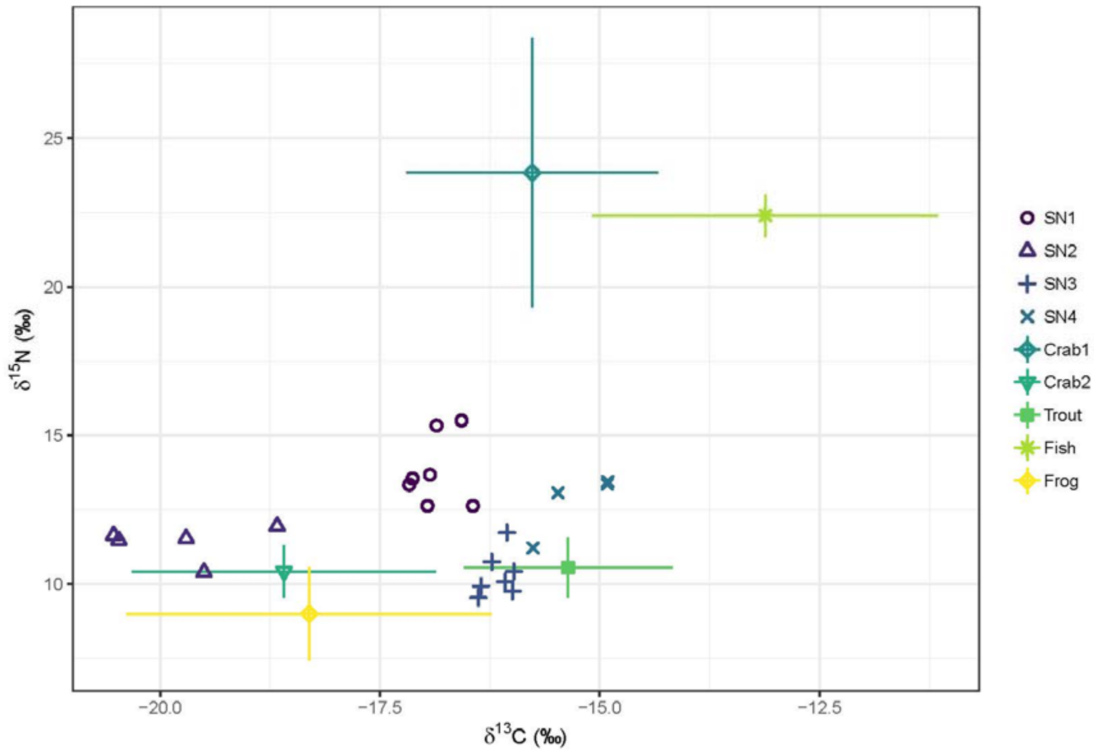

Figure 4. Bivariate isotopic space showing four spotted-necked otters and their potential prey species in the Highlands Meander. The isotopic space that is occupied by potential prey species is displayed as coloured cross-hairs. Otter isotopic values are displayed as various symbols and were obtained from sequential analysis of vibrissae (hence the occurrence of replicas of the same symbol). More detailed information on the prey proportions that make up potential diet (Fig. 3) and time sequence (Fig. 2) are also shown. Details regarding the colour and symbol allocated to each prey species or otter can be found in the key.

Discussion

The overall estimated mean percentages of prey in the diet of spotted-necked otters foraging in and around trout-stocked waters suggests that crab and trout are equally important, followed by frogs. This suggests that trout is more important in the diet of these otters than previously suggested (Rowe-Rowe 1977a). At an individual level, crab dominated the diet of two otters while trout dominated the diet of the other two (Fig. 3). The diet of SN1 and SN4 contained similar proportions of crab1 and crab2, suggesting movement between different foraging systems. These results are not unexpected as a crab dominated diet and temporal dietary variation have previously been found in South African trout waters (Rowe-Rowe 1977a). The remainder of spotted-necked otter diet is made up of frogs (Fig. 3) suggesting that, when compared to African clawless otters, spotted-necked otters feed on more mobile prey that are hunted by sight and caught with the mouth (Rowe-Rowe 1977b; Skinner and Smithers 1990; Nel and Somers 2013; Jordaan et al. 2019).

Due to the small sample size and the limited number of segments obtained in each vibrissa, it is difficult to attribute differences in diet to seasonal differences in prey availability. Seasonal variation in diet is however, thought to result from the inaccessibility of crabs and the reduced locomotion ability of non-trout fish spp. in winter months (Rowe-Rowe 1977a).

Trout mobility would, however, be greatest during winter months when water temperature is at its coldest, while during the summer months, mobility would likely be reduced when water temperature is at its warmest. These changes in water temperature would make trout more difficult and easier to catch in winter and summer respectively (Jonsson and Jonsson 2009). The seemingly high proportion of trout and low proportion of crab in the diet of some otters suggests that these otters can exploit trout, despite their increased mobility, possibly through different foraging strategies.

Although the findings we report here highlight how useful stable isotope techniques are when compared to spraint analysis and other traditional methods, they also illustrate some limitations. The first limitation is that vibrissae samples were not all collected at the same location during the same period. This complicates direct comparisons as a result of non-uniform distribution of otter and prey species (Fry and Wainright 1991; Hemminga and Mateo 1996). Since our prey sampling approach was not exhaustive, it is also possible that not all potential prey items were sampled. However, our prey samples are suggested to appropriately represent the prey items based on prey items previously recorded for spotted-necked otters (e.g. Rowe-Rowe 1977a; Kruuk and Goudswaard 1990; Somers and Purves 1996). Many of these limitations are overcome by our choice of stable isotope mixing model (SIMMR). The SIMMR accounts well for the underdetermination of potential resources and natural variations in stable isotope compositions of prey and consumers through isomeric log-ratio transformation and non-parametric smoothing relationships (Phillips and Greg 2003; Moore and Semmens 2008; Parnell et al. 2010).

In conclusion, the results presented here illustrate intra- and inter-individual dietary variation in spotted-necked otters in the Highlands Meander. These differences can be due to differences in the available prey base and suggest substantial dietary plasticity in this species. These results provide more information on the diet of this understudied small carnivore and suggest that individual animals may show a level of dietary specialisation on trout when available. This is not consistent between individuals and suggests that conflict with freshwater fisheries may be largely due to individual animals adapting to diets consisting largely of farmed trout. Additionally, stable isotope analyses have proved to be a good method to determine intraspecific dietary variation. These results hold implications for the management of stock losses on such properties. However, further investigations on the likely effectiveness and impacts of targeted management actions are required to inform both management and conservation practitioners.

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References

Akpona AH, Djagoun CAMS, Harrington LA, Kabré AT, Mensah GA, Sinsin B. 2015. Conflict between spotted-necked otters and fishermen in Hlan River, Benin. *Journal for Nature Conservation* 27: 63-71.

Angerbjörn A, Hersteinsson P, Lidén K, Nelson E. 1994. Dietary variation in arctic foxes (*Alopex lagopus*) – an analysis of stable carbon isotopes. *Oecologia* 99: 226-232.

Butler JRA, Du Toit JT. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* 24: 41-47.

Cambray JA. 2003. The global impact of alien trout species – a review; with reference to their impact in South Africa. *Journal of Aquatic Sciences* 28: 61-67.

Carrasco TS, Botta S, Machado R, Simões-Lopes PC, Carvalho-Junior O, Ott PH, Colares EP, Secchi ER. 2019. Isotopic niche of the Neotropical otter, *Lontra longicaudis* (Carnivora, Mustelidae), in different coastal aquatic systems in southern Brazil. *Hydrobiologia* 835: 83-100.

Carss DN, Parkinson SG. 1996. Errors associated with otter *Lutra lutra* faecal analysis in assessing general diet from spraints. *Journal of Zoology, London* 238: 301-307.

Coplen TB. 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure and Applied Chemistry* 66: 273-276.

Day CC, Westover MD, McMillan BR. 2015. Seasonal diet of the northern river otter (*Lontra canadensis*): What drives prey selection? *Canadian Journal of Zoology* 93: 197-205.

De Niro MJ, Epstein,S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341-351.

de Vos M. 2018. Human-predator conflict in the South African fly-fishing industry: fish survival probabilities and stakeholder perceptions. MSc dissertation. University of Pretoria, South Africa.

Emmerson W, Philip S. 2004. Diets of Cape clawless otters at two South African coastal localities. *African Zoology* 39: 201-210.

Englund J. 1965. Studies on the food ecology of the Red fox *(Vulpes vulpes)* in Sweden. *Viltrevy* 3: 377-484.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. In: Briggs WR (ed) *Annual review of plant physiology and plant molecular biology, vol 40*. Annual Reviews, Palo Alto, pp 503-538.

Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76: 1456-1471.

Frank L, Hemson G, Kushnir H, Packer C. 2006. Lions, conflict and conservation in Eastern and Southern Africa. In: *Eastern and Southern African Lion Conservation Workshop*. Johannesburg: IUCN.

Fry B, Wainright SC. 1991. Diatom sources of carbon-13 rich carbon in marine food webs. *Marine Ecology Progress Series* 76: 149-157.

Gorgadze G. 2013. Seasonal diet of the otter (*Lutra lutra*) on the Alazani River (Georgia). *Hystrix* 24: 157-160.

Grey J. 2001. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen *Ecology of Freshwater Fish* 10: 168-176.

Hemminga MA, Mateo MA. 1996. Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. *Marine Ecology Progress Series* 140: 285-298.

Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74: 2080-2088.

Hobson KA, Welch HE. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{l3}C$ and $\delta^{l5}N$ analysis. *Marine Ecology Progress Series* 84: 9-18.

Holmern T, Nyahongo J, Røskaft E. 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation* 135: 518-526.

Hoogendoorn G. 2014. Mapping fly-Fishing Tourism in Southern Africa. *African Journal of Hospitality, Tourism and Leisure* 3: 1-13.

Hooker SK, Iverson SJ, Ostrom P, Smith SC. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable isotope analyses of biopsy samples. *Canadian Journal of Zoology* 79: 1442-1454.

Iverson SJ, Frost KJ, Lowry LF. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine Ecology Progress Series* 151: 255-271.

Jenkins D, Walker JGW, McCowan D. 1979. Analysis of otter *(Lurra lutra)* faeces from Deeside, N.E. Scotland. *Journal of Zoology, London* 187: 235-244.

Jonsson B, Jonsson N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* 75: 2381-2447.

Jordaan RK, McIntyre T, Somers MJ, Bester MN. 2015. An assessment of spatial and temporal variation in the diet of Cape clawless otters (*Aonyx capensis*) in marine environments. *African Journal of Wildlife Research* 45: 342-353.

Jordaan RK, Somers MJ, Hall G, McIntyre T. 2019. Plasticity and specialisation in the isotopic niche of African clawless otters foraging in marine and freshwater habitats. *Mammalian Biology* 98: 61-72.

Kelly JF. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1-27.

Klare U, Kamler JF, McDonald DW. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Reviews* 41: 294-312.

Kloskowski J. 2011. Human–wildlife conflicts at pond fisheries in eastern Poland: perceptions and management of wildlife damage. *European Journal of Wildlife Research* 57: 295-304.

KPMG. 1999. Mpumalanga tourism growth plan. Unpublished report. Nelspruit: Mpumalanga Tourism Authority.

Kruuk H, Goudswaard PC. 1990. Effects of changes in fish populations in Lake Victoria on the food of otters *(Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology* 28: 322-329.

Lejeune A. 1990. Ecologie alimentaire de la loutre (*Hydrictis rnuculicollis*) au lac Muhazi. *Mammalia* 54: 33-45.

Lejeune A, Frank V. 1990. Distribution of *Lutra maculicollis* in Rwanda: Ecological constraints *IUCN Otter Specialist Group Bulletin* 5: 8-16.

Lerner JE, Ono K, Hernandez KM, Runstadler JA, Puryear WB, Polito MJ. 2018. Evaluating the use of stable isotope analysis to infer the feeding ecology of a growing US gray seal (*Halichoerus grypus*) population. *PLoS ONE* 13:e0192241.

Lübcker N, Condit R, Beltran RS, de Bruyn PJN, Bester MN. 2016. Vibrissal growth parameters of southern elephant seals *Mirounga leonina*: obtaining fine-scale, time-based stable isotope data. *Marine Ecology Progress Series* 559: 243-255.

Luck GW, Smallbone L. 2010. Species diversity in urban landscapes: patterns, drivers and implecations. In: Gaston K (ed), *Urban Ecology*. Cambridge University Press. pp. 88-119.

Minagawa M, Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* 48: 1135-1140.

Moore JW, Semmens BX. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters* 11: 470-480.

Nel JAJ, Somers MJ. 2013. Family Mustelidae, subfamily Lutrinae – Otters. In: Kingdon J, Happold J, Butynski D, Hoffmann T, Happold M, Kalina J (eds), *Mammals of Africa*, Volume 5. United Kingdom, London: Bloomsbury Publishing. pp. 102-118.

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90: 961-974.

Newsome SD, Bentall GB, Tinker MT, Oftedal OT, Ralls K, Estes JA, Fogel ML. 2010. Variation in $\delta^{13}C$ and $\delta^{15}N$ diet-vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications* 20: 1744-1752.

Norbury GL, Sanson GD. 1992. Problems with measuring diet selection of terrestrial, mammalian herbivores. *Australian Journal of Ecology* 17: 1-7.

O'Leary MH. 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20: 553-567.

Packer C, Ikanda D, Kissui B, Kushnir H. 2005. Lion attacks on humans in Tanzania. *Nature* 436: 927-928.

Parnell AC, Inger R, Bearhop S, Jackson AL. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5: e9672.

Parnell A. 2016. SIMMR: A Stable Isotope Mixing Model. R package version 0.3.

Perez E, Pacheco LF. 2006. Damage by large mammals to subsistence crops within a protected area in a montane forest of Bolivia. *Crop Protection* 25: 933-939.

Phillips DL, Gregg JW. 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologi*a 136: 261-269.

Poledníková K, Kranz A, Poledník L, Myšiak J. 2013. Otters Causing Conflicts. In: Klenke R, Ring I, Kranz A, Jepsen N, Rauschmayer F, Henle K (eds), *Human - Wildlife Conflicts in Europe. Environmental Science and Engineering (Environmental Engineering*). Berlin, Heidelberg: Springer.

Ponsonby DW, Schwaibold U. 2018. Country otter, city otter: The distribution patterns of two otter species in an urbanized area of Gauteng, South Africa. *African Journal of Ecology* 57: 148–154.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosas-Ribeiro PF, Rosas FCW, Zuanon J. 2012. Conflict between Fishermen and Giant Otters *Pteronura brasiliensis* in Western Brazilian Amazon. *Biotropica* 44: 437-444.

Rowe-Rowe DT. 1977a. Food ecology of otters in Natal, South Africa. *Oikos* 28: 210-219.

Rowe-Rowe DT. 1977b. Variation in the predatory behaviour of the clawless otter. *Lammergeyer* 23: 22-27.

Rowe-Rowe DT. 1990. Otter Distribution and Protection in South Africa. *IUCN Otter Specialist Group Bulletin* 5: 17- 23.

Santos-Reis M, Santos R, Antunes P, Sales-Luís T, Gomes J, Freitas D, Madruga L. 2013. Reconciliation of the Conflict Between Otters and Fish Farmers. In: Klenke R, Ring I, Kranz A, Jepsen N, Rauschmayer F, Henle K (eds), *Human - Wildlife Conflicts in Europe. Environmental Science and Engineering (Environmental Engineering)*. Berlin, Heidelberg: Springer.

Skinner D, Smithers HN. 1990. *The Mammals of the Southern African Sub region*. University of Pretoria, Pretoria.

Somers MJ. 2000. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* 35: 261-268.

Somers MJ, Purves MG. 1996. Trophic overlap between three semi-aquatic carnivores: Cape clawless otter, spotted-necked otter and water mongoose. *African Journal of Ecology* 34: 158-166.

Somers MJ, Nel JAJ. 2003. Diet in relation to prey of Cape clawless otters in two South African rivers. *African Zoology* 38: 317-326.

Thirgood S, Woodroffe R, Rabinowitz A. 2005. The impact of human–wildlife conflict on human lives and livelihoods. In: Woodroffe R, Thirgood S, Rabinowitz A (eds), *People and wildlife: conflict or coexistence?* Cambridge: Cambridge University Press. pp. 13–26.

Tinker MT, Costa DP, Estes JA, Wieringa N. 2007. Individual dietary specialization and dive behaviour in the California sea otter: Using archival time-depth data to detect alternative foraging strategies. *Deep-Sea Research Part II: Topical Studies in Oceanography* 54: 330-342.

Thouless CR. 1994. Conflict between humans and elephants on private land in northern Kenya. *Oryx* 28: 119-127.

van Niekerk CH, Somers MJ, Nel JAJ. 1998. Freshwater availability and distribution of Cape clawless otter spraints and resting places along the south-west coast of South Africa. *South African Journal of Wildlife Research* 28: 68-72.

Wang SW, Macdonald DW. 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation* 129: 558-565.