Issues and Perspectives

Measuring Ungulate–Forest Interactions: A Methods Primer

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Introduction

Ungulates interact with their environment through top-down and bottom-up mechanisms. They can play a “keystone” role in ecosystems because of their top-down influences on forest structure, composition, and biodiversity (Rooney 2001). For example, herbivory may significantly affect early successional plant species because young plants have increased nutritional quality and decreased secondary defense compounds, increasing palatability and therefore herbivory (Rhodes et al. 2018). This can affect some species’ regeneration early in the growing season or after disturbance (e.g., aspen *Populus* spp.; Seager et al. 2013), thereby influencing the structure and composition of forests (Rhodes et al. 2018). Similarly, bottom-up changes in vegetation structure, composition, availability, and nutritional content across seasons and weather events (e.g., droughts, floods, etc.; Beck and Peek 2005) can influence ungulate distribution and population dynamics (Rooney 2001). For instance, changes in forest management such as fire suppression may reduce the quality and extent of habitats available to support ungulate populations by limiting the amount of available early successional forage (Proffitt et al. 2016).

Globally, ungulates are native to most forested regions and their densities have increased across the Northern Hemisphere in recent decades (Reimoser 2003; Pellerin et al. 2010). This effect has been especially pronounced in temperate zones with increased agricultural production, conservative management policies, and forestry practices favoring early successional forest stands, in conjunction with increasingly mild winters (e.g., white-tailed deer *Odocoileus virginianus* Kuijper 2011). However, some populations across the northern hemisphere have the opposite trend (Merems et al. 2020) as locations of early successional stands have changed and may no longer occur in areas accessible to ungulates (e.g., elk *Cervus canadensis*; Cook et al. 2016). Because of these differing trends, there has been increased interest in ungulate–forest interactions and their cascading effects, which has motivated the development of methods to address research and monitoring needs. This has resulted in multiple methods addressing similar questions, leading to uncertainty when determining which method is most appropriate for a study’s objectives and spatiotemporal scale.

Here, we review current methods used to answer ecologically important questions of how ungulate populations affect their environment and how environmental conditions affect ungulate populations. We used Web of Science and Google Scholar to search for scientific publications relating to ungulate–habitat interactions in temperate regions using a snowball sampling method (Vogt 2005), collecting relevant papers on the basis of citations within examined manuscripts. In total, we reviewed 274 publications ranging between 1939 and 2020 (Text S2, *Supplemental Material*). For each commonly used method identified in the literature review (Figure S1, *Supplemental Material*), we compiled the type of data required, assumptions, advantages and disadvantages, and research questions addressed. Our goal is to provide a practical guide for researchers to select optimal monitoring techniques to gather data on the basis of their specific research question(s).

Objectives of this primer are to 1) summarize common techniques used to address interactions between ungulates and forested ecosystems from top-down and bottom-up perspectives, 2) present advantages and disadvantages of each technique, and 3) provide examples of research questions appropriate for each method. More information for each method, including additional references, is provided in the supplemental material (Text S1, *Supplemental Material*). We organized this into two broad categories on the basis of the mechanism being investigated: 1) top-down interactions include questions about ungulate impacts on forests, and 2) bottom-up interactions address questions about forest impacts on ungulates. For instance, reduction in average twig age of woody tree species due to high deer browsing (Waller et al. 2017) reflects a top-down effect, whereas the use of denser forest stands during high heat by moose is a bottom-up effect (Borowik et al. 2020). Without commenting on ecological debates about the utility of the top-down/bottom-up framework (Kay 1998; Gandiwa 2013) or the strength or direction of trophic effects (Martin et al. 2010; Nuttle et al. 2011), we adopted the top-down/bottom-up structure as a useful dichotomy for understanding research and monitoring motivations related to ungulate–forest interactions.

Methods Review

Top-down: measuring effects of ungulates on forests

Ungulates may influence the structure, composition, and biodiversity of forests by affecting regeneration, growth, and survival of plant species directly (e.g., browsing) or indirectly (e.g., trampling, competition). This ultimately affects forest structural heterogeneity, the structure of understory plant communities, and other ecological phenomena (Putman 1986; Rooney 2001; Rooney and Waller 2003; Côté et al. 2004), meaning ungulates have important impacts on forest ecosystems, even at low densities (McInnes et al. 1992; Hobbs 1996; Waller and Maas 2013). Furthermore, areas with high ungulate densities or with selective browsers may see a change in plant community composition due to ungulate impacts on sensitive plant species (Rooney 2001; Schumacher and Carson 2013). For example, white-tailed deer tend to favor oaks *Quercus* spp. relative to other available species such as maples *Acer* spp. and ash *Fraxinus* spp., suppressing oak regeneration (Strole and Anderson 1992). Persistent browsing of this nature may lead to an alternative stable state dominated by ferns, graminoids, and shrubs rather than mature hardwoods (Royo and Carson 2006). A growing understanding of the cascading effects of herbivory indicates that ungulates can function as a keystone species in ecosystems because of their disproportionate direct effects on vegetation and indirect effects on other organisms (Waller and Alverson 1997; Rooney and Waller 2003). Therefore, management of ungulate herbivory in forests is critical for biodiversity conservation (Mitchell and Kirby 1990; Gotmark 2013).

Methods for assessing effects on trees

Recruitment: ten-tallest. The ten-tallest method uses the height of focal tree species to understand the influence of ungulate herbivory on population- and site-level forest regeneration and recruitment (Rawinski 2018). This method is based on the heights at which stems are most susceptible to browsing and the point at which they escape browse, representing sapling recruitment (e.g., 0.3–0.6 and 2 m, respectively, for white-tailed deer; Walters et al. 2020). It measures species-specific browse across time in permanent plots to understand if individuals of preferentially browsed species reach recruitment height. This method provides insight into site- and population-level impacts of ungulate browse on forest recruitment. Specifically, the method addresses questions related to recruitment trajectories, long-term trends in forest regeneration, and inter- and intraspecific recruitment comparisons. Example questions include "Are tree saplings on track to grow beyond browse height?" "Is browse damage increasing or decreasing across time within a site?" and "Are there recruitment differences among and within species?" This method can also be adapted to address questions related to shrubs and herbaceous vegetation, as well as dormant-season browsing (Rawinski 2018).

The ten-tallest method is useful for quick, simple, and repeatable evaluation of ungulate browse and its impact on seedling regeneration across time. It can be completed with relatively high accuracy and consistency across field crews without extensive training or experience. As a result, this method is relatively inexpensive and can be done annually. Given that this method focuses on several focal species rather than all species within the plot, it does not provide insight into community-level shifts. Thus, it may not accurately portray future forest conditions or potential interspecific competition from nonfocal species, and it cannot address broader community-level questions without additional work to calibrate it to measure community change.

Regeneration: twig age. The twig age method uses browsing rate (i.e., the length of time a twig grows before it is browsed) to estimate impacts of browsing on seedling development (Waller et al. 2017). In other words, it indicates the duration of time a plant grew before being browsed, which influences seedling survival (Waller 2018). This method addresses questions related to rate of herbivory and tree growth, and changes in herbivory rate and intensity across time. Through a single sampling event, questions such as "Is the frequency of browse significantly inhibiting forest regeneration?" "What is the browse return interval or time between browse events?" or "Is browse consistent across time or does it vary?" can be answered.

Twig age is a relatively quick and easy method to implement but is limited in its inference as it cannot differentiate between browse and other sources of twig damage. It requires limited training and has been shown to produce reliable and consistent estimates of ungulate impacts (Waller et al. 2017). Additionally, it does not require repeated samples or visits to obtain several years of data. It does, however, tend to underestimate mean time between browse events as it cannot differentiate between causes of twig damage (Waller et al. 2017). For example, deer and rabbit browse cannot be distinguished definitively. Thus, it is not an ideal method for a study if a site or tree species are prone to internal or external twig killing phenomena and there is a goal of understanding ungulate browse impacts only.

Regeneration: Forest Inventory Assessment Regeneration Indicator. The Forest Inventory Assessment Regeneration Indicator is a set of standard measurements managed by the U.S. Forest Service. It incorporates a browse index and seedling stem counts to evaluate herbivore impacts on forest regeneration at a landscape scale (e.g., home range or study area). The broad-scale, public nature of Regeneration Indicator data lends itself to landscape-level questions about forest regeneration. Specifically, it can be used independently to address questions related to forest regeneration or can be combined with other regeneration indices to provide a herbivore impact metric across time and space (McWilliams and Westfall 2015). Patton et al. (2018), for instance, used Regeneration Indicator data from across the Great Lakes region to determine the predictive power of socioecological data to forecast deer browsing at the county level. These sorts of analyses may not be possible in all areas as Regeneration Indicator data is only available for the northeastern United States (McWilliams and Westfall 2015).

This method covers a broad spatial scale and is easily combined with other metrics to address complex questions. It can also augment the Forest Inventory Assessment's vegetation profile and invasive plant data to provide a more holistic look at forest communities (McWilliams and Westfall 2015). However, it is relatively simplistic with limited inference and evaluates past, rather than present, browse impacts and it tends to have a high error at the extremes (estimates mid-level browsing impacts the best; McWilliams et al. 2015). Thus, in areas with high browsing, abundant seedlings must be present to accurately estimate the impact of browse (McWilliams et al. 2015).

Methods for assessing impacts on woody and herbaceous vegetation

Herbaceous only: herbaceous indicators. Herbaceous indicator species act as proxies for understory conditions and indicate whether herbivory is driving native species declines or community-level shifts in species composition and structure. Field methods vary depending on research needs, species availability, and plant abundance. The adaptability of this method to various indicator species and experimental designs makes it amenable to a variety of questions across diverse spatial and temporal scales. Questions such as "How does browse affect plant growth across time?" can be addressed without repeated sampling when sampling a long-lived species (Augustine and Decalesta 2003). Likewise, questions addressing multiple spatial scales like "How does browse affect plant communities at local and regional scales?" can be evaluated using indicator species with broad distributions.

However, herbaceous indices have characteristic disadvantages. First, there is a short sampling window because sampling is limited to the focal species' growing season (e.g., a 2- to 3-wk window when flowers are present; Irwin 2000). Second, it may not represent current-year deer browsing because flower production may be limited by the previous year's browsing. This causes a lack of flowers in the present year, representing the effects of both the current and previous year's browsing (Knight 2003). Similarly, flower production can be reduced by intra- and interspecific competition such as plant density (Waller et al. 2017). Last, herbaceous indices may not provide a consistent metric across communities because of variation in growth and reproductive status of the indicator species among communities (Waller et al. 2017).

Woody and herbaceous: *ungulate exclosures*. Exclosures assess plant or plant community responses to the absence of herbivory by excluding ungulates using fencing or other barriers. Studies using exclosures address questions related to the magnitude of browse impacts, alternative plant community trajectories in the absence of ungulate herbivory, and long-term herbivory impacts. Exclosure studies are ideal for direct comparisons between the presence and absence of ungulates, especially when several small permanent plots are used (Augustine and Frelich 1998; Urbanek et al. 2011). For example, Abrams and Johnson (2012) used 30 pairs of fenced and unfenced 2 × 2 m permanent plots to characterize the impact of deer browsing on forest overstory and understory between browsed and unbrowsed plots.

Although several studies have used replicate, small exclosures (Koh et al. 1996; Urbanek et al. 2011; Abrams and Johnson 2012), most studies compare one or two large fenced and unfenced areas (Tanentzap et al. 2011; Long et al. 2012; Shen et al. 2016). This can be useful for gaining long-term data and for demonstration. However, it can lead to pseudoreplication when treating within-exclosure replicates as independent samples rather than subsamples (i.e., sampling occurs among exclosures, whereas subsampling occurs within an exclosure; Hurlbert 1984). Additionally, large exclosures may alter ungulate movement patterns outside the exclosure and in turn, conclusions drawn from sampling outside an exclosure may not be indicative of forest structure under normal browsing conditions (Horsley et al. 2003). Thus, Frankland and Nelson (2003) recommended using several small, replicate exclosures to reduce the probability of pseudoreplication and reduce bias from altered ungulate behavior and movement.

Bottom up: measuring effects of forests on ungulates

Ungulate fitness depends on quantity, quality, and structure of aboveground vegetation in forests. Nutrient availability can influence populations by affecting their survival and reproductive success (Merems et al. 2020). As a result, nutritional measurements are often used as a metric for population health (Cook et al. 2004b; Mosbacher et al. 2016; Cain et al. 2017). Similarly, vegetative structures may affect the demography of ungulates directly by influencing microclimates and mitigating predation risk, and indirectly by altering forage availability (Mysterud and Østbye 1999). For example, a closed forest canopy may reduce the fitness costs of heavy snowfall during winter (Kirchhoff and Schoen 1987; Van Deelen et al. 1998) but may also reduce herbaceous forage production in the summer by limiting light and precipitation penetration (Anderson et al. 1969). This can result in herbivores making trade-offs between forage acquisition and proximity to thermal and escape cover (Reynolds 1966; Lyon and Jensen 1980; Mysterud and Østbye 1999), which can affect reproduction, lactation, and survival, driving population dynamics (Proffitt et al. 2016; Merems et al. 2020).

Methods for assessing nutrition

Composition: observational estimates. Observational estimation of nutritional intake involves watching captive or habituated animals forage while an observer counts individual bites an animal takes during a sampling period (Berry et al. 2019). Direct observation provides insight into mean bite size (g/bite), mean bite rate (bites/min), harvest rate (g/min), and biomass consumed (Berry et al. 2019). Bite count data can be used to rank forage preference by using a relative preference index, which compares the relative percentage of a species in the diet to its availability on the landscape (DeYoung et al. 2019). Specifically, this method quantifies what and how much ungulates are consuming. Example questions include: "How much biomass does an individual consume during a certain time period?" "Which forage species do ungulates prefer?" and "What nutrients are individuals obtaining during a foraging period?"

Captive ungulates are good surrogates for their wild counterparts as their foraging behaviors (e.g., diet selection, encounter rates [rate of encountering forage species], bite rates, and search times [time taken to find forage species]) are similar (Cook et al. 2016). Thus, this method is ideal for understanding fine-scale behaviors and, if combined with other measures of nutrition, can provide information on nutritional quality of each bite acquired by an ungulate (Shipley 2007). Although direct observations occur at fine scales, observed patterns can be extrapolated to larger spatial and temporal scales using statistical inference (e.g., Cook et al. 2016); however, prediction errors may occur and caution is needed (Yates et al. 2018). The main logistical challenges are access to captive or habituated animals, their transition time from supplemental feed to natural forage, and habituation to the new enclosure (Cook et al. 2016). One important consideration is that individual ungulates may have biases in their foraging behavior (e.g., have reduced foraging intensity) because of prior supplemental feeding (Olsen-Rutz and Urness 1987). These limitations may cause direct observation to be time and cost prohibitive.

Composition: microhistological analysis. This method assesses plant fragments found in fresh fecal samples using microhistological identification (Jenkins and Starkey 1993) while providing insight into which plants ungulates are consuming by identifying forage fragments to life form (graminoid, forb, or tree/shrub), genus, and sometimes species. Microhistological analysis can be applied to larger questions about forage selection (i.e., plant species individuals are choosing to forage; Johnson 1980) by comparing what species are consumed to species present on the landscape. Additionally, information on the quality of forage ingested can be inferred by linking the consumed species to its nutritional value. This method addresses questions such as: "Which plant species are ungulates consuming pre- and postwildfire?" and "What is the composition of woody browse in their diet?"

The benefit of this method is that it is noninvasive and cost-effective (Monteith et al. 2014; Mosbacher et al. 2016; Proffitt et al. 2019). However, plant species have differing levels of digestibility on the basis of their fiber content and secondary compounds, meaning highly digestible species may be consumed but not be found in fecal pellets (Monteith et al. 2014; Proffitt et al. 2016; Berini and Badgley 2017; Cain et al. 2017). For instance, less-digestible species such as conifers and evergreen shrubs are often overrepresented in microhistologically-derived diet analyses because of their higher levels of secondary compounds compared with deciduous shrubs. Because of this, it is important to not relate relative abundance of forage in microhistological analysis to forage preference (i.e., the likelihood of an ungulate selecting one species over another when both are equally available: Johnson 1980; Jenkins and Starkey 1991). Another limiting factor is that samples are prone to decomposition and must be refrigerated (17°C) until analysis to ensure that at least two microanatomical epidermal features are maintained for species identification (Hanley and McKendrick 1985; Cain et al. 2017).

Composition: forage biomass. Biomass measuring methods are useful for determining the amount of forage available to ungulates on the landscape; biomass is typically measured at fine scales (e.g., 0.75-m^2 quadrats to 3-m^2 subplots; Lindgren and Sullivan 2018; Robatcek 2019). This method can be combined with quality measurements to address questions such as "How much nutrition are ungulates obtaining from the landscape?" "How is their forage intake affecting their nutritional condition?" and "Is there enough biomass on the landscape to provide adequate nutrition for successful reproduction and survival?" The best method combinations vary on the basis of the focal species and their location on the browser–grazer continuum (e.g., ungulates who feed on woody plants and forbs to ones who feed primarily on graminoids; Hofmann 1973; Bodmer 1990). For example, grazers (e.g., bison) rely more heavily on broad-scale factors such as available forage biomass to maximize intake rate, whereas browsers (e.g., deer) select for fine-scale factors like nutrient quality of plant species, individuals, or plant parts (Bergman et al. 2001).

This method is ideal for understanding fine-scale biomass availability while allowing for extrapolation to larger spatial scales (e.g., landscape level; Merems et al. 2020). Specifically, plant species' mass from a clipped plot can be related to its estimated percent cover within the plot to produce a species-specific cover-weight regression equation. This relationship can be used to estimate plant species' biomass within areas of the study site that were not clipped for biomass (Hanley and McKendrick 1985; Merems et al. 2020). Plant height can also be integrated into the regression equation to produce a more robust estimate of available biomass (Jenkins and Starkey 1993). However, this method can be limiting as it requires prior knowledge of forage species and is labor intensive. Fortunately, new technology is being assessed such as the use of airborne light detection and ranging, which may provide a more accessible method to measure understory biomass in the future (Hull and Shipley 2019).

Quality: *plant samples*. Digestibility (dry matter digestibility and digestible energy) and protein content (crude protein and digestible protein) are common metrics for understanding the nutritional value of forage for ungulates (Cook et al. 2016; Proffitt et al. 2019; Merems et al. 2020; Wisdom et al. 2020). Plant sampling provides insight into the quality of nutrition available to ungulates at the scale at which plants were sampled. Like forage biomass estimations, quality can be extrapolated from fine-scale measurements to larger scales when combined with observational methods and biomass methods. This method can address questions like "Does the habitat have sufficient nutritional value for the ungulates' survival and reproductive success?" "Is there enough crude protein available for a lactating female?" and "Should management work to increase nutritional quality?" This method is important for understanding nutrient acquisition because it directly quantifies nutrition obtained by ungulates; however, it can be time-consuming, costly, and samples must quickly be placed on ice and frozen until analysis.

Quality: fecal samples, *stable isotopes, and urinary analysis*. Fecal nitrogen is a widely used index of diet quality because diets rich in digestible protein have larger concentrations of fecal nitrogen (Monteith et al. 2014; Berini and Badgley 2017; Cain et al. 2017). Urinary analysis, used as a nutritional index, examines the ratio of urinary metabolites derived from urine-saturated snow (Garrott et al. 1997). Two commonly used measurements are 1) urea nitrogen : creatinine ratio (DelGiudice et al. 1996) and 2) allantoin : creatinine ratio, which have been shown to be strongly correlated to daily digestible dry matter intake (Vagnoni et al. 1996; White et al. 2011). Last, stable isotope analysis is a tool for tracking dietary changes and diet history and for monitoring ungulate populations (Mosbacher et al. 2016). Isotopes can be collected from bone collagen, hair samples, or fecal samples. Bone collagen can provide average foraging trends over the ungulate's lifetime (Berini and Badgley 2017). Hair samples provide shorter-term information on dietary changes induced by seasonal and annual fluctuations in ambient temperatures when the hair was growing (Mosbacher et al. 2016). Fecal samples provide information on forage ingested during the previous 24-48 h (Berini and Badgley 2017).

Stable isotope analysis can address dietary questions such as "Are ungulates obtaining enough dietary protein to meet their nutritional requirements?" "Has an individual's diet changed over time?" "How does diet change across seasons?" and "What nutrients have been obtained during a fine-scale period?" However, these measurements are insensitive to animal body conditions (i.e., body fat levels), which can be misleading (Cook et al. 2007). Comparative analysis between species of different body sizes or different life-history stages within a species (e.g., males, nonlactating females, and lactating females) may be challenging because of differences in digestive morphology and function (Monteith et al. 2014). These variations within the study population must be accounted for to make reliable inferences.

Quality: *remote sensing*. Remotely sensed greenness metrics such as normalized difference vegetation index, soil-adjusted vegetation index, and linear spectral unmixing are used as surrogates for nutrition when fine-scale nutritional metrics cannot be obtained (Merkle et al. 2016; Wisdom et al. 2020; Sadeh et al. 2021). In the ungulate literature, normalized difference vegetation index is the most-used proxy for vegetation net primary productivity and phenology across time and space (Espunyes et al. 2019; Olsoy et al. 2020) and can address questions such as "Does ungulate migration match spring green-up?" and "How does quality of forage change across the growing season?" Normalized difference vegetation index is an easily accessible and commonly used metric that is more cost-effective than fine-scale nutritional sampling (Olsoy et al. 2020). Applying this as a metric of nutrition assumes that foraging behavior and associated landscape use by the ungulate match the spatial and temporal grain of the imagery (Wisdom et al. 2020). Many widely used raster data sets use a 30 × 30 m pixel size; however, some ungulate species may forage in very small patches where a smaller grain (e.g., 10 × 10 m pixels) may be more appropriate (Wisdom et al. 2020). Using the larger grain that normalized difference vegetation index provides may lead to misinterpretation of functional traits since ungulates may be selecting or avoiding certain plant species at finer scales (Olsoy et al. 2020), so results should be interpreted with caution (Hebblewhite 2008; Pettorelli et al. 2011).

Methods for assessing thermal cover and shelter

Direct: snow depth and density. Snow interception by forest overstory and snow density may be critically important for overwintering ungulates as deep snow limits access to forage, increases energy required to move, and increases predation risk (Parker et al. 1984; Kirchhoff and Schoen 1987; Van Deelen et al. 1996; Visscher et al. 2006). The depth at which snow inhibits movement and foraging behavior varies with ungulate species and snow density (Parker et al. 1984). Snow tubes estimate snow density (g/cm^3) using marked metal rods to measure the depth (cm) and weight (cm^2) of snow, whereas compaction gauges measure the depth at which a rod penetrates the snow to estimate snow compaction.

These methods are efficient and cost-effective and can address questions such as "Does snow depth or density cause ungulates to use areas with greater canopy cover?" "Does snow interception by forest canopy reduce predation risk?" or "Will timber harvest remove important snow-intercepting canopies on ungulates' winter range?" However, these measurements tend to result in overestimations and can vary on the basis of snow conditions and the type of equipment being used (Work et al. 1965). To mitigate overestimations, researchers should take multiple measurements at a site to create a reasonable average estimation, although this may not be practical at the landscape level. If measurements at the landscape level are necessary, remotely sensed data has emerged as a method for measuring snow cover relative to ungulate habitat use (Maher et al. 2012). For example, Maher et al. (2012) used Landsat data to relate forage availability to snow cover for caribou across the Bathurst Island complex in Canada.

Direct: operative temperature. Operative temperature is the measurement of thermal environments experienced by an animal, which accounts for ambient air temperature and convective heat transfer caused by wind or solar radiation (Demarchi and Bunnell 1993). Demarchi and Bunnell (1993) took this a step further, developing a model for operative temperature that incorporates air temperature, wind speed, and solar radiation. These measurements can answer questions about the physiological stress experienced by ungulates in environments with extreme hot or cold temperatures and to assess the availability of thermal cover (Parker and Gillingham 1990). This method can be applied to questions such as "Does the thermal environment experienced by ungulates differ between habitat types?" "Does thermal stress affect ungulate survival or reproduction?" or "Do habitat management practices alter the thermal landscape experienced by ungulates?" Behavioral or physiological responses to temperature at the population level can be assessed using landscape-level weather data sets (e.g., Borowik et al. 2020), whereas the impact of habitat or timber management on site-specific microclimates is better addressed by fine-scale measurements (e.g., Grace and Easterbee 1979).

It may be necessary to measure several environmental factors to accurately model the operative temperature of the ungulate species being studied if a detailed understanding of physiological stressors is necessary for the research goals (Parker and Gillingham 1990). There is some debate as to whether thermal cover affects operative temperature enough to influence the performance of ungulate species; however, it remains of interest to conservation managers (Cook et al. 2004a). Although ungulates have been observed to use thermal cover to mitigate the effects of extreme heat or cold (e.g., Grace and Easterbee 1979; Borowik et al. 2020), the efficacy of thermal cover to alleviate thermal stress enough to influence survival at the population level is still unknown (Parker and Gillingham 1990). Whether or not thermal stress affects survival at the population level, ungulates are known to respond behaviorally to extreme temperatures by increasing their use of thermal cover (Borowik et al. 2020). As extreme weather conditions increase with climate change, managing wildlife habitat for thermal cover may become more important.

Indirect: visual estimation of canopy cover. Canopy cover can influence ungulate habitat use by providing shade (Borowik et al. 2020), intercepting snowfall (Grace and Easterbee 1979), and reducing the amount of available understory forage (Young et al. 1967). Ocular estimation involves estimating the openness of the tree canopy by naked eye. This method is fast and cost-effective, but it can be influenced by weather conditions and relies on self-calibration by the observers (Jennings 1999). Training could improve consistency in estimates; however, accuracy remains low even when estimates are taken by experienced professionals, and it is likely not accurate enough to produce broad-scale habitat recommendations (Jennings 1999; Korhonen et al. 2006). Robards et al. (2000) found that ocular estimates underestimate canopy cover compared with aided estimates such as spherical densiometers or photography. This method may be appropriate when forming local recommendations and when the observer and weather conditions remain constant during data collection, but it is not recommended when the data will be used more rigorously.

Viewing devices, such as a spherical densiometer, are used to systematically estimate the proportion of sky obscured by vegetative canopy (Lemmon 1956). The densiometer is widely used, durable, easy to carry, relatively inexpensive, and appears to be a reliable method considering the trade-offs of accuracy and time required in the field (Brown et al. 2000; Korhonen et al. 2006; Streich et al. 2015). However, this device has been shown to overestimate canopy cover relative to other devices (Robards et al. 2000; Ko et al. 2009) such as the moosehorn (Robinson 1947; Garrison 1949), vertical densiometer (Stumpf 1993), and canopy-scope (Brown et al. 2000). These devices operate on a similar premise and may be less biased. No matter the device selected, there will still be observer bias, which may produce inaccurate results or obscure patterns (Vales and Bunnell 1988; Cook et al. 1995).

Visual estimation of canopy cover, with or without a viewing device, is an appropriate method for research questions about site-specific habitat characteristics. Example questions include "Do ungulates select bedding sites with greater canopy cover as ambient temperature increases?" "Does the quantity or quality of available forage change with canopy cover?" and "Do ungulates use sites with greater canopy cover during periods of heavy snowfall?" The potential for discrete, point-level estimation of canopy cover makes this method convenient for answering fine-scale research questions, although impractical for addressing questions at the landscape level. This method is prone to observer bias and should therefore be used with caution; some viewing devices have a higher proclivity for observer bias than others (Bunnell and Vales 1990; Korhonen et al. 2006).

Indirect: photography for canopy cover. Wide-angle and hemispherical photography is a method used to quantify canopy closure and light (Leblanc and Fournier 2017). Measurements of canopy openness using photography can vary widely from complex indices (e.g., effective plant area index; Chen et al. 1991) to relatively simple metrics (e.g., percent canopy cover; Kirchhoff and Schoen 1987). Additionally, photographs provide permanent documentation of canopy geometry, and serial photographic sampling can provide data on changes in canopy structure over time (Rich 1990). This method can address research questions similar to visual estimations of canopy cover, although it has potential to answer more in-depth, site-level questions such as "Are long-term changes in canopy cover influencing shifts in ungulate habitat use?" and "Is ungulate habitat selection affected by fine-scale differences in canopy cover?"

It is unclear if photography is less biased than other canopy estimation methods; therefore it should be used with caution (Lindsay 2005; Korhonen et al. 2006). Photography is best suited for studies where a detailed or long-term understanding of canopy effects is required. In other cases, another method will likely be more time- and cost-effective. Camera equipment is relatively costly and fragile, and the time required to set up the camera and process the images is restrictive (Brown et al. 2000). Emerging technology, such as image processing through deep learning (a subfield of machine learning; Díaz et al. 2021) and photo collection and analysis using smartphone cameras apps (Patrignani and Ochsner 2015; Bianchi et al. 2017), may make this method more feasible in the future.

Indirect: standard forestry measurements. Commonly used forest inventory measurements such as diameter at breast height (1.37 m), stem density (stems/ha), tree height (m), and basal area (m^2/ha) can be used to estimate canopy cover. These measurements can be used to investigate questions at a range of geographic scales such as "How does forest structure influence snow interception on ungulates' winter range?" and "How do silvicultural practices influence ungulate habitat selection?" These measures reduce or eliminate the need to take extensive field measurements of canopy cover since they are often collected in forest monitoring programs (Gill et al. 2000). However, in cases where fine-scale canopy estimates are needed, or when stand-level management decisions are being considered, stand- or species-specific regression equations should be developed as the relationship between standard measurements and crown closure may differ on the basis of stand composition and structure (Korhonen et al. 2007; McIntosh et al. 2012). As computing power and modeling processes improve for calibrating models relating canopy cover to standard forestry measurements, this method may become more cost-effective and scalable for estimating canopy cover. Additionally, other habitat characteristics can be derived from the same data, and canopy characterization can be conducted simultaneously to monitor the effects of ungulate browse.

Indirect: remote sensing for canopy cover. Remote sensing using active or passive imagery can be used to explore the relationship between ungulates and canopy cover at site and landscape scales (Long et al. 2005; Melin et al. 2014). Active remote sensing is most appropriate when a detailed measure of the forest canopy is required in areas too large for visual measurements but smaller than the landscape scale. Passive remote sensing can be applied at the site or landscape level depending on image resolution. These methods address similar research questions to visual and photographic estimation but may also provide insight to questions like "How does canopy cover affect ungulate home range selection?" and "How are changes in canopy cover at the landscape level influencing ungulate habitat use or survival?"

These methods offer the ability to scale canopy cover estimations across large spatial extents by providing detailed canopy maps across broad-scale canopy estimates with publicly available data (e.g., tree canopy cover product; Ko et al. 2009; Sexton et al. 2013). The deployment of multispectral imaging technology like Landsat and the development of models to better interpret vegetation reflectance in remotely sensed images have broadened its applicability as a powerful tool for quantifying and monitoring vegetation (Houborg et al.

2015). However, relying on passive remote sensing may underestimate canopy cover compared with estimates from traditional ground-based methods (Ko et al. 2009; Hadi et al. 2016), and it may be limited by the timing, orbit, and resolution of the source satellite (Houborg et al. 2015). Active remote sensing provides more detailed imagery at higher resolutions compared with passive remote sensing (Houborg et al. 2015). Although further calibration may be necessary, remotely sensed data is generally time- and cost-effective, and is suitable for estimating canopy cover over large areas (Hadi et al. 2016).

Method to assess concealment cover

Visual obstruction. Vegetation can provide concealment or hiding cover for ungulates, which may allow them to avoid predation, as well as providing thermal cover from wind (Griffith and Youtie 1988). The most straightforward approach to measuring the visual obstruction characteristics of vegetation (i.e., horizontal cover) is the cover board (Nudds 1977). Because of variability among habitat types and research questions, similar devices have been developed, such as the density board (Wight 1939), Robel pole (Robel et al. 1970), and cover pole (Griffith and Youtie 1988), as well as various shapes including ungulate-shaped cutouts (Griffith and Youtie 1988) and three-dimensional ungulate effigies (Jacques et al. 2011). Cover boards, regardless of type/shape, can provide insight into questions relating to predator avoidance strategies and habitat selection by ungulates. For example, Jacques et al. (2011) measured the visibility of deer decoys with and without radio telemetry collars to assess whether tracking collars increased deer susceptibility to hunting mortality. Other questions of interest could include "Does vegetation density influence the frequency of deer–car collisions?" "Do ungulate dams select habitat with greater concealment cover during parturition?" or "Does vegetative cover reduce predation risk to ungulates?"

These methods are simple to use and cost-effective. They are adaptable to different study species (Nudds 1977) and ecosystems (Coulloudon et al. 1996) and can be modified to fit the needs of the study (Griffith and Youtie 1988). These devices used to assess cover can replace more time-consuming methods for estimating vegetation cover, such as clipping and weighing vegetation (Robel et al. 1970). Similarly, these measurements may be used to estimate the thermal cover benefits of understory vegetation, since shrub height is related to convective heat loss from wind (Grace and Easterbee 1979). These devices can also be photographed in the same location over time to assess long-term changes in cover (Coulloudon et al. 1996). However, some of these devices (e.g., cover boards and three-dimensional deer decoys) may be more cumbersome to transport than others. These devices require little training to achieve consistent measurements, but observer bias should always be considered when collecting data (Griffith and Youtie 1988).

Summary

In this review, we offer a practical guide for understanding methods applicable to studying ungulate–forest interactions. Included are two decision trees (Figures 1 and 2) to help guide method selection on the basis of research questions. Supplemental materials provide more information on each method and their associated references (however, detailed instructions for each method are not provided; Text S1, *Supplemental Material*) and a complete list of manuscripts reviewed for this primer (Text S2, *Supplemental Material*). Last, we created a summary table to help practitioners easily find methods that suit their research needs (Table S1, *Supplemental Material*).

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Text S1. In-depth descriptions of commonly used methods for estimating top-down effects of ungulates on forests and bottom-up effects of forests on ungulates. For each method, references of reviewed manuscripts are provided to easily access additional information.

Available: https://doi.org/10.3996/JFWM-21-091.S1 (99 KB DOCX)

Text S2. A complete list of all 274 manuscripts reviewed for this primer.

Available: https://doi.org/10.3996/JFWM-21-091.S2 (86 KB DOCX)

Table S1. Reference table of methods for estimating top-down effects of ungulates on forests and bottom-up effects of forests on ungulates, including their pros and cons, what they are estimating (e.g., timescale, spatial scale, category), example questions, and relevant citations.

Available: https://doi.org/10.3996/JFWM-21-091.S3 (36 KB DOCX)

Figure S1. This primer reviewed a total of 274 manuscripts to obtain commonly used methods addressing top-down effects of ungulates on vegetation and bottom-up effects of vegetation on ungulates. Top-down methods represented 21.5% of the manuscripts, bottom-up methods represented 67.8% of the manuscripts, and the remaining 10.6% were manuscripts with less common methods and were excluded from the methods review.

Available: https://doi.org/10.3996/JFWM-21-091.S4 (278 KB JPG)

Reference S1. Cook JG, Irwin LL, Bryant LD, Riggs RA, Thomas JW. 2004a. Thermal cover needs of large ungulates: a review of hypothesis tests. Pages 708–726

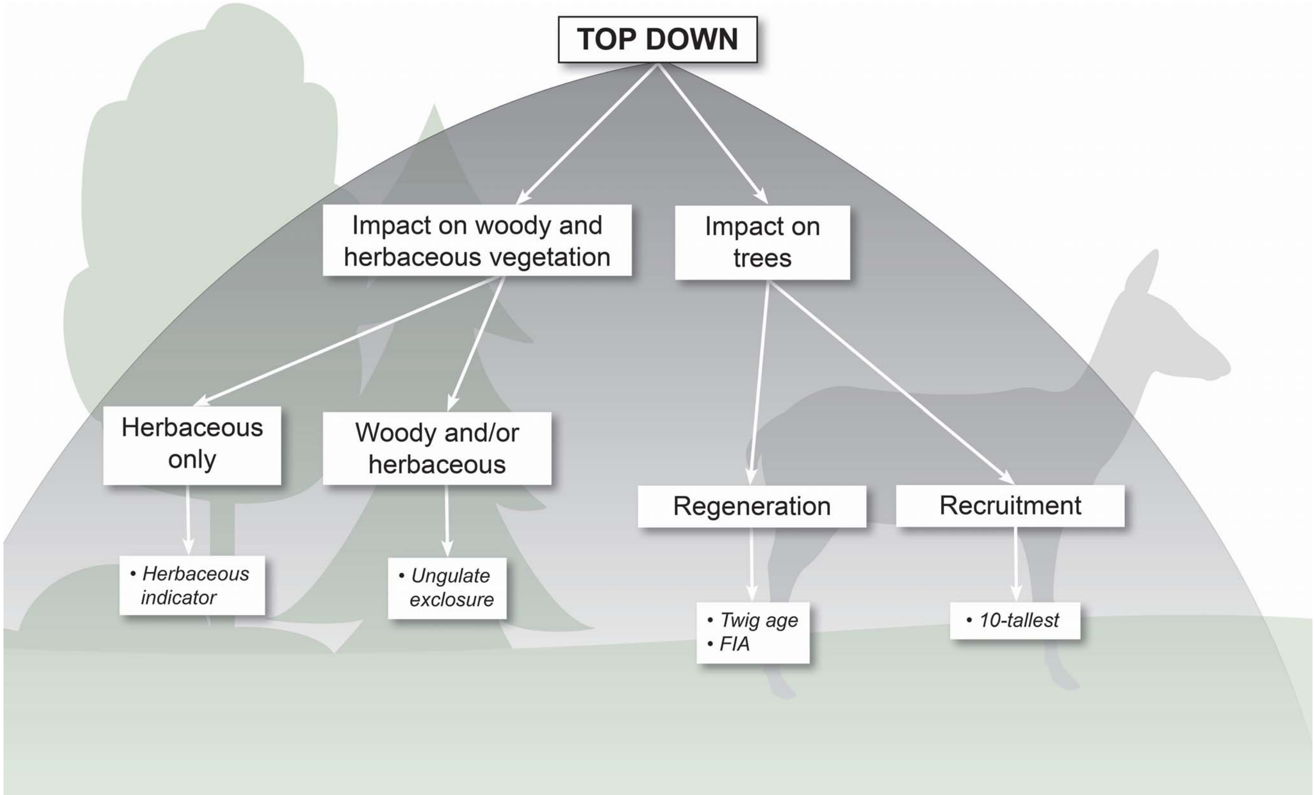

Figure 1. A decision tree for recommended methods based on individual-level research questions regarding top-down effects of ungulates on vegetation. Navigation requires an initial decision about whether the research motivations are better characterized as impacts on forests or impacts on woody or herbaceous vegetation.

in Transactions of the 69th North American Wildlife and Natural Resources Conference, Spokane, Washington.

Available: https://doi.org/10.3996/JFWM-21-091.S5 (1.181 MB PDF) and https://www.fs.fed.us/pnw/pubs/journals/pnw_2004_cook001.pdf

Reference S2. Coulloudon B, Eshelman K, Gianola J, Habich N, Hughes L, Johnson C, Pellant M, Podborny P, Rasmussen A, Robles B, Shaver P, Spehar J, Willoughby J. 1996. Sampling vegetation attributes. Interagency Technical Reference. Denver, Colorado: Bureau of Land Management.

Available: https://doi.org/10.3996/JFWM-21-091.S6 (2.210 MB) and https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1044175.pdf

Reference S3. McWilliams WH, Westfall JA. 2015. An early look at forest regeneration indicator results for the Midwest and Eastern United States. Pages 95–100 in Stanton CSM, Christensen GA, editors. Pushing boundaries: new directions in inventory techniques and applications. Forest Inventory & Analysis (FIA) Symposium 2015. General Technical Report PNW-GTR-931. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Available: https://doi.org/10.3996/JFWM-21-091.S7 (20.236 MB PDF) and http://www.fs.fed.us/pnw/pubs/pnw_gtr931.pdf

Reference S4. McWilliams WH, Westfall JA, Brose PH, Dey DC, Hatfield M, Johnson K, Laustsen KM, Lehman SL, Morin RS, Nelson MD, Ristau TE, Royo AA, Stout SL, Willard T, Woodall CW. 2015. A regeneration indicator for forest inventory and analysis: history, sampling, estimation, analytics, and potential use in the Midwest and Northeast United States. Newtown Square, Pennsylvania: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Available: https://doi.org/10.3996/JFWM-21-091.S8 (3.610 MB PDF) and https://www.fs.fed.us/nrs/pubs/gtr/gtr_nrs148.pdf

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Available: https://doi.org/10.3996/JFWM-21-091.S9 (1.754 MB PDF) and https://hdl.handle.net/2027/umn.31951d02996135d

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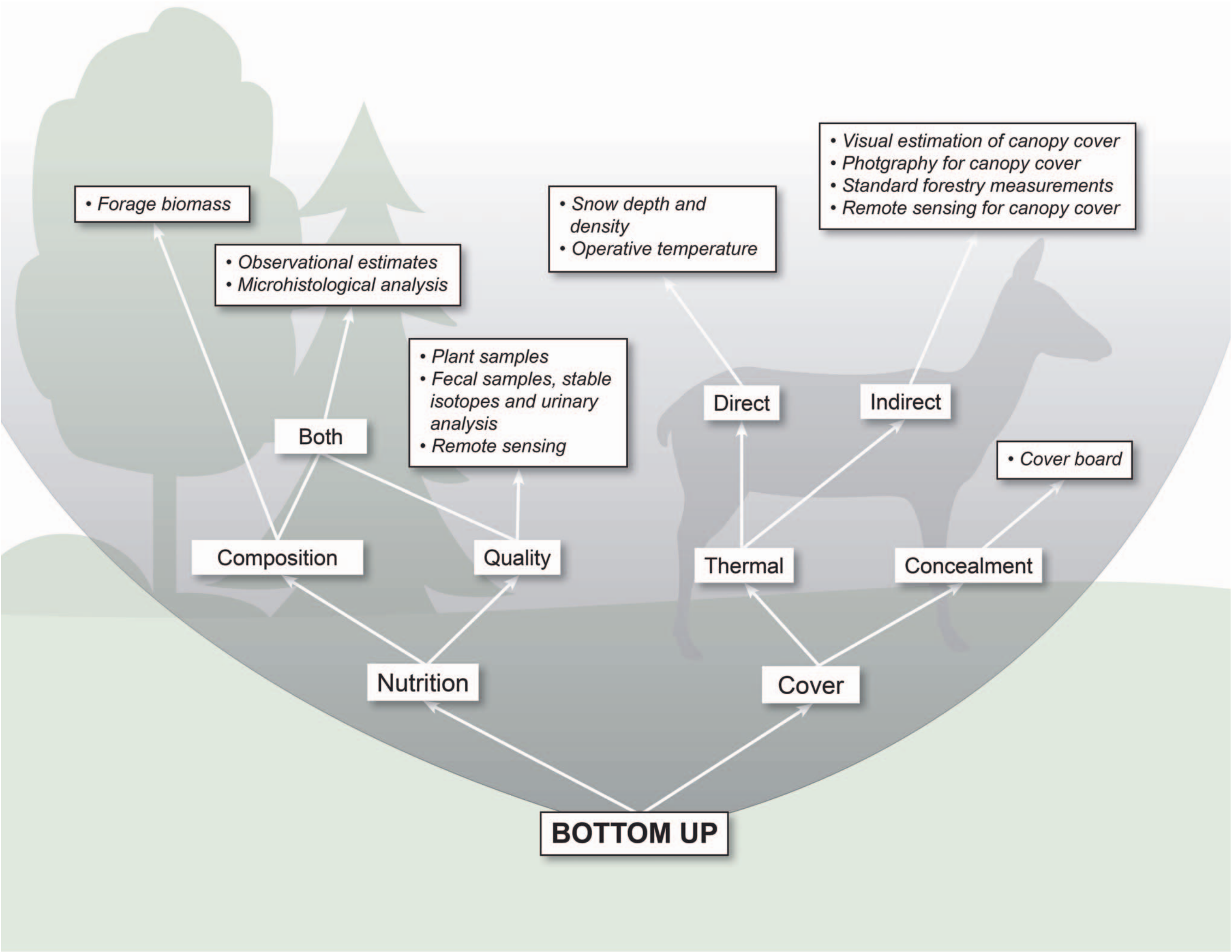

Figure 2. A decision tree for recommended methods based on individual-level research questions regarding bottom-up effects of vegetation on ungulates. Navigation requires an initial decision about whether the research question focuses on cover or nutrition.

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