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Do indirect bite count surveys accurately represent diet selection of white-tailed deer in a forested environment?

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Abstract

Context. Diet selection is studied in herbivores using three predominant methods: (1) microhistological surveys (identification of plants cell walls remaining in gut contents or faecal excretions); (2) direct bite counts (of tame animals); and (3) indirect bite counts (identifying herbivory on damaged plant tissues). Microhistological surveys and direct bite counts are accurate and provide the potential advantage of linking diet selection to particular individuals. Also, they allow diet selection to be measured in systems with sympatric herbivores more easily than indirect bite counts. However, they require expertise in cell wall structure identification or access to tame animals, and generally require greater expense than indirect bite counts. Conversely, indirect bite counts have the advantages of relatively low cost and time commitment for gathering data and do not require animal observation, but may not be accurate.

Aims. We tested for similarity between diet-selection estimates calculated by indirect bite counts and microhistological surveys.

Methods. We performed concurrent indirect bite count and faecal microhistological surveys on white-tailed deer (*Odocoileus virginianus*) at Fort Bragg Military Installation, NC.

Key results. The indirect bite count survey assignment of selection was 48% similar to assignments derived from the microhistological survey, based on Jaccard's similarity index. Out of 23 plant species determined to be selected by indirect bite counts, 15 of those species were selected according to microhistological surveys. According to the microhistological survey, eight of the selected plants made up 51% of the overall diet, and seven of those eight were selected according to the indirect bite counts.

Conclusions. Our data indicate that indirect bite counts may provide a relatively accurate index of the deer-selected plants most important in the white-tailed deer diet, but may be less appropriate to determine selection of plants that infrequently occur in their diet, plants that are typically consumed in entirety, or plants where herbivory damage is poorly identified.

Implications. Indirect bite counts are a relatively inexpensive and time-efficient tool that may be useful to determine plant species most important to white-tailed deer within a forested landscape, particularly if additional research can improve on associated inaccuracies.

Additional keywords: Chesson Index, diet selection transect, herbivory, indirect bite count, microhistological survey, white-tailed deer.

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Introduction

Diet selection in herbivores is a complex process in which animals integrate food quality and quantity, search and handling times, predation risks and nutrient requirements to maximise the net gain of foraging (Hanley 1997; Barboza *et al*. 2009). Despite the complexity of diet selection, measuring diet selectivity is fundamental to understanding animal ecology and management and consequently informs management practices. For example, managers may differentially use disturbances to encourage particular plant species. Thus, determining which plants are important foods for the targeted taxa will guide the application of those disturbance regimes to increased food availability. Understanding diet selection could also be important in the management of problematic herbivores that cause undesirable shifts in plant communities, as the white-tailed deer does in much of eastern North America (Côté *et al*.

2004). However, measuring diet selection may be exceedingly difficult when methods are expensive, time consuming or require extensive expertise in unrelated fields of study (i.e. microscopic cell identification, plant identification and chemical analysis of plant tissue).

To measure diet selection in herbivores, availability and use of foods must be quantified (Norbury and Sanson 1992). Quantifying food availability is commonly accomplished by measuring available biomass of plant species in a given area (Edwards *et al*. 2004; Wam and Hjeljord 2010; Lashley *et al*. 2011) or by counting the relative number of stems available of each species (Lashley *et al*. 2011; Lashley and Harper 2012). Use of foods is measured using three predominant methods: (1) microhistological surveys (identification of plants cell walls remaining in gut contents or faecal excretions; Holechek *et al*. 1982); (2) direct bite counts of tame animals (Wam and Hjeljord 2010); or (3) indirect bite counts (identifying herbivory on damaged plant tissues; Lashley *et al*. 2014*a*). However, techniques to measure use have advantages and disadvantages. The microhistological survey is the most common technique used to measure diet selection in herbivores (Alipayo *et al*. 1992; Marrero and Nogales 2005; Jung *et al*. 2015). It has the advantage of detecting plants that may be consumed in entirety, and also accounts for the differences in bite sizes between plants, a distinction that may be lacking in bite count surveys. However, they have potential biases associated with differential digestibility of plant materials (Gill *et al*. 1983; Spalinger *et al*. 1986), and hence require that correction factors based on the relative digestibility of plant materials be accurate (Pulliam 1978; Holechek *et al*. 1982). Furthermore, the technique either requires expertise in identification of plant cell structures or necessitates additional costs associated with contracting that expertise. Directly observed bite counts of animals are rarely used with success unless tame animals are available or wild animals can be followed. Moreover, tame animals may not select all the same plants as wild animals in some cases (Spalinger *et al*. 1997), and direct observation of wild animals is normally restricted to less elusive mega-herbivores such as the giraffe (*Giraffa camelopardalis*; Parker and Bernard 2006). New technology may provide an exciting way to mitigate issues with tame or elusive animals by videoing animal selection with cameras installed on gps-radio-tags (Newmaster *et al*. 2013). However, this technology is relatively new and costly, labour intensive (from tagging animals and sorting videos) and still requires expertise in plant identification. Indirect bite counts rely on the identification of herbivory from the species of interest based on the structure of damage on remaining plant tissues (Lashley *et al*. 2014*a*). Biases associated with consumption of whole plants, differential ability to detect herbivory among plant species and inability to distinguish between species of herbivores may reduce the accuracy of indirect bite counts. Importantly, neither type of bite count can account for differential volumes of bites from one plant to the next. Despite these flaws, the indirect bite count method is potentially useful because of decreased time commitment for data collection, lack of need for animal observation and lower overall cost when compared to other methods. Therefore, the accuracy of the indirect bite count survey warrants further investigation. To determine the accuracy of indirect bite counts in estimating diet selection, we used a site with a single primary herbivore, the white-tailed deer (*Odocoileus virginianus*). We compared the diet selection measured via indirect bite count to a concurrent faecal microhistological survey.

Materials and methods

Study area

Fort Bragg Military Installation (Fort Bragg; 73 469 ha; 35.1°N, 79.2°W) is located in the Sandhills physiographic region in the northern-most remnants of the longleaf pine (*Pinus palustris*) ecosystem in North Carolina. Fort Bragg is managed primarily on a 3-year growing-season prescribed fire regime (Lashley *et al*. 2014*b*). Fort Bragg was primarily forested (65%), with non-forested areas primarily being maintained in grasslands and firebreaks (mineral soil roads) (Lashley *et al*. 2014*b*). The average winter temperature was 6.9°C and the average summer temperature was 26.0°C. On average, rainfall was 120 cm, snowfall was 7.5 cm, and there were ~175 frost-free days per year (Sorrie *et al*. 2006). Fort Bragg was considered an important contributor to the floristic diversity of the longleaf pine ecosystem. It comprised more than 1200 plant species, 61 of which were rare, and three of which were federally endangered (see Sorrie *et al*. 2006 for detailed floristic accounts). Overall, Fort Bragg is floristically diverse compared to other sites in the longleaf pine ecosystem, which has been commonly regarded as one of the most floristically diverse ecosystems in the temperate zone (Platt 1999). Thus, Fort Bragg is floristically diverse in comparison to other ecosystems in the temperate zone. We confined all sampling to one of five areas on the study site to ensure that indirect bite counts and faecal microhistological surveys were comparable (Fig. 1). Each of these areas included all forest types occurring on the study site and no sample for one method was more than 1km from a sample of the other method. Thus, we considered the sampling conducted for the indirect bite counts and the faecal microhistological surveys to be directly comparable given the scale of sampling was well within the concurrent average summer home-range size of white-tailed deer on the study site (~2 km^2; Lashley *et al*. 2015).

Indirect bite count surveys

In mid-June and mid-August 2011, we randomly placed 120 50-m line transects within the five sampling areas to determine plant use by deer as well as stems available within reach of deer at Fort Bragg. In each of three 1.5-m × 1.2-m × 1.2-m plots centred at 10, 25 and 40 m along each transect ($n = 360$), we recorded all stems (i.e. availability) of each species and number of stems showing evidence of deer herbivory (i.e. use), and extrapolated the measurements to stems per hectare. Between 70 and 75 transects were systematically located in a grid pattern across each of the five sampling areas. Because of small sample sizes in each plot, we pooled all detections of a plant species across the plots. We used the structure of damage in remaining forage tissues and the foraging ecology of deer and other wildlife to distinguish herbivory between deer and other wildlife species (Lashley *et al*. 2014*a*). This method was particularly useful in distinguishing between lagomorphs

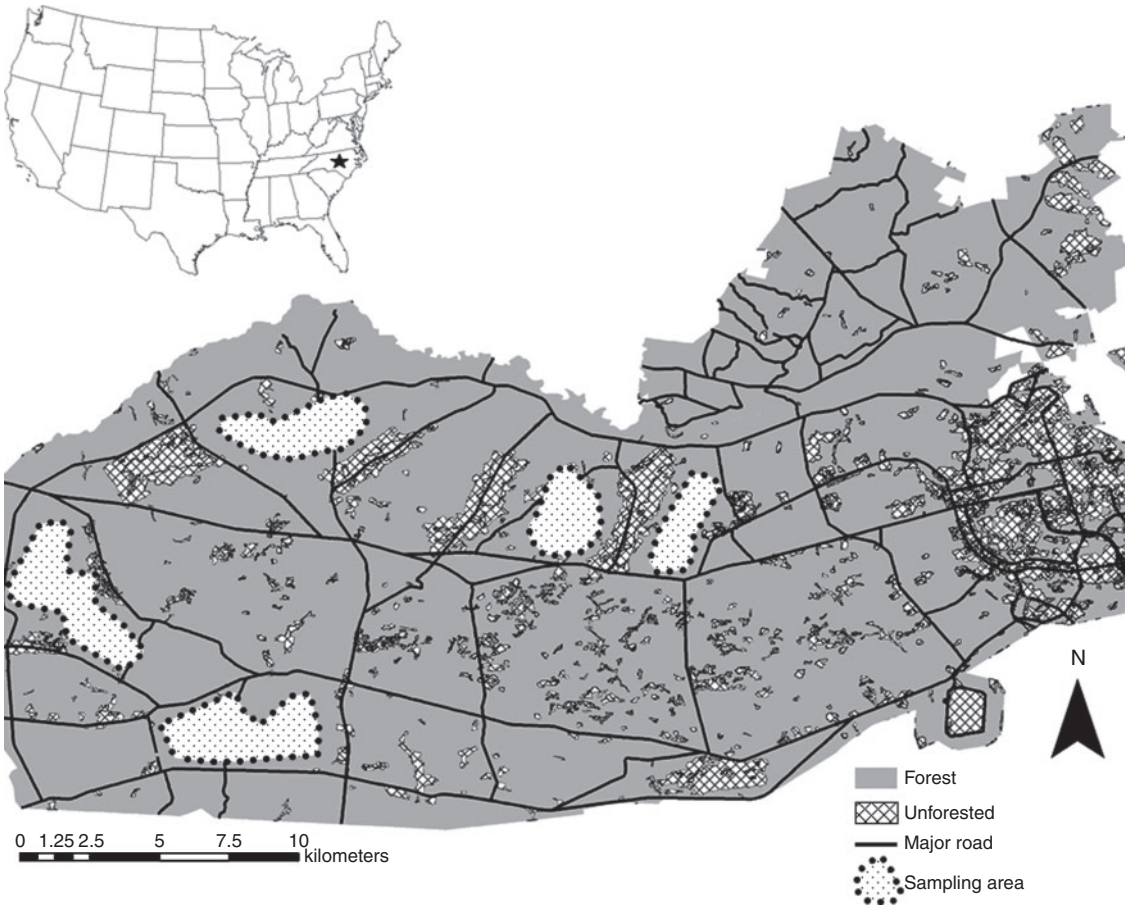

Fig. 1. Areas sampled during indirect bite count and faecal microhistological surveys at Fort Bragg Military Installation, NC. Dots within sampling areas represent the design used when establishing indirect bite count surveys.

and ungulates but may also be useful to identify insect damage as well (Lashley *et al.* 2014*a*). However, Lashley *et al.* (2014*a*) noted that distinguishing herbivory between wildlife species may be difficult in some cases, and this method likely contains sampling error related to damage detectability that may change with leaf morphology between plant species. Because our study area was primarily forested, all areas sampled for indirect bite counts represented forested areas. Therefore, we limited subsequent comparisons of the two methods to forest-dwelling plants to determine the indirect bite count's utility to establish selection of plants within a single vegetation type. The ability to assess diet selection by vegetation type was important in comparing the relative importance of plants within treatments (e.g. Lashley *et al.* 2011) and within a single vegetation type (e.g. Lashley and Harper 2012).

Faecal microhistological surveys

We collected deer faecal samples May–August 2011 and 2012 opportunistically across the five sampling areas at Fort Bragg to perform a microhistological survey, which gave the proportion of each plant species in the diet based on the remaining undigested plant cells in the faeces (Vavra and Holechek 1980). We collected at least five faecal samples >1 km apart, attempting to distribute samples across the areas as equally as possible for each week from 15 May to 31 August. We also formed weekly composite samples (mean = 12.2 faecal samples per composite sample for 30 composite samples). We sent all composite faecal samples to the Wildlife Habitat and Nutrition Laboratory at Washington State University (Pullman, WA), where microhistological surveys were conducted. Because various plant species may have been digested differently by deer, we collected samples of plants (72 genera) representing the plant-part selectivity of deer, dried the samples and submitted them to the Clemson Agricultural Service Laboratory (certified by the National Forage Testing Association) to determine the acid detergent fibre (ADF) of each plant during each month of faecal sample collection. ADF, a measure of undigestible fibres in plants, was used to standardise use based on the proportion of the plant that remained distinguishable in the microhistological survey (Vavra and Holechek 1980). After receiving diet compositions for each composite faecal sample, we weighted each plant-use percentage by the respective ADF to correct for differential digestibility of plants (Holechek *et al.* 1982). After correcting

for differential digestibility in each month, we calculated the average proportion of each plant across all composite samples (i.e. use).

To determine availability, we randomly placed 160 1.2-m × 1.2-m × 1.2-m woven-wire panel exclusion cages across the five sampling areas in forested areas of Fort Bragg in January–March 2011. Cages were designed to exclude deer, thereby allowing us to measure any effect of herbivory on understory biomass. From 1 to 14 August 2011, we collected all leafy biomass from woody species and entire herbaceous plants (excluding fibrous stems) within cages and from 160 paired uncaged plots placed at a randomly generated distance (10–100 m) and bearing (0–360 degrees) from the caged plot. We repeated the sampling protocol in 2012 by redeploying the cages to new random locations. We separated samples by plant species, bagged them in small paper bags, and dried them in an air-flow dryer at 50°C (Lashley *et al.* 2014*a*). We weighed dried samples to the nearest 0.01 g and calculated understory leafy biomass per hectare by summing plant weights from a plot and extrapolating to kg/ha. Thus, availability metrics of the indirect bite counts and microhistological survey were standardised to account for the different volume of the respective sampling methods.

Data analysis

For each method, we calculated a selection index (Chesson index; Chesson 1978, 1983) by dividing the ratio of use (i.e. stems browsed for bite count and the proportion of the diet for microhistological survey) and availability (i.e. total number of stems for bite count and available biomass for microhistological survey) for a given species by the sum of ratios for all species. We calculated the Chesson index allowing only use and availability of forest-dwelling plants to be considered in calculations. This was necessary to avoid biases that may be associated with animals having access to non-forested areas and the potential for consumption of plants that only occur in those areas. After deriving the selection index for each plant species for each of the two methods, we used Jaccard's similarity coefficient (J) to determine similarity between the lists of selected species as determined by each method. The J coefficient measures similarity between finite sample sets (in our case the list of selected plants from each method) and is defined as the size of the intersection divided by the size of the union of the sample sets (Jaccard 1901), or $J = \frac{C}{A+B+C}$, where A is the number of observations in the first sample (here, the microhistological survey) but not in the second (here, the indirect bite counts), B is the number of observations in the second sample but not in the first, and C is the number of observations in both samples. Following Real and Vargas (1996), assuming equal likelihood of detecting a given observation between both samples, the probability of finding a value of J less than the observed value is $P(J<J_{obs}) = \frac{\sum_{x=0}^{C-1}(\frac{N!}{x!(N-x)!})N-x}{3^N}$, where J_{obs} is the observed value of J, N is the total number of observations in either sample, C is the number of observations detected in both samples and x is a vector of values from 0 to C–1. We calculated $P(J<J_{obs})$ as a measure of accuracy of our comparative approach (i.e. high values of $P(J<J_{obs})$ correspond to a high degree of accuracy).

Results

Deer selected 36 plants based on the microhistological survey and 24 plants based on the indirect bite count. Fifteen plants were shared across both methods. Of the plants selected based on microhistology but not according to indirect bite counts, 14 of 21 occurred only in non-forested areas. When limiting the microhistological survey to only forest-dwelling plants, it identified 23 plants selected by deer, 15 of which overlapped with those selected according to the bite count survey (Table 1). Eight of the selected species in the microhistological survey made up the majority of the deer diet (51%) and seven of those species were also deemed selected by the bite count survey (Table 1). Of the nine indirect bite count selected plants, seven were used but not selected according to the microhistological survey, and the other two plant species (one shrub and one forb) were not detected in the microhistological

Table 1. Forest-dwelling plants selected by white-tailed deer as indicated by microhistological survey and indirect bite counts in 2011 at Fort Bragg Military Installation, NC

Bold text indicates both methods identified the plant as selected

Common name	Scientific name	Microhistological survey	Indirect bite count
Alder	*Alnus* spp.		X
Aster	***Aster* spp.**	**X**	**X**
Indigo	*Baptisia* spp.		X
Sedge	***Carex* spp.**	**X**	**X**
Hickory	*Carya* spp.	X	
Butterfly pea[A]	***Centrosema* spp.**	**X**	**X**
Partridge pea[A]	***Chamaecrista* spp.**	**X**	**X**
Pepperbush[A]	***Clethra* spp.**	**X**	**X**
Nettle	*Cnidoscolus* spp.		X
Dogwood[A]	***Cornus* spp.**	**X**	**X**
Dwarf Hawthorne	*Crataegus uniflora*	X	
Titi[A]	***Cyrilla* spp.**	**X**	**X**
Tick-trefoil	***Desmodium* spp.**	**X**	**X**
Milk pea	*Galactia* spp.		X
Bushclover	*Lespedeza* spp.	X	
Fetterbush	*Lyonia* spp.		X
Waxmyrtle	*Morella* spp.	X	
Blackgum	*Nyssa sylvatica*		X
Virginia creeper[A]	*Parthenocissus quinquefolia*	X	
Common pokeweed[A]	***Phytolacca americana***	**X**	**X**
Silkgrass	*Pityopsis* spp.		X
Black cherry	*Prunus serotina*	X	
Sumac	***Rhus* spp.**	**X**	**X**
Locust	*Robinia* spp.		X
Blackberry	***Rubus* spp.**	**X**	**X**
Sassafras	*Sassafras albidum*	X	
Rosinweed	***Silphium* spp.**	**X**	**X**
Greenbrier[A]	***Smilax* spp.**	**X**	**X**
Goldenrod	*Solidago* spp.	X	
Common sweatleaf	***Symplocos tinctoria***	**X**	**X**
Blueberry	*Vaccinium* spp.		X
Grape	***Vitis* spp.**	**X**	**X**

[A]Plants collectively representing 51% of the diet composition based on microhistological surveys.

survey (i.e. no plant cells were found), indicating herbivory may have been misidentified or the plants were a negligible proportion of the diet. The lists of selected species from each method had a Jaccard coefficient of 0.469 ($P(J<J_{obs})$ = 0.92), indicating the methods were 46.9% similar in their determination of selected plants, with a high probability of obtaining more dissimilar samples by chance alone. Additionally, a plot of the empirical cumulative distribution function for all possible values of J at our sample size indicated a cumulative probability of 0.74 to the left of J_{obs} (Fig. 2).

Discussion

The indirect bite count was relatively accurate in identifying the selected species representing the majority of the deer diet, only failing to rank one species as selected that was selected by microhistology. However, the indirect bite counts did incorrectly classify several plants as selected that were not selected by microhistology. Thus, researchers and managers may be able to use the indirect bite count surveys to determine the most important plants to deer but may simultaneously falsely identify other plants. This is obviously problematic in some cases, but in other instances this may be unimportant. For example, if the plants (both correctly and falsely identified as selected) responded similarly to management actions, then the list of plants would be beneficial to direct management. The problem would arise when the manager is tasked with managing for plants with very different life-history strategies (e.g. early versus late successional plants), and unknowingly some of those plants are not selected or important. Thus, the misidentification of selected plants by the indirect bite counts could be problematic. We were not able to find any trends in those misidentifications in terms of life history traits of the plants as they occurred with annual and perennial forbs and woody plants. However, the misidentifications tended to be plants that were infrequently detected (i.e. we detected <100 stems on five of nine misclassified plants). Thus, simply increasing the sampling intensity of indirect bite count surveys may increase the precision of estimates or provide more insight into patterns of misidentification and thus alleviate problems with misidentifying selected plants. Conversely, if plants were rare enough on the landscape that they were not detected in faecal samples, they may have not been detected because they were rarely available rather than not selected. It is likely that the methods would be more complementary in less floristically diverse systems. Regardless, our findings suggest that this method is reliable, considering the high probability of obtaining a smaller value by chance alone (or, conversely, the low probability of obtaining a value greater than or equal to that observed, $1–P(J<J_{obs})$; also, Fig. 2. Future research is needed to understand whether the inconsistencies we observed between the methods can be reconciled by altering sampling intensity to accommodate the site-specific floristic diversity.

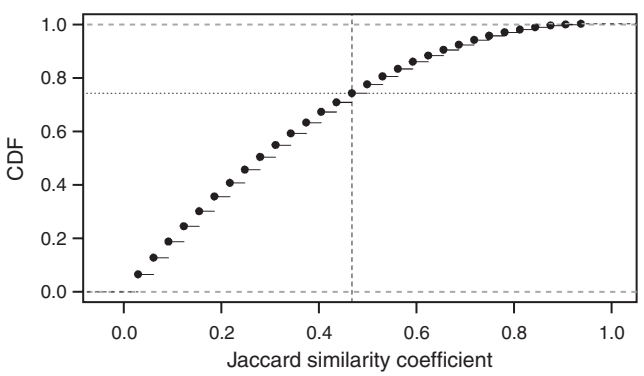

Fig. 2. Empirical cumulative distribution function for all possible values of Jaccard's similarity coefficient (J), given $N = 32$ and $C = 15$. The vertical dashed line represents our observed value, J_{obs}, and the horizontal dotted line the cumulative probability at J_{obs}.

Although the indirect bite count method had a much better agreement with the microhistological survey than should be expected by random chance, we could not account for biases associated with inability to distinguish between herbivores, inherent differences between stem count and biomass metrics to estimate availability (i.e. biomass per stem may vary within a species; Poorter *et al*. 2012), and the amount of the plant consumed, which probably accounted for some of the inconsistencies among methods that we observed (Hewitt 2011). Two plants identified as selected in the indirect bite count were never detected in the microhistological survey, which may indicate that some herbivory misidentification was occurring in our relatively simple herbivore system (i.e. deer, lagomorphs and insects), or that plants were selected but were in low enough abundance that they were not detected in the microhistological survey. More complex systems with sympatric herbivores that share similar mouth morphology likely would lead to more inaccurate indirect bite count surveys (Lashley *et al*. 2014*a*). However, in situations with multiple sympatric herbivores, bite counts still may be useful when combining them with other data such as the presence of tracks (Vivas and Sæther 1987; Sæther *et al*. 1989; Shipley *et al*. 1998). Also, stem counts and biomass measurements may not predict the same availability because of the inherent differences in biomass allocation per stem across plant species (Poorter *et al*. 2012). However, the indirect bite count must rely on the proportion of stems bitten and stems available to calculate the selection index because the bite count method cannot account for the biomass removed per bite. Therefore, if precise measurements of selectivity are needed, microhistological surveys with the necessary biomass and digestibility data are likely a better option.

Cost efficiency of the indirect bite count method is superior to the microhistological survey, making it a more practical method when resources are limited (Table 2). The time commitment and manpower needed to conduct indirect bite count surveys were minor in comparison to the microhistological survey. Also, the microhistological survey required simultaneous collection of representative plant samples to determine availability, contracted services to measure plant digestibility (i.e. 5 USD per sample), microhistological analysis (i.e. ~100 USD per sample) and 6–12 months to acquire laboratory results. Undoubtedly, the indirect bite count survey is more efficient in almost all metrics of efficiency. Moreover, indirect bite count surveys are more convenient because one can simultaneously measure plant use and availability as opposed to the multiple steps required with other methods of

Table 2. Estimated time commitment (Hours) and costs (USD) of the microhistological survey and indirect bite count survey used to determine white-tailed deer diet selection in the current study at Fort Bragg Military Installation, NC

Item	Microhistological Survey		Indirect Bite Count	
	Time	Cost	Time	Cost
Labour	873	8730	60	600
Materials		2000		50
Contracted Services		3360		
Total	773	14 090	60	650

determining diet selection. Therefore, indirect bite count surveys represent a time and cost-efficient tool that may be used to study diet selection and related research questions, if some accuracy can be spared. These potential advantages warrant further investigations to improve the inaccuracies associated with the indirect bite count survey method.

Implications

Indirect bite counts identified the majority of selected plants, which may be useful for comparing diet selection across years and vegetation types (Lashley and Harper 2012), for informing estimates of nutritional carrying capacity in silvicultural treatments (Edwards *et al*. 2004; Lashley *et al*. 2011) and for identifying important plants to target with management practices. However, the method also falsely identified some plants as selected, indicating further development of the methods is needed to improve usefulness. Furthermore, indirect bite counts may provide a useful index to measure relationships between animal density and carrying capacity or to identify plants vulnerable to deer browsing pressure. For example, surveying the percentage of stems browsed may allow managers to assess the likelihood that herbivores are limiting plant regeneration (Gill 1992). Researchers and managers should consider the indirect bite count method to determine diet selection when time and cost are of concern, but should beware of the inherent inaccuracies.

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