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Effects of prey size on scat analysis to determine river otter *Lontra* canadensis diet

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We conducted a controlled feeding trial using two captive river otters *Lontra canadensis* to determine how prey size may introduce bias into frequency of occurrence analysis using otter scats. Otters were fed specific prey across a range of sizes. We then collected all scats deposited by the otters to determine how many defecation events occurred to remove the prey item from the digestive system. We found a strong, positive relationship between prey item size and the number of scats required to excrete the item. We then examined how the results, of an actual river otter feeding habits study using frequency of occurrence analysis of scats, could be biased towards an over-representation of larger prey items by using a correction factor for prey item size developed from our feeding trials. Frequency of occurrence suggested a strong preference for mid-range size of prey items and a strong avoidance of smaller prey items. Our corrected results indicated that otters exhibit little preferential feeding based on prey item size in the Missouri Ozarks. Our results suggest that bias associated with frequency of occurrence analyses may severely limit the robustness of inferences that can be made from such analyses.

Key words: feeding habits, frequency of occurrence, Lontra canadensis, prey size, river otter, scat analysis

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Dietary studies are critical for understanding animal ecology and conserving animal populations (Martin et al. 1961, Litvaitis et al. 1996, Litvaitis 2000). Such studies are increasingly based on the identification of prey remains found in scats, especially in studies of carnivore diets (Reynolds & Aebischer 1991, Hewitt & Robbins 1996, Browne et al. 2002). Many alternative methods for assessing feeding habits exist including direct observations of foraging (e.g. Bielefeldt et al. 1992), examination of stomach contents (e.g. Perez & Bigg 1986), and stable isotope analysis (e.g. McFadden et al. 2006). Litvaitis (2000)

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highlighted many of the advantages and disadvantages for several of these methods. Its non-destructive nature often makes scat analyses preferable to studies of gastrointestinal tracts, and its low cost and logistical ease make it an appealing method to many biologists. Scat analyses are also recommended because of their comparability to previous studies (van Dikj et al. 2007). However, it is important to note that these considerations do not account for accuracy or reliability of the method. Scat analyses have been commonly used to assess food habits in several mustelid species, including mink *Mustela vison* (Ferreras & Macdonald 1999, Bartoszewicz & Zalewski 2003), American marten *Martes americana* (Bull 2000), and river otters *Lontra canadensis* (Pardini 1998, Crait & Ben-David 2006).

Most scat-based diet studies quantify dietary composition based on frequency of occurrence, and is expressed as the proportion of scats collected which contain a particular species (Trites & Joy 2005). The issues associated with estimating food habits from frequency of occurrence analyses have been addressed by previous researchers (Litvaitis et al. 1996). Most of this research has focused on the differential digestibility of specific previtems, or the relative importance of certain prey items based on biomass remains (Floyd et al. 1978, Dickman & Huang 1988). Several comparisons of frequency of occurrence to other methods have been made. For example, Mersmann & Buehler (1992) found that frequency of occurrence analysis of bald eagle Haliaeetus leucocephalus scats vielded highly biased results compared to direct observations. However, in a study of wolverine Gulo gulo diet, van Dijk et al. (2007) found that frequency of occurrence analysis performed better than several other methods in a controlled setting.

River otters are the apex predator in many aquatic systems in North America, therefore understanding their functional role in these systems is critical for proper management (Melquist et al. 2003). Studies of otter feeding habits have been conducted throughout North America, yielding great regional variation (Gilbert & Nancekivell 1982, Anderson & Woolf 1987, Reid et al. 1994). Many studies that have assessed river otter feeding habits have been based on frequency of occurrence analysis of scats (e.g. Crait & Ben-David 2006, Roberts et al. 2009). However, little information exists on biases that may be associated with frequency of occurrence analyses for river otter diets derived from scat samples. Our objectives were to determine: 1) if the size of a prey item affects the number of scats in which it could be found, and 2) how this relationship could affect the results in the frequency of occurrence analysis of food habits in river otters.

Material and methods

Feeding trials

We used two captive river otters legally owned by a private citizen to conduct controlled feeding trials. Both river otters were adult animals in good physical condition which were primarily used for public outreach events sponsored by the Missouri Department of Conservation. Both otters were housed in a small $(<100 \text{ m}^2)$ semi-natural enclosure. One day prior to each feeding trial, their normal ground-beef based diet was withheld and their enclosures were cleaned of all remnant scat. On five occasions, each otter was fed one smallmouth bass Micropterus dolomieu of known length (10-18 cm) and allowed to completely digest and excrete the fish (N = 10 trials). We recorded the number of scats excreted by each otter for 24 hours after consuming the fish that contained identifiable remains, during which time the study animals were not given any additional food. The small size of the enclosures facilitated the collection of all scats with minimal probability that any scats were not located.

Example data

In order to assess how prey item size may influence the results of feeding habits studies, we used an existing data set containing 4,750 river otter scats collected in southern Missouri during 2001-2002 (Roberts et al. 2009). Scats were collected from the Big Piney River and Osage Fork of the Gasconade River in the winter (January-March) and summer (June-August), along 30 randomly selected 0.4 km survey sections of each river. Frequency of occurrence analysis was conducted using diagnostic materials extracted from scats (e.g. fish scales, reptile bones and bird feathers), and these materials were used to identify prey species. Once located, fish scales were pressed on acetate plates and the impressions were viewed using a microfiche reader. Scale morphometric characteristics were used to determine species (Roberts et al. 2007). Fish age was determined using annulus counts. For this study, we focused only on the frequency of occurrence and age estimates for smallmouth bass remains.

Data analysis

We examined the relationship between smallmouth bass length and the number of scats in which remains were found during our feeding trials using simple regression analysis. This model allowed us to predict the number of scats in which a smallmouth bass of known mass could be found (Fig. 1). We then used standard growth models developed by Jackson et al. (2008) to estimate the length of smallmouth bass recovered in otter scats as a function of age, which were based on samples collected throughout North America, and thus represented a general yet plau-

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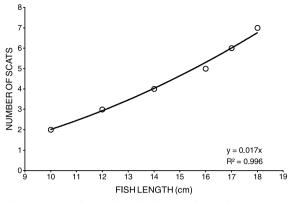


Figure 1. Regression model estimating number of river otter scats deposited as a function of fish length (in cm). Points at length 10 cm and 12 cm each represent three points with the same value (N = 10 total).

sible relationship between smallmouth bass age and length in our study area. We then combined the standard growth equation of Jackson et al. (2008), which allowed us to estimate mass of smallmouth bass based on age, with our regression model. This allowed us to estimate the number of otter scats in which we could expect to find remains of a smallmouth bass of a known age using the following equation:

$$N_i = \frac{n_i}{0.0177 \times (498.6 \times [1 - e^{-0.229(i - 0.141)}])^{2.0566}}$$

where N_i is the actual number of smallmouth bass consumed in age class i, and n_i is the number of scats containing smallmouth bass remains of age class i.

We used this equation as a correction factor in our frequency of occurrence analysis. We based our frequency of occurrence analysis on the assumption that each sample containing smallmouth bass remains represented a single fish. Such assumptions are common in frequency of occurrence analyses. Of the 4,750 scats collected, 261 contained remains of smallmouth bass that could be assigned to a specific age class (Table 1), thus we assumed this to represent 261 fish consumed. We then applied our correction

Table 1. Total numbers (N) of river otter scats containing smallmouth bass remains according to age class.

Age	Ν	% of total
0	3	1.2
1	45	17.2
2	71	27.2
3	94	36.0
4	37	14.2
5	8	3.1
6	3	1.2

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factor to these results to create a size-adjusted estimate of the minimum number of fish consumed in each age class. We then compared the resulting estimated smallmouth bass age class distributions from the frequency of occurrence analysis and our sizecorrected estimate to the observed age class distribution in our study area (Missouri Department of Conservation, unpubl. data). In this case, the age class distributions from frequency of occurrence and our size correction represented estimated age distributions of consumed fish, whereas the observed distribution represented the true age class distribution of the prey population. We calculated Pearson's correlation coefficient between estimated and observed age distributions as an overall measure of departure between age distributions of consumed and available fish.

Results

There was a very strong relationship between fish length and the number of scats deposited during our feeding trials despite our relatively small sample size (see Fig. 1). There was minimal variability in the results of our feeding trials, indicating a stable relationship between prey item size and digestive capabilities. The number of scats required to excrete a prey item increased by approximately 250% for every 50% increase in prey item length (see Fig. 1). When correcting for size-based bias using our correction factor, the estimated age distribution of smallmouth

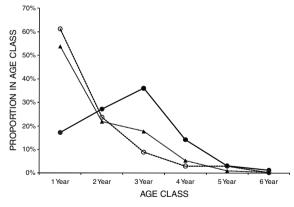


Figure 2. Observed age class distribution $(- - - \blacktriangle - -)$, estimated age class distributions from frequency of occurrence analysis $(-- \diamondsuit)$, and size-corrected scat analysis $(- \cdot \bigcirc -)$. Estimated distributions from scat analyses represent percentages of prey consumed in each age class. Observed distribution represents age class distribution of available prey population from electrofishing surveys.

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bass consumed by otters closely matched their availability. Conversely, estimated age distributions of smallmouth bass consumed based on frequency of occurrence analysis indicated that otters consumed a much higher number of 3-5 year old fish than available (Fig. 2). Correlation was substantially higher between corrected age distributions and observed age distributions (r = 0.983) than between age distributions estimated from frequency of occurrence and observed age distributions (r = 0.287).

Discussion

Dietary investigations of carnivores are often prompted by interest in the potential predation of a single taxa of interest; examples include river otter predation of sportfish (Roberts et al. 2009), coyotes Canis latrans predation of deer Odocoileus spp. (S. Crimmins, unpubl. data), and wolf *Canis lupus* predation of livestock (Chavez & Gese 2005). Scats provide a convenient and relatively assessable sampling unit from which to characterize the diet of a given species. Diets are often analyzed using frequency of occurrence analyses due to an uncomplicated methodology, computational ease and simple interpretation (Litvaitis 2000). However, this method is recognized as being subject to several sources of bias that can influence its results (van Dijk et al. 2007). Despite this, little research has been conducted to identify potential solutions to these sources of bias. Fundamental to describing an organism's diet from indirect observations, such as scats, is appreciating and quantifying sources of sampling bias.

Controlled feeding studies of captive animals have been used to assess accuracy of dietary analyses for a variety of carnivorous and piscivorous species including wolverine (van Dijk et al. 2007) and harbour seals Phoca vitulina (Cottrell et al. 1996). Our study is, to our knowledge, the only study to conduct controlled feeding trials of captive river otters. Although our feeding trials did not account for scat deposition rates when multiple prey items were consumed, the observed positive relationship between prey item size and the number of scats in which it could be detected would likely remain. Our results indicate a clear prey-size specific bias associated with the frequency of occurrence analysis of river otter scat. By applying a correction weight to account for the observed bias to the results of a previous study (Roberts et al. 2009), we demonstrated that the interpretation of results regarding prey selectivity can be dramatically different from naïve estimates based on frequency of occurrence. In fact, the limited range of prey sizes used in our feeding trials indicates that bias from frequency of occurrence analysis would be even greater in situations where larger prey items were consumed. Although the scats used in our frequency of occurrence analysis were collected across multiple seasons, the age ratios of smallmouth bass remains were similar across seasons and sites, meaning that the trend in estimated age ratios across seasons would be similar. Most carnivores consume a variety of prey that range considerably in size. Given this, it is reasonable to assume that the inherent difficulties with frequency of occurrence analysis are not limited by prey taxa. If researchers desire to more accurately quantify overall dietary patterns using scat analysis, correction factors would need to be developed for several prey species (Rühe et al. 2008). We suggest that researchers should acknowledge the potential of prey-size specific bias when employing frequency of occurrence derived diet analysis and, preferably, attempt to quantify and correct for these biases. Previous research has indicated that other factors can influence the results of scat-based dietary studies including total meal size (Marcus et al. 1998), specific prey remains recovered (Cottrell et al. 1996), level of digestion (Tollit et al. 1997), and specific analysis technique (van Dijk et al. 2007). When considered along with our results, studies such as these suggest that caution should be used when conducting frequency of occurrence analysis to determine dietary composition.

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