Wildlife Society Bulletin 43(4):651–660; 2019; DOI: 10.1002/wsb.1021

Original Article

Comparing Methods of Estimating Carnivore Diets with Uncertainty and Imperfect Detection

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ABSTRACT Carnivore diet-selection studies based on scat analyses are frequently used to elucidate predator ecology, predict potential effects on prey populations, and inform management decisions. However, accuracy of results and the following inference are contingent on multiple sources of sampling error including missed detections and pseudoreplication in statistical comparisons that assume independence within scat samples. We compared a repeated-sampling occupancy framework intended to estimate detection and occurrence rates for diet items with a multinomial modeling approach intended to estimate diet selection while accounting for nonindependence of diet items within samples. Both methods allowed for multimodel inference to specifically test hypotheses about differences in diet. We applied each method to 2 example data sets, a bobcat (*Lynx rufus*) scat data set ($n = 101$) collected in western Virginia, USA, from 2011 to 2013 with morphological identification of diet items, and a coyote (*Canis latrans*) scat data set ($n = 50$) collected in Tooele County, Utah, USA, in 2014 with molecular identification of diet items, and compared results with those commonly implemented in diet studies (frequency of occurrence calculations). We found imperfect detection of diet items was not a major source of bias in either the morphological or molecular data set results, but grouping similar or indistinguishable diet items in the morphological data set affected estimates when there was heterogeneity in detection among items. Using the occupancy approach on the morphological data set demonstrated that presence or amount of some diet items could decrease detection of other items and bias occurrence estimates. Furthermore, comparing multiple models of bobcat diet using Akaike's Information Criterion with either approach revealed no support for seasonal differences, even though traditional frequency of occurrence calculations differed by almost 10%. Thus, we suggest even moderate trends in diet based on frequency of occurrence calculations without incorporating measures of uncertainty may represent sampling error, and not true differences in diet. When detection is not conditional on other diet items, comparison of multinomial models will typically be sufficient to make accurate inference about carnivore diets without requiring additional processing of scat samples.

KEY WORDS bobcat, capture–mark–recapture, carnivore diet, coyote, frequency of occurrence, molecular diet analysis, morphological diet analysis, multinomial models, occupancy, scat analysis.

Diet studies are useful approaches for evaluating wildlife resource requirements (Carbone et al. 1999), niche partitioning among competitors (Breuer 2005, Vieira and Port 2007), and potential effects to prey populations and other natural resources (Allen and Leung 2012, Latham et al. 2013). As such, many methods exist to elucidate patterns in diet including direct observation; examination of stomach, scat, or pellet contents; or analysis of stable isotopes from animal hair or fatty acid signatures (Putman 1984, Iverson et al. 2004, Dalerum and Angerbjörn 2005, Azevedo et al. 2006, Monterroso et al. 2019). Collection and analysis of scats for diet selection studies is noninvasive, can result in large sample sizes, and be relatively inexpensive. As a result, scat analysis is the most commonly utilized method for carnivore diet assessment (Klare et al. 2011). However, there are multiple potential sources of sampling error and bias when using scats to analyze carnivore diet selection. Ultimately, the effectiveness of management and conservation actions based on the findings of diet studies are

Received: 13 September 2018; Accepted: 29 June 2019
Published: 06 November 2019

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contingent on the sampling design, methods of analysis, and inference and interpretation of dietary metrics.

Sampling error and misinterpretation in scat-collection–based diet studies can occur at 4 different steps in the process. Firstly, there is inherent sampling error in the collection of scats from a study area (Reynolds and Aebischer 1991). In most studies, we assume that the scats represent an independent sampling of all available diet items in accurate proportions. However, sampling intensity, study area extent, and resolution of scat collection activities will influence the number of samples, number of individuals sampled, and proportional contribution of each sampled individual to the final diet metrics (Trites and Joy 2005, Byerly et al. 2017). Ideally, a study is designed to minimize these potential sources of error, although adequate sample sizes and individual contributions to diet samples are rarely considered (Reynolds and Aebischer 1991, Trites and Joy 2005).

Secondly, once samples are collected, error and bias may be introduced through misidentification of the predator species (Reed et al. 2004, Monterroso et al. 2013, Lonsinger et al. 2015*b*, Morin et al. 2016*a*). Implications for this type of error have been well-studied and can depend on the number and size of sympatric carnivores, amount of dietary overlap, and the proportional representation of each species in the local carnivore community (Farrell et al. 2000, Prugh and Ritland 2005). Increasing use of molecular identification of predator scats in diet studies can reduce the bias introduced from this source of error (McVey et al. 2013; Monterroso et al. 2013, 2019; Morin et al. 2016*a*; Byerly et al. 2017).

Thirdly, there may be errors in how we find, identify, and quantify diet items found in scat (Spaulding et al. 2000). Not all diet items within a scat sample may be detected equally (Casper et al. 2007, Balestrieri et al. 2011, Mumma et al. 2015, Gosselin et al. 2017). In traditional diet analysis where remains are washed and visually identified, diet item representation in a scat can be influenced by digestibility, which can result in unobserved presences (false negatives) and inaccurate relative proportions of prey consumed. Accuracy can also be affected by identifiability of diet items, which is typically handled by grouping prey into categories based on taxonomy (Morin et al. 2016*a*). Using molecular methods to identify prey DNA within scat samples can improve upon visual identification methods (Casper et al. 2007, Gosselin et al. 2017), but can present other errors in detection (Mumma et al. 2015).

Lastly, interpretation and inference from diet study data may not acknowledge limitations of sampling (Klare et al. 2011). Diet studies typically report deterministic metrics including frequency of occurrence (i.e., the percent of scat samples in which a diet item is found; Pianka 1974) and relative percent occurrence of diet items (i.e., contribution proportional to all diet items detected; Pianka 1974), or dietary niche breadth (based on relative percent occurrence; Levins 1968) without acknowledging stochasticity in the sampling process. In addition, diet metrics are often compared using frequentist statistical tests that assume independence among diet items and samples, which is clearly violated because multiple diet items occur in multiple scats that are then considered repeatedly as independent samples (Thomas and Taylor 1990, Lemons et al. 2010). Thus, resulting diet metrics may be unreliable and result in subjective interpretation because they are deterministic, do not account for bias in diet item detection, do not fully express the uncertainty in estimates as a result of sampling error, and are often compared using statistical tests resulting in pseudoreplication (Hurlbert 1984). The relative contribution of each source of error to overall diet estimation and inference is unknown.

There is a rich history of methodologies accounting for imperfect detection in species distributions and population parameters (Seber 1965, Otis et al. 1978, MacKenzie et al. 2002). These methods use repeated sampling of the same sites or populations to estimate detection and correct for biases in raw counts or presence-only data, and can be readily applied to scat-based diet studies if scat samples are considered sites and repeatedly sampled to estimate detection of diet items. Alternatively, maximum likelihood methods for estimation using multinomial data already exist in the capture–recapture literature and can be applied to scat-based diet studies to account for nonindependence of samples—in this case, multiple diet items within the same scat sample (Lemons et al. 2010).

We compared 2 approaches for estimating diet selection from scat-based studies, a novel occupancy-based approach and a multinomial modeling approach. We selected 2 data sets that each used a different methodology for identifying diet items in scat samples (visual identification of diet items and molecular identification of diet items). The occupancy framework implements repeated-sampling of each scat sample to estimate diet item occupancy while accounting for imperfect detection (MacKenzie et al. 2002). The multinomial modeling approach (implemented in a closed population capture–mark–recapture framework) estimates the proportional occurrence of diet items in a species' diet while accounting for nonindependence of diet items within samples (Lemons et al. 2010). Using the occupancy approach allows comparisons of competing hypotheses about trends in diet, including seasonal differences, or tests of whether the presence of some diet items might obscure detection of other diet items. The multinomial modeling approach also allows for comparison of competing hypotheses about differences in diet while accounting for nonindependence of diet items within samples, but, in this application, does not account for imperfect detection (only exploits the multinomial modeling framework available in the capture–mark–recapture Program MARK; White and Burnham 1999). We compared both approaches to traditional calculations of frequency of occurrence based only on detected diet items (Pianka 1974).

We hypothesized some diet items such as white-tailed deer (*Odocoileus virginianus;* deer) could obscure the detection of other similar diet items (other mammal hair). We expected the occupancy-based approach would perform better than other methods if imperfect detection of diet items was a substantial source of error in quantifying diet selection, but that multinomial approaches would produce

similar results if it was not. We used our findings to suggest the possible extent of bias and misinterpretation of results, and identify study objectives and circumstances for which each method may be most appropriate.

STUDY AREA

We used 2 existing carnivore diet data sets (a morphological diet data set and a molecular diet data set) to compare different methods of diet estimation. The morphological diet data set consisted of a random subset of 101 bobcat (*Lynx rufus*) scats collected as part of a larger carnivore study in the Ridge and Valley province of the central Appalachian Mountains in Bath and Rockingham counties, Virginia, USA (described in detail in Morin et al. 2016*a*, *b;* 2018). The land-cover was primarily even-aged forests consisting of chestnut oak (*Quercus montana*), red oak (*Q. rubra*), white oak (*Q. alba*), tulip poplar (*Liriodendron tulipifera*), rhododendron (*Rhododendron maximum*), and eastern mountain laurel (*Kalmia latifolia*). Elevation ranged from 350 m to 1,365 m, temperature ranged from a mean minimum of −5° C in January to a mean maximum of 32° C in July, and annual precipitation was approximately 98 cm (National Oceanic and Atmospheric Administration, public data 2012, https://www.noaa.gov/climate). The molecular diet data set consisted of a subset of 50 coyote (*Canis latrans*) scats collected as part of a larger canid study at the U.S. Army Dugway Proving Ground in the Great Basin Desert of western Utah, USA (described in detail in Lonsinger et al. 2017, 2018). The study area was characterized by low-lying basins separated by abrupt range formations with an elevational range of approximately 1,200–2,100 m (Arjo et al. 2007). Temperature ranged from a mean minimum of 0° C in January to a mean maximum of 36° C in July, and average annual precipitation was approximately 20 cm (Arjo et al. 2007).

METHODS

Sample Collection and Laboratory Methods

Morphological diet analysis.—We collected carnivore scats for the morphological diet analysis from 16 established 5-km transects in western Virginia from June 2011 to May 2013. We collected a 0.5-mL sample from each scat for molecular identification of the carnivore. The remainder of the sample was collected for morphological diet analysis, stored in a plastic bag and frozen at −20° C. We identified bobcat scats using a mtDNA species-identification multiplex (De Barba et al. 2014; described in Morin et al. 2018). Bobcat scats represented >50% of the carnivore scats collected in the study area, in addition to coyotes and black bears (*Ursus americanus;* Morin et al. 2016*a*).

For morphological diet analysis, we thawed samples and divided each scat into 5 approximately equally sized subsamples. We analyzed each subsample for contents separately following methods described in Morin et al. (2016*a*). We included 22 diet items (unique species or groups of species) found in bobcat scats in the diet analyses, including deer, rabbits (*Sylvilagus* spp.), rodents, soft and hard mast seeds, insects, grass, birds, and reptiles (Table 1).

Molecular diet analysis.—We collected carnivore scats for the molecular diet analysis from January to March 2014 along 270 km of randomly selected transects established to monitor canid occupancy and density (Lonsinger et al. 2017, 2018). We measured diameter, length, and number of disjoint segments, then sampled approximately 0.5 mL of fecal material from the side of each scat for molecular identification of the carnivore; the remainder of the scat was collected and stored frozen at −20° C (Gosselin et al. 2017). We distinguished coyote scats from sympatric wild and domestic carnivores using a mtDNA species-identification test (De Barba et al. 2014; described in Lonsinger et al. 2015*b*).

We then identified coyote scats of similar size, thawed scats, and collected 4 additional fecal samples of approximately 0.5 mL; we collected one sample from each end, one from the center, and one from the side, as well as a homogenized sample that consisted of equal parts from the side, center, and ends (Gosselin et al. 2017). We conducted a morphological diet analysis on each coyote scat following procedures of Byerly et al. (2017) to identify 25 scats with, and 25 scats without, morphological detection of leporid (rabbit) prey, designed to allow for a balanced comparison of morphological and molecular detection of diet items in a previous study (Gosselin et al. 2017). For each of the 50 scats, we analyzed each fecal sample separately for the presence of leporid mtDNA using a multiplex designed to identify 6 leporid species: mountain (*S. nuttallii*) or desert cottontails (*S. aududonii*), eastern cottontails (*S. floridanus*), black-tailed jackrabbits (*Lepus californicus*), white-tailed jackrabbits (*L. townsendii*), and pygmy rabbits (*Brachylagus idahoensis;* Adams et al. 2011, Gosselin et al. 2017).

We expected each of the cottontail species, black-tailed jackrabbits, and potentially pygmy rabbits to be present within the study extent, though we did not detect pygmy rabbits (Gosselin et al. 2017). Each scat and fecal sample represented primary and secondary sampling occasions in the occupancy modeling framework, respectively. We stored all fecal samples in DETS buffer (20% DMSO, 0.25 M EDTA, 100 mM Tris, pH7.5, and NaCl to saturation; Seutin et al. 1991). All DNA extraction methods, polymerase chain reaction (PCR) conditions and procedures, and scoring are detailed in Gosselin et al. (2017).

Methods of Diet Estimation

Diet item occupancy.—We estimated detection and probability of occurrence (occupancy rate) for each identified species and taxon, for both the morphological and molecular diet data sets. For the morphological diet data set, we used the 5 subsamples to construct a detection history for each scat, similar to repeatedly sampling the same location in site occupancy studies (MacKenzie et al. 2002). Occupancy in this case is the occurrence of a diet item in a scat, and detection of the diet item is estimated by the repeated sampling to allow for estimation of the probability a diet item occurred in a sample when it was

Table 1. Frequency of occurrence calculations compared with estimates using an occupancy modeling approach (accounting for imperfect detection) and a closed capture–recapture approach (accounting for nonindependence within samples) for morphological and molecular diet analyses. The morphological data set consisted of 101 bobcat scat samples collected on standardized transects from June 2011 to May 2013 in Bath and Rockingham counties, Virginia, USA. The molecular data set included 50 coyote scat samples collected on standardized transects from January to March 2014 in Tooele County, Utah, USA. For the occupancy modeling approach, species were considered separately when identifiable, or grouped by taxon as is common in many diet studies. In the morphological data set, we considered support for the presence and count of subsamples containing white-tailed deer remains as covariates in detection model structures within the species candidate sets using Akaike's Information Criterion (AIC_c). For the capture–mark–recapture (CMR) approach, we considered the 3 lagomorph species as separate diet items in the molecular data set, but grouped by taxonomy in the morphological data set because of the unwieldy number of parameters required to consider all species separately.

Diet analysis type	Diet item	Diet item grouping	Frequency of occurrence (naïve detection)[a]	CMR estimate (95% CI)	Detection (95% CI)	Occupancy (95% CI)	Occupancy accounting for deer (95% CI)
Morphological	*Odocoileus virginianus*		0.42 (0.79)	0.42 (0.32–0.51)	0.79 (0.73–0.84)	0.42 (0.32–0.51)	NA
	Sylvilagus spp.		0.20 (0.84)	0.20 (0.13–0.29)	0.84 (0.75–0.90)	0.20 (0.13–0.29)	count: 0.24 (0.15–0.35)
	Sciurus spp.	squirrels	0.45 (0.75)		0.75 (0.69–0.80)	0.45 (0.35–0.54)	count: 0.58 (0.47–0.70)
	Tamias striatus	squirrels	0.17 (0.45)		0.42 (0.31–0.54)	0.18 (0.11–0.27)	count: 0.24 (0.15–0.37)
	Glaucomys spp.	squirrels	0.01 (0.60)		0.59 (0.19–0.90)	0.01 (0.00–0.07)	NA
		squirrels	0.48 (0.79)	0.47 (0.38–0.57)	0.75 (0.69–0.80)	0.48 (0.38–0.57)	count: 0.63 (0.51–0.74)
	Myodes gapperi	voles	0.17 (0.55)		0.54 (0.43–0.65)	0.17 (0.11–0.30	NA
	Microtus spp.	voles	0.32 (0.80)		0.80 (0.73–0.86)	0.32 (0.23–0.41)	presence: 0.32 (0.24–0.42)
		voles	0.40 (0.83)	0.40 (0.31–0.49)	0.80 (0.74–0.85)	0.40 (0.31–0.49)	presence: 0.40 (0.31–0.50)
	Zapus hudsonius	mice and rats	0.02 (0.40)		0.36 (0.11–0.71)	0.02 (0.01–0.09)	NA
	Napaeozapus insignis	mice and rats	0.02 (0.20)		NA[b]	NA[b]	NA
	Reithrodontomys spp.	mice and rats	0.10 (0.44)		0.41 (0.27–0.57)	0.11 (0.06–0.19)	NA
	Sigmodon hispidus	mice and rats	0.14 (0.31)		0.23 (0.13–0.38)	0.19 (0.10–0.32)	NA
		mice and rats	0.26 (0.48)	0.26 (0.18–0.35)	0.32 (0.23–0.43)	0.30 (0.21–0.41)	NA
	Ondatra zibethicus		0.01 (0.60)	0.01 (0.001–0.07)	NA[b]	NA[b]	NA
	Blarina brevicauda		0.01 (1.00)	0.01 (0.001–0.07)	1.00	0.01 (0.001–0.07)	NA
	unknown mammal		0.89 (0.59)	0.90 (0.81–0.94)	0.58 (0.54–0.63)	0.90 (0.82–0.94)	presence: 0.90 (0.82–0.95)
	Amelanchier arborea	soft mast	0.01 (0.20)		NA	NA	NA
	Lonicera morrowii	soft mast	0.02 (0.30)		0.20 (0.03–0.66)	0.03 (0.01–0.14)	NA
	Acer spp.	soft mast	0.09 (0.36)		0.29 (0.16–0.47)	0.11 (0.05–0.20)	presence: 0.13 (0.07–0.27)
	unknown seeds	soft mast	0.23 (0.34)		0.27 (0.18–0.38)	0.29 (0.19–0.42)	presence: 0.28 (0.19–0.40)
		soft mast	0.29 (0.50)	0.29 (0.21–0.38)	0.36 (0.27–0.45)	0.32 (0.23–0.43)	count: 0.38 (0.26–0.61)
	grass		0.40 (0.53)	0.40 (0.31–0.49)	0.51 (0.44–0.58)	0.41 (0.31–0.51)	NA
	insect		0.26 (0.35)	0.26 (0.18–0.35)	0.28 (0.19–0.38)	0.32 (0.22–0.44)	NA
	bird		0.15 (0.60)	0.15 (0.09–0.23)	0.59 (0.47–0.70)	0.15 (0.09–0.24)	count: 0.16 (0.10–0.25)
	reptile		0.09 (0.56)	0.09 (0.05–0.16)	0.55 (0.39–0.69)	0.09 (0.05–0.17)	count: 0.10 (0.05–0.19)
Molecular	*Lepus californicus*	rabbits	0.20 (0.40)	0.19 (0.10–0.35)	0.36 (0.22–0.52)	0.23 (0.12–0.38)	NA
	Sylvilagus audubonii	rabbits	0.68 (0.53)	0.66 (0.36–0.86)	0.52 (0.44–0.59)	0.70 (0.55–0.81)	NA
	Sylvilagus floridanus	rabbits	0.04 (0.20)	0.04 (0.01–0.15)	NA[b]	NA[b]	NA
		rabbits	0.76 (0.52)	NA[c]	0.51 (0.43–0.58)	0.78 (0.64–0.88)	NA

[a] Scat samples commonly contain multiple diet items; therefore, frequency of occurrence for all diet items and groupings often sums to >100%. Naïve detection is the number of subsamples a diet sample was identified in divided by the total number of subsamples within a sample.
[b] Unable to estimate because of small sample size.
[c] Not estimated at the grouping scale.

not detected. There were 26 occupancy model sets in the morphological data set (17 for diet items identified at the species- or genus-level and 9 for taxonomic groupings).

To demonstrate the utility of multimodel inference for inferring trends in diet, we compared 4 models representing hypothesized differences in bobcat consumption of deer over time. Assuming detection was imperfect but consistently so ($p(\cdot)$), we compared models where deer occupancy in bobcat diet was consistent over time ($\psi(\cdot)$), differed by month (ψ(month)), different when deer fawns were most available during the fawn least-mobility period (Apr, May, and Jun: ψ(LMP)), or different during peak hunting season when scavenging was expected to be greatest (Oct, Nov, Dec: ψ(hunting)). We compared models using Akaike's Information Criterion corrected for small sample size (AIC_c) to assess support for each competing model and make inference about patterns in deer occurrence in bobcat scats.

Additionally, deer were the most common species detected and represented the largest biomass in predator scats in the study area (Morin et al. 2016*a*); therefore, we hypothesized the presence of deer hair might hinder detection of other species, especially those also commonly identified by hair samples. Thus, for remaining species and taxa in the morphological data set, we estimated consistent diet item occupancy $\psi(\cdot)$ and compared that null model with models estimating a difference in detection based on 1) presence of deer hair (p(presence)) or 2) number of subsamples of a sample in which deer hair was present (p(count)). We selected scat samples for the molecular data set to create a balanced design for a previous methodological comparison and not for inference about any biological hypotheses (detailed in Gosselin et al. 2017). Thus, for the molecular data set, we used the 5 subsamples to construct a detection history for each scat and estimated occupancy of each of the 3 leporid species in coyote diet and for leporids as a group using the null model ($\psi(\cdot)p(\cdot)$).

Multinomial modeling of diet.—The multinomial modeling approach considers the presence and absence of each diet item as multinomial data and uses the Huggins closed-capture, capture–mark–recapture model in Program MARK to estimate probability of occurrence as the detection probability (White and Burnham 1999, Lemons et al. 2010). In this case, we considered each scat an "individual" and each potential diet item an encounter occasion, indicating with a 1 if an item occurred in any of the subsamples for a scat and a 0 if it was not detected in that scat.

Each diet item was considered an occasion in this framework, so we fit a "time"-dependent model to allow for estimation of probability of occurrence for each diet item (modeled with probability of "initial detection" and probability of "recapture" equivalent because there would be no trap response). Thus, in this approach, detection is the probability of a diet item occurring in a predator scat, and not an estimate of how often an item is detected. The resulting occurrence rate estimates and 95% confidence intervals allow for assessment of differences in estimated frequency of occurrence among diet groups (as would comparison with a null detection model). For the morphological diet data set, we also compared models constraining samples into groups by month, least-mobility period for deer fawns, and hunting seasons to test for evidence of seasonal differences in bobcat diet. We fit multinomial models using RMark, a wrapper package for Program MARK (White and Burnham 1999, Laake 2013).

Frequency of occurrence calculations.—We calculated frequency of occurrence as the number of whole samples in which a diet item or grouping was present divided by the total number of samples (Pianka 1974). Scat samples commonly contain multiple diet items, so frequency of occurrence for all diet items and groupings often sum to >100%. We also calculated frequency of occurrence by month and season for white-tailed deer for comparison with the 2 diet estimation approaches detailed above. Finally, we calculated naïve detection as the number of subsamples with the diet item present divided by total number of subsamples to compare with detection rates using the occupancy framework.

RESULTS

The multinomial model and occupancy estimates of probability of occurrence tracked closely with the traditional frequency of occurrence calculations for both data sets (Table 1). There were differences in detection estimates across species for both the morphological and molecular data sets, but detection estimates from occupancy models for each species were similar to naïve detection rates. However, when we grouped diet items in the morphological data set such as soft mast, insects, or mice and rats, heterogeneity in species-specific detection rates resulted in slight differences in frequency of occurrence estimates compared with traditional calculations. Conversely, detection and occupancy estimates for the 3 leporid species in the molecular data set were unaffected by grouping the 3 species together.

In the morphological data set, there was support for inclusion of presence or count of deer detections in a sample as a detection covariate for rabbits, *Sciurus* spp., eastern chipmunks (*Tamias striatus*), a grouping of all squirrels (including *Sciurus* spp., eastern chipmunks, and *Glaucomys* spp.), voles, unknown mammal, soft mast, bird, and reptile (Supporting Information, available online). Accounting for an effect of deer detection in these models resulted in slight decrease in detection estimates and greater estimates of probability of occurrence for rabbits, *Sciurus* spp. and eastern chipmunks, and soft mast (Table 1; Fig. 1).

Although there was temporal variability in the monthly and seasonal traditional frequency of occurrence calculations, neither the closed-capture multinomial model nor occupancy model set showed support for a monthly or seasonal difference in probability of deer occurrence in the morphological data set (Table 2). The null model (consistent diet item occupancy across samples) was ranked highest for candidate sets for both approaches, providing no evidence deer consumption changed over the time periods evaluated. There was a model in the occupancy candidate set with $\Delta AIC_c < 2$, suggesting a decrease in deer

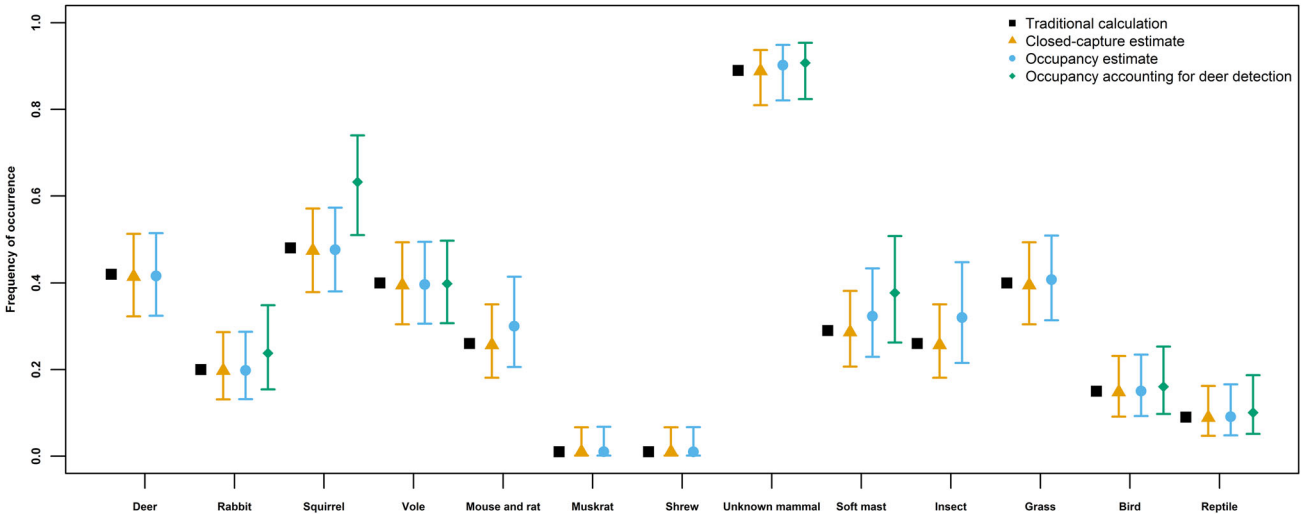

Figure 1. Comparison of frequency of occurrence estimates for grouped diet items found in bobcat scats collected on standardized transects from June 2011 to May 2013 in Bath and Rockingham counties, Virginia, USA. Diet items were identified visually based on morphological features. Frequency of occurrence was calculated as the number of scats a diet item was found in divided by the total number of scats (traditional) and estimated using a closed-capture multinomial modeling approach and an occupancy framework. Within the occupancy framework, detection was held constant or included the presence or number of subsamples white-tailed deer (deer) remains were detected in as a covariate on detection. Estimates accounting for an effect of deer remains on detection of a diet item are only included if there was support for those models over the null detection model based on Akaike's Information Criterion (AIC_c). Error bars represent 95% confidence intervals.

occurrence during fawn least-mobility period compared with other months. However, this model contains an additional parameter compared with the higher ranked null model and does not sufficiently improve the negative log-likelihood to be considered a competing model (Arnold 2010).

DISCUSSION

Our results suggested that imperfect detection of diet items is not a substantial source of error in studies using scat to estimate carnivore diet. Estimates of diet item occupancy and the multinomial model estimates of diet item occurrence were similar to the traditional frequency of occurrence calculations for both the morphological and molecular diet data sets. However, we were able to identify potential biases in the morphological data analysis that demonstrated the need for thoughtful consideration when grouping species and when the presence of some species may obscure the detection of others. Additionally, both the occupancy and closed-capture multinomial model approaches represent an improvement over frequency of occurrence calculations. These estimation approaches accounted for uncertainty in point estimates and provided a framework to assess possible differences in diet among groups of samples, whereas interpreting differences in traditional calculations is subjective or subject to issues of pseudoreplication.

Typically, in morphological diet analysis, diet items are grouped based on inconclusive taxonomic identifications or for ecological reasons such as by guild (Klare et al. 2011). For example, although dental occlusal patterns allow for species- or genus-level identification, small mammal species are commonly grouped to allow for equivalent comparison to taxa that are less easily identified by undigested remains, such as birds or reptiles (Athreya et al. 2016, Morin et al. 2016*a*, du Preez et al. 2017). Grouping diet items is also used to facilitate inference about predator diet. For example, Lagos and Barcena (2018) suggested gray wolves (*Canis lupus*) in the northwestern Iberian Peninsula selected wild

Table 2. Akaike's Information Criterion (AIC_c) table for 4 competing hypotheses about temporal differences in bobcat diet. For occupancy models, detection was fit as constant (i.e., p(null)), while occupancy (ψ) of white-tailed deer remains was fit as constant over time (null) or constrained to be different depending on month or season including least mobility period for fawns (LMP; Apr–Jun) or peak hunting season (Oct–Dec). For closed-capture multinomial models, all diet items are included in the analysis and detection is fit as a temporal model (p(t) = c(t)) with each "occasion" representing a diet item. Scat samples were collected on standardized transects from June 2011 to May 2013 in Bath and Rockingham counties, Virginia, USA. Deer remains were identified visually based on morphological features.

Approach	Model	ΔAIC_c	Model AIC_c weight	No. of parameters
Occupancy	ψ(null) p(null)	0.00	0.497	2
	ψ(LMP) p(null)	1.38	0.249	3
	ψ(hunting season) p(null)	2.12	0.172	3
	ψ(month) p(null)	3.61	0.082	13
Capture–recapture	p(null)	0.00	0.96	22
	p(LMP)	6.24	0.04	44
	p(hunting season)	24.38	<0.01	44
	p(month)	308.81	<0.01	264

ponies (*Equus ferus atlanticus*) over domestic livestock, and roe deer (*Capreolus capreolus*) over other wild ungulates. However, our results suggest careful thought should be applied to grouping diet items into categories such as domestic livestock or wild ungulates in morphological diet analysis, potentially including pilot investigation of specific diet item detection, because inherent heterogeneity in detection of diet items may bias estimates and resulting comparisons.

Results of the morphological diet-analysis evaluation suggest the presence of deer hair in a sample was easily detected and often obscured detection of hair of smaller species occurring in scant amounts. Identification of ungulate guard hair is generally straightforward because of its distinctive medulla structure and scaling, whereas hairs of small mammals can be less characteristic (Day 1966, Debelica and Thies 2009). Furthermore, ungulates are commonly much larger than other mammalian prey species, so there may be many more guard hairs consumed and therefore available for detection, creating a dilution effect in detecting smaller species. Biased detection may also be an issue when many or all species are identified only by hair but not all hairs are examined, and when there is not consistent training and experience among observers (Spaulding et al. 2000, du Preez et al. 2017).

Biases in probability of occurrence resulting from grouping and detection of other species were small in our examples. However, errors could accumulate in metrics derived from frequency of occurrence including relative percent occurrence of diet items, dietary niche breadth, niche overlap, or biomass calculations (Levins 1968, Pianka 1974, Jędrzejewska and Jędrzejewski 1998, Atkinson et al. 2004). For example, the reduced detection of each small mammal species in samples with deer could culminate in reduced relative occurrence for each species, which would result in inflated relative percent occurrences for deer. These errors would be amplified by biomass calculations and corrections because consumption of white-tailed deer relative to amount of hair collected is high (Powers et al. 1989). Thus, based on our current results, we may have slightly overestimated the relative frequency of occurrence of white-tailed deer in coyote, bobcat, and black bear diets in a previous study, potentially inflating the degree of dietary overlap (Morin et al. 2016*a*). The greater the number of diet items and disparity in proportional representation, the greater the risk of bias in derived estimates. Derived estimates of niche breadth and overlap between species may also be at risk of misinterpretation due to accumulating biases originating from imperfect detection of diet items. Hierarchical community models are an extension of occupancy modeling that allow for estimation of species richness and diversity with imperfect detection and could be modified to infer diet breadth and overlap without relying on potentially biased frequency of occurrence metrics (Royle and Dorazio 2008).

Molecular approaches to diet analysis do not depend on the presence of indigestible prey remains, they can alleviate many of the limitations of morphological diet analysis (Corse et al. 2010, Gosselin et al. 2017). This may be particularly valuable when indigestible prey remains are regurgitated, unidentifiable, or masked by the presence of prey remains from a larger prey item, as demonstrated in this study with deer.

Grouping was not required for molecular identification of most species, and presence of particular species should not bias detection of others unless taxon-specific primers are not suitably designed and tested for matching alleles. In addition, diet items may be identified at a greater rate than visual identification in morphological analysis (Gosselin et al. 2017; but see Braley et al. 2010). If researchers desire to identify threats to prey populations, use of species-specific markers can be a targeted approach resulting in a lower chance of false negatives (missed detections). If instead, researchers are interested in composition of predator diet, universal primers can be employed to compare DNA barcodes with reference databases to identify multiple prey species (Corse et al. 2010, Smith et al. 2018).

However, there are limitations associated with molecular diet analyses. Molecular approaches may have greater costs when species-specific primers need to be developed or universal primers identified, and when acquisition or processing of reference samples and sequences for prey are required. Costs (per scat) for consumable supplies necessary for DNA extractions and PCR would generally be greater and analyses require more labor than for morphological diet analyses. Molecular techniques also require greater expertise and necessary training for processing fecal samples. Additionally, prey DNA may not be evenly distributed within a scat and multiple fecal samples may need to be collected and analyzed to effectively detect prey, further increasing costs (Gosselin et al. 2017). It is still unknown how relative size of prey may influence the distribution of prey DNA within a scat, or how scat size may influence detection probabilities for prey DNA under different sampling designs (e.g., taking subsamples vs. homogenization of the entire scat).

Molecular diet studies also introduce a fifth step in which dietary sampling error can occur; that is, during replication of the DNA amplification process (Furlan et al. 2016). We attempted to minimize stochastic sampling errors during replicated amplifications by using the freshest scats and reamplifying samples that failed prey species identification during initial amplifications (Gosselin et al. 2017). Molecular diet studies using scats of variable ages or sizes could improve inferences by empirically estimating the level of replication necessary to obtain reliable results (Ficetola et al. 2015). Finally, DNA in scats is also subject to degradation, limiting the application of molecular diet analyses to relatively fresh scats (Tollit et al. 2009), and failure to consider degradation rates can result in false negatives (i.e., prey present in scats goes undetected due to DNA degradation). Thus, studies employing molecular diet analyses should perform pilot studies similar to those used to identify the species depositing the scat (e.g., Lonsinger et al. 2015*a*) to understand DNA degradation rates and minimize the risk of false negatives.

The greatest advantage in using the occupancy or multinomial model estimation methods was the ability to make

comparisons accounting for uncertainty in estimates and evaluate hypotheses about differences in diet using multimodel inference (Burnham and Anderson 2003, Lemons et al. 2010). The traditional frequency of occurrence calculations for deer in bobcat scats could be interpreted to be lower during least-mobility period for fawns (0.37), compared with other months (0.46). However, inference based on these calculations is subjective, and there is no way to account for uncertainty resulting from sources of sampling error without introducing pseudoreplication (Lemons et al. 2010). Both the multinomial modeling and occupancy approach suggested there was little support for a difference between the 2 time periods and provided standard errors and confidence intervals to reflect the uncertainty in the point estimates leading to more objective inference. Uncertainty in estimates will be partly dependent on sample size, so precision in estimates and power to identify trends could be improved with greater sampling effort.

Both the multinomial modeling and occupancy approaches performed equally well, and choice of method will depend on type of diet analysis and parameters of interest to answer specific questions about a population's diet. The occupancy approach must be planned prior to field work for molecular analysis and prior to laboratory work for morphological analysis because of the required subsampling. The occupancy approach is also more intensive and requires more time for additional extractions and PCR reactions, or for washing, sorting, and identifying multiple subsamples. When grouping diet items is required (as it often is for morphological diet analysis with uncertain diet item identification), the occupancy approach, at least for a subsample, will elucidate whether there are differences in detection of diet items and whether some items may obscure detection of other items. However, we were unable to estimate occupancy for trace diet items such as eastern cottontail for the molecular data set and muskrat (*Ondatra zibethicus*) in the morphological data set.

If detection rates across grouped species can be assumed equal and unbiased by other diet items or there is no need to group species as with the molecular approach, the closed-capture multinomial modeling approach is less intensive and provides similar results. In addition, because of how capture histories are created for this method, it may be used on existing data sets in addition to new projects. All diet items are considered at the same time with the capture–mark–recapture approach; thus, testing for differences in frequency of occurrence of specific diet items will require some creative use of interaction terms in design matrices and sufficient samples and detections to estimate additional parameters. Using this approach, we were able to estimate the frequency of occurrence for trace diet items, although standard errors and resulting confidence intervals were large. Finally, this approach can be implemented *post hoc*; therefore, standardization across methods is possible and could enhance our ability to draw comparisons between different studies.

Based on our results, imperfect detection of diet items did not contribute substantially to sampling error relative to other potential sources. With the increased use of molecular identification of predators from their scat, sampling error at the scale of the study design may be the greatest source of error and potential bias (Reynolds and Aebischer 1991, Steenweg et al. 2015). Imperfect detection at this scale results from the inability of researchers to sample every scat on the landscape, which is further exacerbated by subsampling from scat samples that were collected (e.g., to reduce laboratory effort or only using target species samples identified with "high confidence" by observers). Further, imperfect detection is only one form of observational bias present in scat studies. Repeatedly collecting scat samples from the same individual or habitat type can bias diet results by creating a narrower representation of diet items than are actually consumed across the entire landscape by many individuals with differing dietary preferences or access to resources (Ciucci et al. 1996, Steenweg et al. 2015, Gable et al. 2017). Similar issues may arise when sampling occurs seasonally or sample size is not appropriate (Trites and Joy 2005, Byerly et al. 2017). Even slight biases from multiple potential sources could compound into severe biases, resulting in an inaccurate understanding of diet. Further evaluation of sampling design is needed to improve accuracy of diet studies and prevent misguided management efforts.

MANAGEMENT IMPLICATIONS

Scat-based diet studies are a common research tool for understanding wildlife resource requirements and potential effects to prey populations because collection of samples is typically easy and relatively inexpensive. However, inference and application of information gained from these studies will only be appropriate when analyses provide accurate and unbiased information correctly assessing the uncertainty in potential trends uncovered. As such, caution should be exercised in interpreting study results that only present calculations and do not estimate diet metrics with a measure of uncertainty. Future studies should be designed to better account for all sources of error in scat-based diet studies to provide the most critical information for wildlife management decisions.

ACKNOWLEDGMENTS

Financial support provided by the Virginia Department of Game and Inland Fisheries (VDGIF) came from the U.S. Fish and Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Additional funding sources included Virginia Deer Hunter Association, The Nature Conservancy (TNC), the Edna Bailey Sussman Foundation, the Student Undergraduate Research Foundation, the Cunningham Fellowship (Virginia Tech Graduate School), USDA National Institute of Food and Agriculture, McIntire Stennis project (1020959), the Curt and Adele Berklund Undergraduate Research Scholar Award, the U.S. Army Research Laboratory and the U.S. Army Research Office (RC-201205), the U.S. Department of Defense Environmental Security Technology Certification (12 EB-RC5-006) and Legacy Resource Management (W9132T-12-2-0050) programs, and the National

Geographic Society's Conservation Trust (C248-13). We thank landowners, collaborators, and technicians including the VDGIF, U.S. Forest Service, TNC, Dugway Proving Ground, Green Valley Hunters Paradise, the Laboratory for Ecological and Evolutionary Conservation Genetics, R. Alonso, D. Montague, R. Montague, J. Holub, S. Webster, J. Kinkead, B. Martini, S. Perkins, J. Hody, C. Maynard, J. Estienne, S. Hovendon, C. Helmke, M. Lopez, M. Smith, and M. Melham. Finally, we thank the Associate Editor and 2 anonymous reviewers for contributions that improved the quality of the manuscript.

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Associated Editor: Messmer.

SUPPORTING INFORMATION

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Table S1. Akaike's Information Criterion (AICc) for occupancy candidate sets including the presence and count of white-tailed deer remains in morphological diet analysis subsamples as covariates on diet item detection.