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Original Article

Bias in Carnivore Diet Analysis Resulting from Misclassification of Predator Scats Based on Field Identification

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ABSTRACT Diet studies are frequently used to improve understanding of predator ecology, potential effects of carnivores on prey populations, and competition among predators. However, field identification of carnivore scat typically relies on scat morphology, size, and contents resulting in possible subjective predator identification and potentially biased results. Advancements in noninvasive genetic sampling allow for molecular identification of predator scat, eliminating many issues associated with field identification methods. We collected scat samples once per month from June 2011 to May 2012 in western Virginia, USA, using morphological characteristics for field identification of the predator. We then used mitochondrial DNA to identify the predator species of each scat and identified prey remains visually. Using confusion matrices, we found a range of accuracy in field identification for the 3 target species: coyotes (*Canis latrans*; 54.0%), bobcats (*Lynx rufus*; 57.1%), and black bears (*Ursus americanus*; 95.2%), even though we only considered samples with high-confidence field identification. We found a high coyote false-positive rate (52.7%), indicating we often incorrectly identified scats as coyote (98% of misidentified bobcat scats and 75% of misidentified black bear scats were recorded as coyote in the field). This asymmetrical bias in predator identification resulted in inaccurate estimates of dietary niche breadth and overlap between competitors. Our results suggest that caution should be exercised when interpreting results from studies in which carnivore species are identified by scat morphology. Future studies should employ noninvasive genetic sampling for carnivore scat identification, especially in areas with sympatric predator species that have similar scat morphology.

KEY WORDS *Canis latrans*, carnivore diet analysis, diet bias, *Lynx rufus*, molecular species identification, morphological scat identification, noninvasive genetic sampling, *Ursus americanus*.

Diet analysis is a commonly used tool in carnivore ecology studies (Klare et al. 2011). Researchers have used results from diet analyses to estimate required resources for carnivore species (Carbone et al. 1999), determine the effects of habitat and community changes on carnivores (Novaro et al. 2000, Phillips et al. 2007, Larson et al. 2015), evaluate interspecific competition between species (Jones and Barmuta 1998, Fedriani et al. 2000), and predict potential human–wildlife conflict and effects on prey populations (Risbey et al. 1999, Bagchi and Mishra 2006). Although carnivore diet analysis can provide valuable insight into population resource requirements and interactions among species, accuracy during each step of the analysis is critical for correct interpretation of results and prediction of effects (Reynolds and Aebischer 1991, Iverson et al. 1996, Marucco et al. 2008, Klare et al. 2011).

There are many methods available to study carnivore diets, including direct observation of feeding behavior (Huegel and Rongstad 1985, van Valkenburgh 1996), examination of stomach contents (Azevedo et al. 2006), isotope analysis (Dalerum and Angerbjörn 2005), fatty acid analysis (Iverson et al. 1996), molecular genetic approaches (Symondson 2002, Deagle et al. 2005, King et al. 2008, De Barba et al. 2014*b*,

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Egeter et al. 2015), and scat (feces) analysis (Reynolds and Aebischer 1991). Scat analysis is by far the simplest and least expensive method, and thus the most commonly used (Klare et al. 2011). Scat analysis typically involves collection and identification of scat in the field, with field identification based on morphology (i.e., shape, diameter, length, mass, color, and odor) and context, including presence of tracks or location near dens (Larson et al. 2015, Lonsinger et al. 2015). Although scat analysis is frequently used to study carnivore diets, several studies have reported variable success correctly identifying the source of the scat using morphological attributes and measurements, particularly in areas with sympatric predators of similar size (Davison et al. 2002, Reed et al. 2004, Harrington et al. 2010, Lonsinger et al. 2015).

Recent advancements in molecular ecology allow for accurate predator species identification using noninvasive genetic sampling (Dalén et al. 2004, Beja-Pereira et al. 2009, De Barba et al. 2014*a*). We compared field identification with molecular species identification for scats collected on transects in western Virginia, USA, a region with 3 apex predators: coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). We then analyzed these samples, visually identified diet contents, and used both data sets (field identification and molecular identification) to quantify dietary niche breadth and niche overlap and assess potential competition among predator species. There was large size overlap of coyote and bobcat scats, and collected scats were highly variable in appearance and condition; therefore, we hypothesized field identification would not reliably distinguish among these species. However, we hypothesized field identification of black bear scat would be more accurate because of its larger size and visual differences in consistency resulting from a highly plant-based diet (Beeman and Pelton 1980, Graber and White 1983). Finally, we predicted that misidentifications of carnivore scats in the field would result in incorrect conclusions about dietary niche breadth for each carnivore species and the degree of potential competition between those species.

STUDY AREA

The study area was located in Bath and Rockingham counties, Virginia, in the Ridge and Valley region of the central Appalachians (Fig. 1). The George Washington National Forest was the largest public landholder in the region. The landscape consisted primarily of contiguous, even-aged forests including a canopy of chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), white oak (*Q. alba*), and tulip poplar (*Liriodendron tulipifera*), and an understory

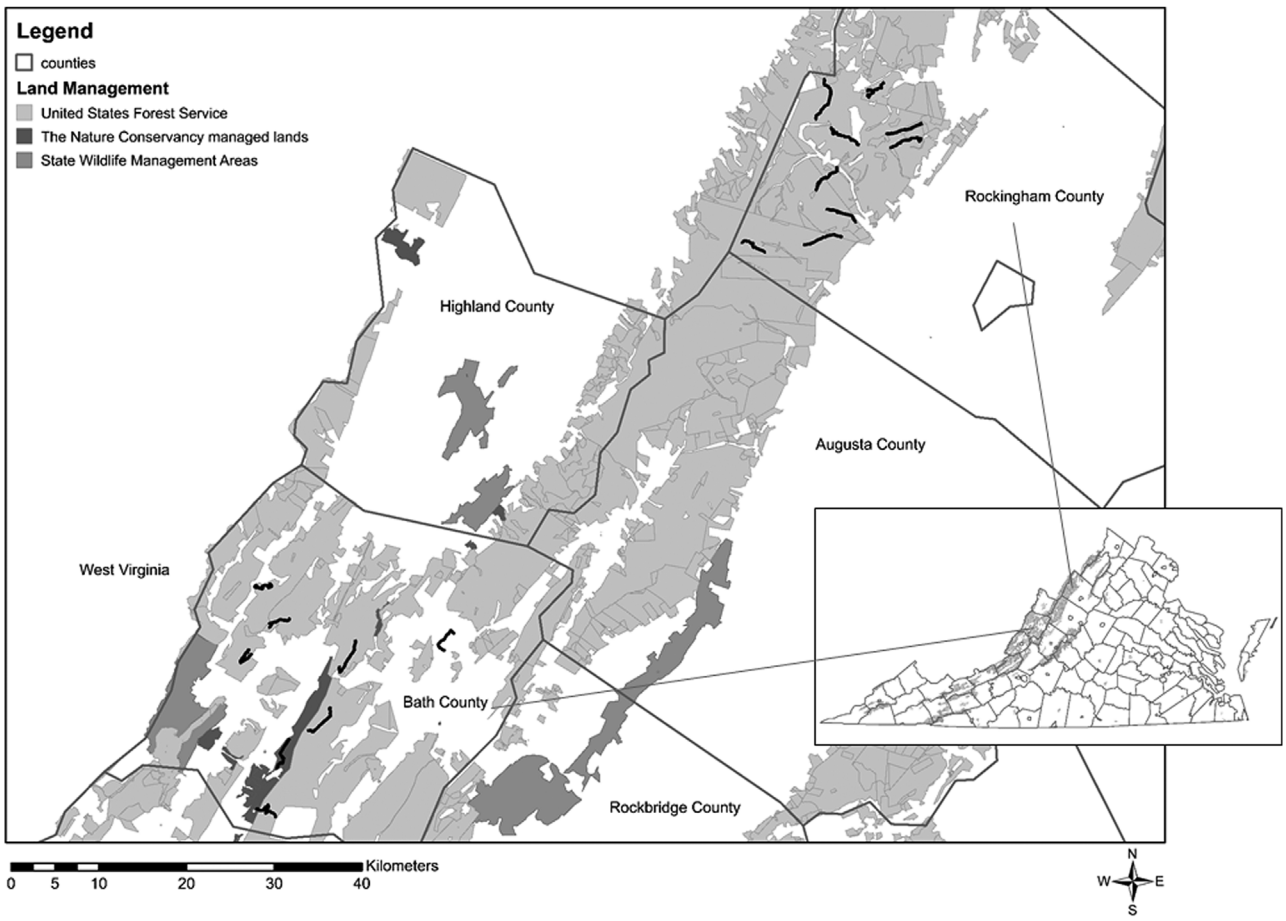

Figure 1. The study area in the western mountains of Virginia, USA, includes 8, 5-km scat transects in Bath County, and 8, 5-km transects in Rockingham County. Carnivore scats were collected from all transects once per month from June 2011 to May 2012.

primarily composed of rhododendron (*Rhododendron maximum*) and eastern mountain laurel (*Kalmia latifolia*). Elevation ranged from 350 m to 1,365 m and temperature can range from a mean minimum temperature of −4.6° C in January to a mean maximum temperature of 31.6° C in July (National Oceanic and Atmospheric Administration, public data 2012; www.noaa.gov). In addition to the 3 target carnivore species (coyotes, black bears, and bobcats), other carnivores in the study area included gray foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), river otters (*Lontra canadensis*), mink (*Neovison vison*), long-tailed weasels (*Mustela frenata*), least weasels (*M. nivalis*), raccoons (*Procyon lotor*), and domestic dogs (*Canis familiaris*) and cats (*Felis catus*).

METHODS

Field Methods

We collected carnivore scat samples along 16 established 5-km transects once per month from June 2011 to May 2012. We used morphology, size, and shape to assign a field identification of the predator when the scat was collected, and recorded a confidence ranking for the field identification (low, medium, or high). We assigned scat identification with high confidence when we thought it was from one specific predator, and not likely to be from any other predator. We used length and diameter size ranges from the literature and field guides as well as overall shape descriptions such as constricted tubules and twisted cords and scents (Halfpenny 1986, Rezendes 1999, Elbroch 2003, Reed et al. 2004, Prugh and Ritland 2005). We identified scats with medium confidence when we thought scats likely to be from a specific predator species based on the above criteria, but it had some slightly ambiguous characteristics that led us to believe it could be from another predator. We identified scats with low confidence when a scat did not have many distinguishing characteristics and could not be easily identified to species based on common field assessments. We collected an approximate 0.5-mL sample from the side of each scat and stored it in 1.5 mL of DETS buffer (20% DMSO, 0.25 M EDTA, 100 mM Tris, pH 7.5, and NaCl to saturation; Frantzen et al. 1998). We stored the remainder of the scat in a plastic bag in a freezer prior to diet analysis. During a concurrent study at the same 2 sites, additional scat samples were collected for carnivore population density surveys and identified using the same field and molecular methods, but the remainder of the scat sample was not collected for diet analysis (Morin et al. 2016). We included these additional samples in our assessment of field identification to improve sample size, but these samples were not used in the diet analysis described below, resulting in a larger data set available for estimating accuracy as compared to diet metrics.

Laboratory Methods

We extracted DNA and identified the predator using a mitochondrial DNA (mtDNA) control-region species-identification multiplex (De Barba et al. 2014*a*), as described in Morin et al. (2016). We removed 39 samples that amplified DNA from more than one predator species because it was not possible to determine from which species the scat originated (territorial carnivores may investigate or mark scat from other species, potentially resulting in DNA cross-contamination).

We stored diet scat samples at −20° C, then thawed and washed scats through a series of progressively finer mesh sieves, manually separating diet items into piles of materials such as bones, teeth, hair, feathers, fruits, seeds, and debris. We dried, weighed, and identified diet contents using medulla and scaling patterns and cross-sections of hairs, occlusal patterns of teeth, and other items including bones, hooves, and claws. We identified diet items based on a reference key developed specifically for the region using published dichotomous keys, and field guides, as well as a reference collection of hair, bones, teeth, and seeds collected from the field (Spiers 1973, Jones and Manning 1992, Hillson 2005, Elbroch 2006, Debelica and Thies 2009). Sample handling and collection methods were approved by and conducted in accordance with Virginia Tech Institutional Animal Care and Use Committee permit 10-172-FIW.

Statistical Methods

To evaluate accuracy of field identification of scat samples, we subsampled the data set to include only those samples that had both high-confidence field identifications and definitive mtDNA molecular identifications. We tabulated field identifications and molecular identifications for each sample to create confusion (error) matrices for coyote, black bear, and bobcat (Hay 1988, Congalton 1991). We used the confusion matrices for each species to calculate accuracy, true- and false-positive rates, and true- and false-negative rates for field identifications for each predator species. Using coyotes as an example, if a sample was identified in the field as a coyote scat and confirmed to be a coyote scat with molecular identification, the outcome was a true positive. But if the molecular identification determines the scat identified in the field as a coyote was from a bobcat, bear, or another species, the outcome was a false positive. There are 2 additional possible outcomes: a sample could be identified as another species in the field but determined to be a coyote scat using molecular identification (false negative); or, molecular identification could confirm a scat identified in the field as another species is not a coyote scat (true negative). For any given species, confusion matrices allow for assessment of all 4 possible outcomes of field identification (see Table 1 for calculations). We calculated accuracy as the sum of true positives and true negatives divided by the sum of all possible outcomes (true positive, true negative, false positive, false negative). Thus, accuracy decreases with high false-positive or false-negative rates, and increases with high true-positive and true-negative rates.

For diet analysis, we divided diet items into 16 categories (Table S1, available online in Supporting Information). For each predator species (coyote, bobcat, and bear), we

Table 1. Confusion (error) matrix tables and calculated accuracy and error rates for coyote (top), bobcat (middle), and black bear (bottom) scat samples collected in the western mountains of Virginia, USA, June 2011–May 2012. A total of 315 scat samples were identified in the field with high confidence (predicted count in the error matrix) and also amplified successfully to allow for molecular identification (actual count in the error matrix).

		Predicted (field identification)			
Coyote		**Not a coyote (negative)**	**Is a coyote (positive)**	**Total**	**Accuracy[e] 0.54**
Actual (molecular identification)	Not a coyote (negative)	105[a]	117[b]	222	True-positive rate[f] 0.70 True-negative rate[g] 0.47
	Is a coyote (positive)	28[c]	65[d]	93	False-positive rate[h] 0.53 False-negative rate[i] 0.30
	Total	133	182	315	
Bobcat		**Not a bobcat (negative)**	**Is a bobcat (positive)**	**Total**	**Accuracy 0.57**
Actual (molecular identification)	Not a bobcat (negative)	124	23	147	True-positive rate 0.33 True-negative rate 0.84
	Is a bobcat (positive)	112	56	168	False-positive rate 0.16 False-negative rate 0.67
	Total	236	79	315	
Black bear		**Not a black bear (negative)**	**Is a black bear (positive)**	**Total**	**Accuracy 0.95**
Actual (molecular identification)	Not a black bear (negative)	254	7	261	True-positive rate 0.85 True-negative rate 0.97
	Is a black bear (positive)	8	46	54	False-positive rate 0.03 False-negative rate 0.15
	Total	262	53	315	

[a] True negative (predicted it was not a coyote scat and it was not a coyote scat).
[b] False positive (predicted it was a coyote scat but it was not a coyote scat).
[c] False negative (predicted it was not a coyote scat and it was a coyote scat).
[d] True positive (predicted it was a coyote scat and it was a coyote scat).
[e] Accuracy = (true positive + true negative)/(true positive + true negative + false positive + false negative).
[f] True-positive rate = true positive/(true positive + false negative): how often did we identify a coyote scat correctly?
[g] True-negative rate = true negative/(true negative + false positive): how often did we correctly predict a scat was not a coyote scat?
[h] False-positive rate = false positive/(true negative + false positive): how often did we incorrectly identify scat from another species as coyote?
[i] False-negative rate = false negative/(true positive + false negative): how many times did we incorrectly predict a scat was not a coyote scat?

calculated frequency of occurrence as the number of times a diet category was present in a sample divided by the total number of samples for that predator. Scat samples often contain multiple food items; therefore, frequency of occurrence of all diet items for a predator species can sum to >100%. Thus, we also calculated relative percent occurrence by dividing frequency of occurrence for each diet category by the sum of all frequency of occurrences of diet categories for each predator species to provide an indication of proportional occurrence of diet items in coyote, bobcat, and black bear diets (Pianka 1973). We estimated dietary niche breadth and niche overlap (Levins 1968, Pianka 1974) among coyotes, black bears, and bobcats, first using the predator field identifications (high-confidence field identifications only) and then using the correct molecular identifications to assess potential bias that can occur when relying solely on field identifications. We estimated dietary niche breadth by considering the number of different diet items as well as the proportions in which those items were found; this can range from 1 to the total number of diet items found for a predator species (Levins 1968). An estimate close to 1 indicates a narrow dietary niche with a large proportion of the diet consisting of just a few items. An estimate close to the total number of possible diet items suggests all possible diet items are being consumed in equal proportions. Niche overlap is derived from the dietary-niche breadth estimates for 2 different predators (Pianka 1974). Niche overlap can range from 0 (no diet items shared between 2 predator species) to 1 (complete diet overlap between 2 species; see Table 2 for calculations).

RESULTS

Combining diet transects and concurrent carnivore density surveys, we collected 315 samples confirmed to be coyote, bobcat, or black bear scat using mtDNA that were also identified with high confidence in the field (including several scats identified as species other than coyote, bobcat, or black bear). Field identification methods of these scats predicted 181 of the samples were from coyotes, 79 from bobcats, 53 from black bear scats, and 2 from foxes. In contrast, molecular identification of the 315 samples revealed 93 scat samples were coyote, 168 samples were bobcat, and 54 samples were black bear. Accuracy for black bear scat field identification was high (95.2%; Table 1). The high true-positive rate (85.2%), and low false-negative rate (14.8%) suggested we were often able to accurately identify black bear

Table 2. Dietary niche breadth and overlap for coyotes, bobcats, and black bears estimated from scat samples collected in western Virginia, USA, June 2011–May 2012 (spring: Mar, Apr, May; summer: Jun, Jul, Aug; autumn: Sep, Oct, Nov; winter: Dec, Jan, Feb). Diet metrics were calculated using both molecular identification and high-confidence field identification.

Metric		Molecular identification	High-confidence field identification	Change in metric[a]
Dietary niche breadth[b]	Coyote	4.27	6.02	−1.75
	Spring	4.11	6.67	−2.56
	Summer	3.83	5.64	−1.81
	Autumn	4.45	7.59	−3.14
	Winter	3.41	4.57	−1.16
	Bobcat	6.69	6.97	−0.28
	Spring	6.62	6.41	0.21
	Summer	6.49	6.36	0.13
	Autumn	4.55	4.25	0.30
	Winter	6.49	6.12	0.37
	Black bear	4.33	1.14	3.19
	Spring	4.21	1.80	2.41
	Summer	3.86	4.04	−0.18
	Autumn	4.35	3.93	0.42
	Winter	3.57	3.27	0.30
Niche overlap[c]	Coyote–bobcat	0.73	0.95	−0.22
	Spring	0.67	0.98	−0.31
	Summer	0.82	0.95	−0.13
	Autumn	0.39	0.81	−0.42
	Winter	0.72	0.67	0.05
	Coyote–black bear	0.69	0.50	0.19
	Spring	0.96	0.32	0.64
	Summer	0.55	0.50	0.05
	Autumn	0.65	0.54	0.11
	Winter	0.90	0.70	0.20
	Bobcat–black bear	0.47	0.48	−0.01
	Spring	0.46	0.42	0.04
	Summer	0.60	0.52	0.08
	Autumn	0.24	0.14	0.10
	Winter	0.60	0.24	0.36

[a] Metric for molecular identification—metric for field identification.

[b] $\frac{1}{\sum \%\text{occurrence for each diet item}^2}$.

[c] $\frac{\Sigma\%\text{ccurence for each diet item for predator A} \times \%\text{ccurence for each diet item for predator B}}{\sqrt{\Sigma\%\text{ccurence for each diet item for predator A}^2 \times \Sigma\%\text{ccurence for each diet item for predator B}^2}}$.

scat samples when collected in the field. In addition, we did not often identify scat samples from other predator species as black bear, as demonstrated by the low false-positive rate (2.7%) and high true-negative rate (97.3%).

Field identification accuracy was much lower for bobcat (57.1%; Table 1) and coyote (54.0%; Table 1) scat samples. Low accuracy in bobcat scat field identification was a result of both a low true-positive rate (33.3%) and high false-negative rate (66.7%), indicating many of the bobcat scat samples we collected in the field were misidentified as another species. Although the true-positive rate in coyote field identification was relatively high (69.9%), accuracy in coyote field identification was low because the false-positive rate was also high (52.7%). In fact, almost all false negatives for bobcat and black bear scat samples were misidentified in the field as coyote (98.0% of misidentified bobcat samples and 75.0% of misidentified black bear samples). This asymmetrical bias in field identification resulted in the perception that 58.0% of the scat samples identified with high confidence in the field were from coyotes and 25.1% were from bobcats. Molecular identification of these scats, however, revealed the proportions were reversed with 29.5% of scats collected with high confidence determined to be from coyotes and 53.3% of scats collected with high confidence determined to be from bobcats.

For the scat data set used for diet analysis, 657 coyote, bobcat, and bear samples amplified successfully (225 coyote, 348 bobcat, 84 black bear), of which only 302 samples were identified with high confidence in the field (174 coyote, 77 bobcat, 51 black bear). We estimated dietary niche breadth to be 4.27 for coyotes, 6.69 for bobcats, and 4.33 for black bears based on molecular identification of scat. These niche breadth estimates suggest that, even though there was a broad variety of food items in each predator's diet (13 in coyote, 12 in bobcat, and 10 in black bear diets), all 3 predators were eating a few diet items in large proportions (Fig. 2). White-tailed deer (*Odocoileus virginianus*), voles (*Microtus* spp., *Myodes gapperi*), mast (soft and hard), and insects comprised 77.4% of coyote diet. Squirrels (*Sciurus* spp., *Glaucomys* spp.), chipmunks (*Tamias striatus*), white-tailed deer, voles, and rabbits (*Sylvilagus* spp.) comprised 67.4% of bobcat diet. Mast, insects, and white-tailed deer comprised 84.1% of black bear diet.

As a result of shared diet items found in differing proportions across predator species, dietary overlap was variable among the 3 predators (0.73 for coyotes and bobcats,

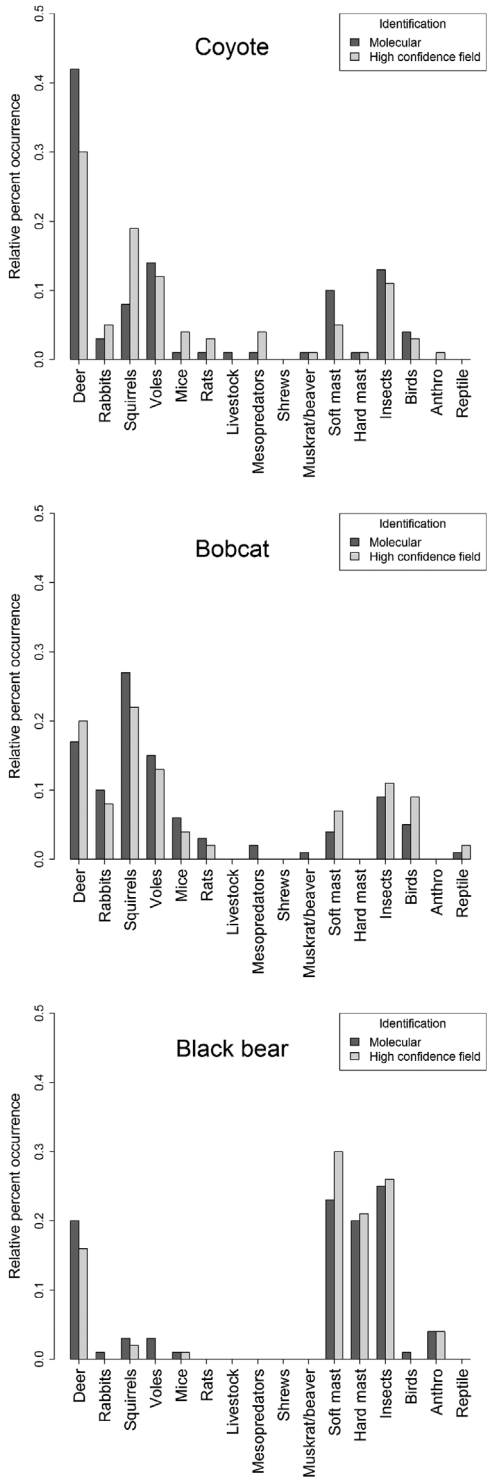

Figure 2. Relative frequency of occurrence of diet items based on molecular identification and high-confidence field identification for coyotes, bobcats, and black bears scat samples collected in western Virginia, USA, from June 2011 through May 2012.

0.69 for coyotes and black bears, and 0.47 for bobcats and black bears). The large amount of dietary overlap between coyotes and bobcats based on molecular identification explains why estimated dietary niche breadth for bobcat and coyote using field identification (6.02 for coyotes, 6.97 for bobcats) were similar compared to the estimate using molecular identification (Table 2). However, the niche breadth for black bears was more narrow with high-confidence field identification methods (1.14), because some diet categories present in scat samples confirmed to be black bear using molecular identification methods were not found in the samples with high-confidence field identification. In addition, dietary niche overlap using high-confidence field identification was similar for the 2 species with the least amount of true overlap—bobcats and black bears (0.48). However, field identification overestimated niche overlap for bobcats and coyotes (0.95), because a large number of bobcat scats were falsely identified as coyotes, and underestimated niche breadth for coyotes and black bears (0.50), which was a result of the missing categories in bear diet when using high-confidence field identification.

DISCUSSION

Our results concur with other studies that found it is difficult to reliably differentiate between scats for carnivore species of similar size (Farrell et al. 2000, Davison et al. 2002). We commonly misidentified coyote and bobcat scat samples in the field using size, morphology, scent, and context criteria. Coyotes and bobcats demonstrated relatively broad overlap in proportions of and types of diet items consumed, so misidentification of coyote scat as bobcat, or more often bobcat scat as coyote, did not result in different composition of food items attributed to the falsely identified predator's diet and estimates of dietary niche breadth were similar. However, misidentification resulted in overestimation of coyote dietary niche breadth and underestimation of black bear dietary niche breadth. Misidentification also resulted in overestimation of niche overlap between coyotes and bobcats, and erroneously suggested a greater degree of interspecific competition as a result of estimated nearly complete dietary niche overlap.

Published field identification methods for bobcat scats are very detailed, including specific shapes and a scent-test commonly cited by trackers as a definitive diagnostic for felid scats (Halfpenny 1986, Rezendes 1999, Elbroch 2003). However, the high false-negative rate for bobcat scat samples (66.7%) suggests that many bobcat scats did not fit this descriptive definition and were misidentified as another predator. In addition, we found evidence of bias in diet analyses utilizing field identifications, even for black bears with high field identification accuracy. Quite possibly, this bias may have been related to the presence of a few diet items not normally expected to be found in bear scats (Beeman and Pelton 1980). We found voles, rabbits, and bird feathers in bear scat identified with molecular methods, but not in bear scat identified using field methods. It is possible that unexpected diet items resulted in a lower assigned confidence ranking and exclusion from the high-confidence field identification data set. Thus, the use of confidence rankings may unintentionally bias results because atypical samples may be excluded from analyses. Culling samples of uncertain species origin also reaffirms biased perceptions of expected diet for a species, even when

high-confidence field identifications are accurate. For example, black bear dietary niche breadth calculated from field-identified scat only resulted in underestimation of food resources utilized by black bears and the possible degree of competition between black bears and other sympatric predators in the region.

Bias in identification of black bear and bobcat scats also resulted in the high false-positive rate for scats misidentified as coyote. Field identification of coyote may have served as a catch-all for scats with ambiguous features in our study. The overwhelming number of bobcat scats misidentified as coyote provides strong evidence for an underlying biased perception influencing field identifications. Bobcats are often considered to be completely carnivorous; therefore, technicians may have inadvertently considered scats with certain diet items (such as soft mast) more likely to be coyote scats and unlikely to be bobcat scats (Litvaitis and Harrison 1989, Anderson and Lavallo 2003, Melville et al. 2015). Finally, technicians may have been less likely to identify scat as bobcat because of a possible perception that coyotes were common and bobcats were rare in the study area.

Misidentification of predator scats could also bias other types of carnivore surveys, as well as public perceptions. Counts or presence of scats are sometimes used in spoor or sign surveys to infer relative activity, abundance, or habitat use of predators (Crooks 2002, Balme et al. 2009, Bauer et al. 2014, Gulsby et al. 2015). Attempts to quantify activity of each species using field identified scat collected in this study would likely have resulted in erroneous conclusions.

In addition, if our study had targeted only a single predator species (i.e., coyote), either at the time of sample collection or during molecular identification, inaccuracies in amplification success rates would have occurred because many scats originating from nontarget species would have been considered failed samples. As a result, researchers could mistakenly believe their study system or marker set was unsuitable for noninvasive genetic sampling. Also, perceptions of coyote abundance held by local residents, hunters, and trappers can be influenced by misidentified bobcat and coyote scat, resulting in the misconception that coyotes are more abundant than they really are. Coyotes are frequently blamed for decreased numbers of deer and other game species in many regions. However, bias associated with coyote scat identification potentially masks the importance of predation by other large carnivore species.

Finally, molecular identification of scats increased the total sample size for diet analysis because many samples identified in the field with medium or low confidence would likely have been culled from analyses. In our study, there were 657 samples in the molecular identification data set and only 302 samples in the high-confidence field-identification data set, with many of these misidentified. Even for black bear samples for which accuracy in field identification was high, fewer black bear scat samples were identified with high confidence using field identification (51) compared with the number of scats that were successfully identified with molecular identification (84).

Our results suggest that field identification of scat based on morphology is inherently subjective and illustrates the limitations of comparing results among previously published scat-analysis studies, especially those that relied on field identification of the predator source and confirm what researchers expected. Diet composition results vary substantially depending on identification methods used; therefore, comparisons among studies are potentially problematic or invalid. We suggest managers should exercise caution when interpreting results from diet analysis studies that used subjective scat-identification methods, especially those conducted in areas with sympatric carnivore species with morphologically similar scat.

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LITERATURE CITED

Anderson, E. M., and M. J. Lavallo. 2003. Bobcat and lynx. Pages 758–786 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Mammals of North America: biology, management, and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Azevedo, F. C. C., V. Lester, W. Gorsuch, S. Larivière, A. J. Wirsing, and D. L. Murray. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. Journal of Zoology 269:127–135.

Bagchi, S., and C. Mishra. 2006. Living with large carnivores: predation on livestock by the snow leopard (*Uncia uncia*). Journal of Zoology 268:217–224.

Balme, G. A., L. T. B. Hunter, and R. Slotow. 2009. Evaluating methods for counting cryptic carnivores. Journal of Wildlife Management 73:433–441.

Bauer, D., M. Schiess-Meier, D. R. Mills, and M. Gusset. 2014. Using spoor and prey counts to determine temporal and spatial variation in lion (*Panthera leo*) density. Canadian Journal of Zoology-Revue Canadienne De Zoologie 92:97–104.

Beeman, L. E., and M. R. Pelton. 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. Fourth International Conference on Bear Research and Management 4:141–147.
Beja-Pereira, A., R. Oliveira, P. C. Alves, M. K. Schwartz, and G. Luikart. 2009. Advancing ecological understandings through technological transformations in noninvasive genetics. Molecular Ecology Resources 9:1279–1301.
Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.
Congalton, R. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment 37:35–46.
Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.
Dalén, L., A. Götherström, and A. Angerbjörn. 2004. Identifying species from pieces of faeces. Conservation Genetics 5:109–111.
Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.
Davison, A., J. D. S. Birks, R. C. Brookes, T. C. Braithwaite, and J. E. Messenger. 2002. On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. Journal of Zoology 257:141–143.
Deagle, B. E., D. J. Tollit, S. N. Jarman, M. A. Hindell, A. W. Trites, and N. J. Gales. 2005. Molecular scatology as a tool to study diet: analysis of prey DNA in scats from captive Steller sea lions. Molecular Ecology 14:1831–1842.
De Barba, M., J. R. Adams, C. S. Goldberg, C. R. Stansbury, D. Arias, R. Cisneros, and L. P. Waits. 2014*a*. Molecular species identification for multiple carnivores. Conservation Genetics Resources 6:821–824.
De Barba, M., C. Miquel, F. Boyer, C. Mercier, D. Rioux, E. Coissac, and P. Taberlet. 2014*b*. DNA metabarcoding multiplexing and validation of data accuracy for diet assessment: application to omnivorous diet. Molecular Ecology Resources 14:306–323.
Debelica, A., and M. L. Thies. 2009. Atlas and key to the hair of terrestrial Texas mammals. Special publication of The Museum of Texas Tech University, Number 55, Lubbock, USA.
Egeter, B., P. J. Bishop, and B. C. Robertson. 2015. Detecting frogs as prey in the diets of introduced mammals: a comparison between morphological and DNA-based diet analyses. Molecular Ecology Resources 15:306–316.
Elbroch, M. 2003. Mammal tracks & sign: a guide to North American species. Stackpole, Mechanicsburg, Pennsylvania, USA.
Elbroch, M. 2006. Animal skulls: a guide to North American species. Stackpole, Mechanicsburg, Pennsylvania, USA.
Farrell, L. E., J. Roman, and M. E. Sunquist. 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. Molecular Ecology 9:1583–1590.
Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.
Frantzen, M. A. J., J. B. Silk, J. W. Ferguson, R. K. Wayne, and M. H. Kohn. 1998. Empirical evaluation of preservation methods for fecal DNA. Molecular Ecology 7:1423–1428.
Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. Fourth International Conference on Bear Research and Management 5:1–10.
Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39:248–255.
Halfpenny, J. C. 1986. A field guide to mammal tracking in western America. Big Earth Publishing, Boulder, Colorado, USA.
Harrington, L. A., A. L. Harrington, J. Hughes, D. Stirling, and D. W. Macdonald. 2010. The accuracy of scat identification in distribution surveys: American mink, *Neovison vison*, in the northern highlands of Scotland. European Journal of Wildlife Research 56:377–384.
Hay, A. M. 1988. The derivation of global estimates from a confusion matrix. International Journal of Remote Sensing 9:1395–1398.
Hillson, S. 2005. Teeth. Cambridge manuals in archaeology series. Cambridge University Press, Cambridge, United Kingdom.
Huegel, C. N., and O. J. Rongstad. 1985. Winter foraging patterns and consumption rates of northern Wisconsin coyotes. American Midland Naturalist 113:203–207.
Iverson, S. J., C. Field, W. D. Bowen, and B. Wade. 1996. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs 74:211–235.
Jones, J. K., and R. W. Manning. 1992. Illustrated key to skulls of genera of North American land mammals. Texas Tech University Press, Lubbock, USA.
Jones, M. E., and L. A. Barmuta. 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. Journal of Animal Ecology 67:410–421.
King, R. A., D. S. Read, M. Traugott, and W. O. C. Symondson. 2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology 17:947–963.
Klare, U., J. F. Kamler, and D. W. Macdonald. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Review 41:294–312.
Larson, R. N., D. J. Morin, I. A. Wierzbowska, and K. R. Crooks. 2015. Food habits of coyotes, gray foxes, and bobcats in a coastal southern California urban landscape. Western North American Naturalist 75:339–347.
Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.
Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180–1188.
Lonsinger, R. C., E. M. Gese, and L. P. Waits. 2015. Evaluating the reliability of field identification and morphometric classifications for carnivore scats confirmed with genetic analysis. Wildlife Society Bulletin 39:593–602.
Marucco, F., D. H. Pletscher, and L. Boitani. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. Journal of Mammalogy 89:665–673.
Melville, H. I. A. S., W. C. Conway, M. L. Morrison, C. E. Comer, and J. B. Hardin. 2015. Prey selection by three mesopredators that are thought to prey on eastern wild turkeys (*Meleagris gallopavo sylvestris*) in the pineywoods of East Texas. Southeastern Naturalist 14:447–472.
Morin, D. J., M. J. Kelly, and L. P. Waits. 2016. Monitoring coyote population dynamics with fecal DNA and spatial capture–recapture. Journal of Wildlife Management 80:824–836.
Novaro, A. J., M. C. Funes, and R. Susan Walker. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation 92:25–33.
Phillips, R. B., C. S. Winchell, and R. H. Schmidt. 2007. Dietary overlap of an alien and native carnivore on San Clemente Island, California. Journal of Mammalogy 88:173–180.
Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology, Evolution, and Systematics 4:53–74.
Pianka, E. R. 1974. Niche overlap and diffuse competition. Ecology 71:2141–2145.
Prugh, L. R., and C. E. Ritland. 2005. Molecular testing of observer identification of carnivore feces in the field. Wildlife Society Bulletin 33:189–194.
Reed, J. E., R. J. Baker, W. B. Ballard, and B. T. Kelly. 2004. Differentiating Mexican gray wolf and coyote scats using DNA analysis. Wildlife Society Bulletin 32:685–692.
Reynolds, J. C., and N. J. Aebischer. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Review 21:97–122.
Rezendes, P. 1999. Tracking and the art of seeing: how to read animal tracks & sign. HarperCollins, New York, New York, USA.
Risbey, D. A., M. C. Calver, and J. Short. 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. Wildlife Research 26:621–630.
Spiers, J. K. 1973. A microscopic key to the hairs of Virginia land mammals. Virginia Polytechnic Institute and State University, Blacksburg, USA.
Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. Molecular Ecology 11:627–641.
van Valkenburgh, B. 1996. Feeding behavior in free-ranging, large African carnivores. Journal of Mammalogy 77:240–254.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. We provide a complete list of diet items and species detected, and how we grouped them for diet analysis calculations (Table S1). We also provide a detailed table (Table S2) of the number of occurrences, frequency of occurrence, and relative percent occurrence for diet item categories in coyote, bobcat, and black bear scat from the study.