

LETTER

Sampling bias exaggerates a textbook example of a trophic cascade

Elaine M. Brice¹  | Eric J. Larsen² | Daniel R. MacNulty¹ 

¹Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah, USA

²Department of Geography and Geology, University of Wisconsin – Stevens Point, Stevens Point, Wisconsin, USA

Correspondence

Elaine M. Brice, Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT 84322, USA.
Email: elbrice92@gmail.com

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Abstract

Understanding trophic cascades in terrestrial wildlife communities is a major challenge because these systems are difficult to sample properly. We show how a tradition of non-random sampling has confounded this understanding in a textbook system (Yellowstone National Park) where carnivore [*Canis lupus* (wolf)] recovery is associated with a trophic cascade involving changes in herbivore [*Cervus canadensis* (elk)] behaviour and density that promote plant regeneration. Long-term data indicate a practice of sampling only the tallest young plants overestimated regeneration of overstory aspen (*Populus tremuloides*) by a factor of 4–7 compared to random sampling because it favoured plants taller than the preferred browsing height of elk and overlooked non-regenerating aspen stands. Random sampling described a trophic cascade, but it was weaker than the one that non-random sampling described. Our findings highlight the critical importance of basic sampling principles (e.g. randomisation) for achieving an accurate understanding of trophic cascades in terrestrial wildlife systems.

KEYWORDS

aspen, carnivore, elk, non-random sampling, predator indirect effects, preferred browsing height, sampling bias, trophic cascade, ungulate, wolf

INTRODUCTION

Knowledge about the occurrence and strength of trophic cascades (indirect effects of predators on plants and abiotic processes) is vital to understand the forces that structure food webs. Much of the empirical information about trophic cascades derives from tractable systems that are variously small scale, aquatic, invertebrate and captive (Alston et al., 2019; Ford & Goheen, 2015; Piovia-Scott et al., 2017). Less is known about trophic cascades in terrestrial wildlife systems due in part to the difficulty and cost of measuring these large and uncontrolled systems in accordance with basic principles of sampling design, including control of variation, replication and

randomisation (Allen et al., 2017; Ford & Goheen, 2015; Hayward et al., 2019).

A textbook example of a trophic cascade in a terrestrial wildlife community is the interaction between wolves (*Canis lupus*), elk (*Cervus canadensis*) and woody deciduous plants (*Populus* spp., *Salix* spp.) in northern Yellowstone National Park (YNP). In this system, the trophic cascade hypothesis states that reintroduced wolves scared away and/or killed enough elk to allow plants to recover from decades of unchecked browsing. A main support for this hypothesis is time series data showing annual decreases in browsing and annual increases in plant height following wolf reintroduction (Beschta et al., 2018; Beschta & Ripple, 2016; Painter et al., 2018;

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Painter & Tercek, 2020). A negative correlation between browsing and plant height is considered critical evidence of a trophic cascade because it demonstrates the mechanism connecting the lower two trophic levels: reduced browsing increases plant growth, leading to escape from browsing if plants grow tall. The operative assumptions are that plants taller than 200 cm escape the reach of elk and recruit into the overstory, whereas plants shorter than 200 cm are browsed with equal intensity (Beschta et al., 2018; Beschta & Ripple, 2016; Beyer et al., 2007).

An underappreciated problem with reports of decreased browsing and increased plant height after wolf reintroduction is that many violate basic principles of sampling design (Fleming, 2019; Kauffman et al., 2013; Peterson et al., 2014; Winnie, 2014). In particular, non-random sampling underlies nearly every published annual trend in browsing and height of young aspen (*Populus tremuloides*) that has been attributed to a cascading effect of wolves (Table 1). In this case, non-random sampling is the practice of measuring the three or five tallest young aspen within a stand. Five tallest data comprise most trends and they originate from one of two time series (Painter et al., 2014; Ripple & Beschta, 2007). A third time series uses three tallest data (Halofsky et al., 2008). All three time series were built from a single year of sampling by retrospectively inferring the past browsing and height of sampled aspen using plant architecture methods (Keigley & Frisina, 1998). Only one time series was built by randomly sampling young aspen each year: an unpublished data set from E. Larsen that has received limited attention (Peterson et al., 2014, 2020). No time series involved marked plants.

Although the first study that sampled the tallest young aspen acknowledged that such 'data are only representative of the first recovering aspen ... and not an estimate of aspen population response across Yellowstone's northern range' (Ripple & Beschta, 2007), subsequent studies emphasised that the tallest young aspen represent a 'leading edge' indicator of the future condition of the aspen population (e.g. Beschta et al., 2018; Painter et al., 2014; Ripple & Beschta, 2012). Peterson et al. (2020) explained that sampling the tallest young aspen 'allows investigators to document the occurrence of any young aspen exceeding the upper browse level of elk (i.e. ~200 cm) in a given stand years before the average stem height attains this metric'. However, the fate of the tallest young aspen may not represent that of the average young aspen if the former are exposed to more favourable growing conditions than the latter. For example, if the tallest young aspen exceed the preferred browsing height (PBH) of elk, which is potentially as low as 50–100 cm (Konôpka et al., 2018; Maxwell et al., 2019; Motta, 2003; Renaud et al., 2003; Rounds, 1979), they may realise a faster growth rate, via progressively less browsing as they grow taller, that leads to a level of overstory recruitment that is unattainable for the average young aspen. If so, sampling the tallest young aspen will exaggerate the average increase in overstory recruitment and the extent

that this increase is due to wolf-caused reductions in browsing.

Here, we use E. Larsen's time series data to clarify annual trends in browsing and height of young aspen after wolf reintroduction, and to assess how and why these trends differ between random samples of all plants versus non-random samples of the tallest plants. Both sets of samples show browsing and height trends consistent with a trophic cascade, but these trends are weaker in the random sample partly because relatively few of these plants exceeded the PBH of elk. Our results emphasise how basic sampling principles like randomisation are vital to resolving the complexity of trophic cascades in terrestrial wildlife systems.

MATERIALS AND METHODS

Study area

We measured young aspen in the portion of the northern Yellowstone elk winter range that lies within YNP (Figure 1). This 995-km² area is defined by low-elevation (2000–2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries near the Park's northern border. A variety of ungulates spend winter in the area including elk, *Bison bison*, *Odocoileus hemionus* and *Alces alces*. Elk and bison were the most abundant ungulate in the area during winter (1200–6000 elk; 1400–3200 bison), and bison numbers exceeded those of elk beginning winter 2011–2012 (Tallian et al., 2017). Wolves were reintroduced to YNP in 1995–1997 (Bangs & Fritts, 1996) and their annual distribution was concentrated in the study area (Cassidy et al., 2020) where they hunted mainly elk (Metz et al., 2020). Other elk predators included *Puma concolor*, *Ursus arctos* and *Ursus americanus* (Barber-Meyer et al., 2008; Ruth et al., 2019). Humans hunted elk that moved beyond the study area into adjacent areas of Montana (MacNulty et al., 2020).

Study population

Aspen is one of the few upland deciduous tree species in YNP and is scattered across the study area in discrete stands on relatively moist mid-elevation benches, near streams and along conifer forest/shrub steppe ecotones (Houston, 1982). Aspen is a clonal species that mainly regenerates by root sprouting, which produces genetically identical trees from a common root system that may be substantially older than the age of the oldest tree, which rarely exceeds 150 years. Aspen requires moist soils and occurs mostly in areas with ≥ 38 cm of annual precipitation (Jones & DeByle, 1985); the study area is near this lower limit (Larsen & Ripple, 2003). Although aspen is a minor cover type in the arid portions of its range,

TABLE 1 Peer-reviewed publications showing annual trends in height and (or) browsing of young aspen in Yellowstone National Park linked to the cascading effects of wolves

| Authors (Year) | Fig. | Data Source | Data Years | Data Type | | Sampling Method | |
|------------------------------------|-------|---|-------------------------------------|-----------|----------|-----------------|--------|
| | | | | Height | Browsing | Tallest* | Random |
| Ripple & Beschta (2007) | 1c-d | Original data (98 stands) | 1998-2006 | ✓ | ✓ | ✓ | |
| Beschta & Ripple (2009) | 8b | Ripple & Beschta (2007) | 1999-2005 | ✓ | ✓ | ✓ | |
| Ripple & Beschta (2012) | 1c-d | Ripple & Beschta (2007) Original data (resampled 98 stands) | 1998-2006 2010 | ✓ | ✓ | ✓ | |
| Beschta & Ripple (2016) | 3g | Ripple & Beschta (2007, 2012) | 1998-2006, 2010 | ✓ | | ✓ | |
| Beschta et al. (2018) | 2b-c | Ripple & Beschta (2007, 2012) Original data (60 additional stands) | 1999-2006, 2010 2005-2015 | ✓ | ✓ | ✓ | |
| Painter et al. (2014) [†] | 7a | Original data (87 stands) | 2003-2012 | ✓ | ✓ | ✓ | |
| Peterson et al. (2014) | 1c | <u>Painter et al. (2014) Original data (113 stands)</u> | 2003-2012 1999-2013 [‡] | ✓ | | ✓ | ✓ |
| Painter et al. (2015) [†] | 2a | Painter et al. (2014) | 2003-2012 | ✓ | | ✓ | |
| Beschta et al. (2016) | 5c | Painter et al. (2014) | 2002 [§] -2012 | | ✓ | ✓ | |
| Painter et al. (2018) [†] | 3a | Ripple & Beschta (2007, 2012) Painter et al. (2014) | 1999-2006, 2010 2005-2012 | | ✓ | ✓ | |
| Halofsky et al. (2008) | 3a-b | Original data (44 stands) | 1995-2004 | ✓ | ✓ | ✓ | |
| Peterson et al. (2020) | 15.4a | <u>Painter et al. (2014) Original data (113 stands)</u> | 2003-2012 2001-2016 [¶] | ✓ | ✓ | ✓ | ✓ |

Note: Listed are the authors and publication year (Authors [Year]), number of the relevant data figure in the article (Fig.), source of data shown in relevant data figure (Data Source), timespan covered by the data (Data Years), type of data collected (Height, Browsing) and method of data collection (selective sampling of the tallest young aspen [Tallest] or random sampling of all young aspen [Random]). Checkmarks indicate which data were collected and with which sampling method. Shaded cells indicate articles that reproduced or extended data originating in Ripple and Beschta (2007), and dashed-outlined cells indicate articles that reproduced or extended data originating in Painter et al. (2014). Underlined data in Peterson et al. (2014, 2020) were unpublished data from E. Larsen and are the subject of this article.

*The authors sampled the five tallest young aspen within a stand, except for Halofsky et al. (2008) who sampled the three tallest young aspen.

[†]Included data from a random sample that provided no information on annual trends in height and little or no information on annual trends in herbivory; the latter was limited to changes in browsing during 1997–1998 and 2011–2012 reported in Painter et al. (2014, 2015).

[‡]Did not include data for 2000 and 2003.

[§]Did not specify the data source for 2002.

[¶]Did not include data for 2015.

it is a major source of biological diversity, providing habitat for numerous plants and animals (DeByle, 1985; Mueggler, 1985). Various ungulates eat the leaders of young stems, especially during winter. Persistent browsing of a stem's leader prevents its growth to tree height, a process that has contributed to loss of overstory aspen in portions of western North America, including the study area (National Research Council, 2002).

Historic landscape photographs suggest that overstory aspen covered ~4%–6% of the study area during 1880–1900 (Houston, 1982; Meagher & Houston, 1999), and aerial photographs indicate that aspen coverage

decreased to ~1% by the 1990s (Larsen & Ripple, 2005). Pre-wolf reintroduction studies predicted no cascading effects of wolves on aspen (reviewed in Yellowstone National Park, 1997), but subsequent studies proposed that regeneration of overstory aspen depended on wolves reducing elk browsing (Ripple & Larsen, 2000; White et al., 1998). The first evidence of substantial numbers of unprotected aspen reaching tree height since the early- to mid-20th century (Kauffman et al., 2010; Larsen & Ripple, 2003) occurred about a decade after wolf reintroduction (Ripple & Beschta, 2007). See Appendix S1 for additional context.

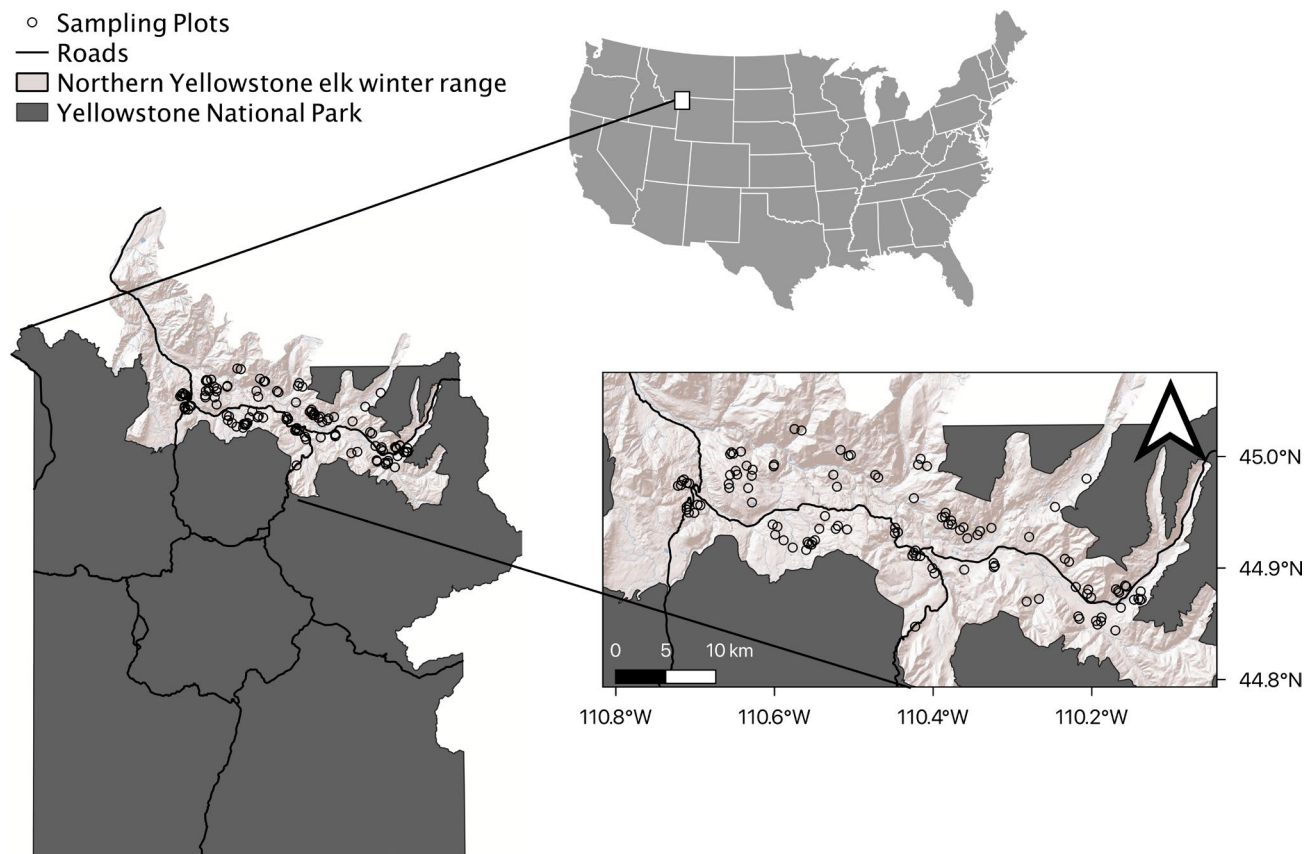


FIGURE 1 Locations of randomly sampled aspen stands in northern Yellowstone National Park. The northern Yellowstone elk winter range is the maximum distribution of the northern Yellowstone elk population during winter when elk often browse young aspen (shaded relief from Esri)

Data collection

We measured browsing and height of young aspen in 113 plots distributed randomly across the study area (Figure 1). Each plot was a 1×20 m belt transect located randomly within an aspen stand that was itself randomly selected from an inventory of stands with respect to high and low wolf-use areas (Ripple et al., 2001). The inventory was a list of 992 grid cells (240×360 m) that contained at least one stand (Appendix S1). A ‘stand’ was a group of tree-size aspen (>10 cm diameter at breast height) in which each tree was ≤ 30 m from every other tree. One hundred and thirteen grid cells were randomly selected from the inventory ($\sim 11\%$ of 992 cells), one stand was randomly selected from each cell, and one plot was randomly established in each stand. Each plot likely represented a genetically independent sample (Appendix S1).

We measured aspen at the end of the growing season (late July–September), focusing on plants ≤ 600 cm tall and ≥ 1 year old, which we termed ‘young aspen’. For each stand, we measured every young aspen within a plot (‘random stems’) and each of the five tallest young aspen within the stand (‘5T stems’). For all young aspen, we measured browsing status (browsed or unbrowsed) and height of the leader (tallest) stem. A leader was ‘browsed’ if its growth from the previous

growing season had been eaten, which we identified by a sharp, pruned edge at the base of the current year’s growth. Most plots were measured nearly every year since 1999 (Ripple et al., 2001) and our analysis focused on data from 10 years (2007–2014, 2016–2017) in which sampled stands included measurements of random and 5T stems. Elk were likely the primary ungulate species browsing young aspen in our plots during the study (Figure S1).

Data analysis

First, we built empirical distributions of browsing levels and stem heights to visualise how these characteristics differed between 5T and random stems within and across years (Appendix S1). Second, we modeled annual changes in browsing and stem height, and tested how these changes differed between 5T and random stems. Third, we modelled the influence of stem height on browsing to identify the PBH (height at which browse probability is greatest) and browse escape height (BEH: height at which browse probability nears zero). We used these results to assess the prevalence of non-preferred stems in samples of 5T and random stems, and to test how estimates of overstory recruitment differed between random and 5T stems.

Annual changes in browsing, stem height and overstory recruitment

We combined measurements of 5T and random stems into one data set of all stems ($N = 18,623$) across all years ($N = 10$ years) and used generalised linear mixed models (GLMMs) to test how the effect of year on browsing, height and recruitment of stems differed by the sampling method. We treated the stem as the unit of analysis and used GLMMs with a Bernoulli distribution and a logit link to separately analyse the probability a stem was browsed (1 = browsed; 0 = not browsed) and recruited (1 = recruited; 0 = not recruited), and GLMMs with a gamma distribution and a log link to analyse stem height (cm), which took only non-negative values that were strongly right-skewed. A stem 'recruited' if it exceeded the commonly assumed BEH of 200 cm or our estimated BEH of 300 cm (see Results). Year was an integer that ranged from 1 (2007) to 11 (2017) and sampling method was a dummy variable (1 = 5T sampling; 0 = random sampling). If 5T sampling estimated a faster annual decrease in browsing and faster annual increase in height and recruitment compared to random sampling, we expected (i) models with a year \times method interaction fit the data better than models with only main effects for these variables and (ii) the sign of this interaction to be negative in the browsing model and positive in the height and recruitment models. We used likelihood ratio tests to compare models.

All GLMMs included a random intercept for stand identity, and GLMMs of browsing and stem height also included a random slope for year. We observed too few stems >200 or >300 cm to estimate a GLMM of recruitment with a random slope for year. The random intercept controlled for correlation among measurements of the same stand in multiple years and unmeasured stand-related effects including soil, water and light conditions; the random slope permitted stand-specific annual trends in browsing and stem height. Analysis of standardised Pearson residuals from the best-fit GLMMs indicated a lack of temporal autocorrelation (Appendix S1, Figure S2). We estimated average marginal effects (AMEs) from GLMMs to quantify and compare annual changes of 5T and random stems. AMEs describe the average effect of changes in explanatory variables on the change in a response variable and are useful for interpreting generalised linear models (Leeper, 2021). We used z -scores to test how the AMEs of year on browsing, stem height and recruitment differed between 5T and random stems.

We calculated population-averaged fitted values from best-fit GLMMs by deriving marginal expectations of the responses averaged over the random effects but conditional on the observed variables. We refit year as a categorical factor and plotted the associated fitted values to illustrate the distribution of the underlying data after controlling for stand-level

heterogeneity, and to assess the negative correlation between mean annual browsing and mean annual stem height.

Following previous studies (Beschta et al., 2016; Painter et al., 2014, 2015, 2018), we also estimated recruitment at the stand level as the percentage of sampled stands with stems taller than the presumed reach of elk. We calculated this separately for 5T and random stems as the annual percentage of sampled stands in which the median stem height exceeded 200 or 300 cm. Consistent with previous studies, recruitment estimates from 5T stems excluded stands that produced no young aspen.

Preferred browsing height and browse escape height

We modelled the effect of stem height on browsing to estimate PBH and BEH. We estimated separate GLMMs for 5T stems ($N = 4265$) and random stems ($N = 14,358$), and included crossed random intercepts for stand identity and year to account for (i) correlation between measurements taken on the same stand in multiple years and on multiple stands in the same year, and (ii) unmeasured stand- and year-related effects.

We used piecewise linear splines to identify the PBH, which we defined as the height threshold beyond which browsing probability decreased with further height increase. We compared models with a single height threshold placed from 10 to 200 cm (first at 10 cm and then 1 cm intervals), a model with no height threshold and an intercept-only model. We selected thresholds a priori based on the traditional assumption that stems taller than 200 cm escape browsing (Kay, 1990). We constructed variables containing a linear spline for stem height so that the estimated coefficients measure the slopes of the segments before and after the threshold. We evaluated competing models using marginal likelihoods and information-theoretic statistics (AIC_c; Burnham & Anderson, 2002), and used AMEs of the best models to estimate how browsing probability changed with increasing stem height. We also used the best models to identify the BEH.

RESULTS

Empirical distributions of browsing and stem height

Probability densities indicate that minimal browsing ($\leq 20\%$ stems browsed) and tall height (>100 cm) were more characteristic of 5T stems than of random stems, and that these differences increased from 2007 to 2017 (Figure 2; Figure S3). During this period, median height of 5T stems tracked increases in the 85–90th percentile height of random stems, which increased four to five times faster than did the median height of random stems (Figure S4).

Annual changes in browsing and stem height

GLMMs of browsing and stem height with a year \times method interaction fit the data better than did those with only main effects for these variables (browsing: $\chi^2_1 = 140.4$, $p < 0.001$; height: $\chi^2_1 = 48.9$, $p < 0.001$). The interaction was negative in the browsing model ($\beta = -0.19$; 95% CI = $-0.22, -0.16$; $p < 0.001$) and positive in the height model ($\beta = 0.016$; 95% CI = $0.012, 0.021$; $p < 0.001$), which indicates that 5T sampling estimated a faster decrease in browsing and a faster increase in height compared to random sampling (Figure 3a,b). Specifically, browsing decreased 4.0 percentage points \cdot year $^{-1}$ (95% CI = $3.2, 4.7$) for 5T stems versus 1.7 percentage points \cdot year $^{-1}$ (95% CI = $0.86, 2.5$) for random stems ($z = 11.5$, $p < 0.001$). Height increased 20.9 cm \cdot year $^{-1}$ (95% CI = $16.1, 25.8$) for 5T stems versus 8.0 cm \cdot year $^{-1}$ (95% CI = $6.0, 10.0$) for random stems ($z = -7.0$, $p < 0.001$). The negative correlation between estimates of mean annual browsing (points in Figure 3a) and mean annual height (points in Figure 3b) was 19% stronger for 5T stems (Pearson's correlation coefficient, $r = -0.94$; $p < 0.001$) compared to random stems ($r = -0.78$; $p = 0.02$; Figure 3c).

Preferred browsing height and browse escape height

The best-fit GLMMs ($\Delta AIC_c = 0$) indicate that the PBH was 132 cm for 5T stems and 122 cm for random stems

(Figure 4a; Tables S1 and S2). Below these heights, each 10 cm increase in height increased browsing by 0.3 percentage points for 5T stems (95% CI = $-0.2, 0.9$; $p = 0.27$) and 0.5 percentage points for random stems (95% CI = $0.1, 0.8$; $p = 0.005$). Above these heights, each 10 cm increase in height decreased browsing by 3.5 percentage points for 5T stems (95% CI = $3.3, 3.8$; $p < 0.001$) and 4.1 percentage points for random stems (95% CI = $3.6, 4.5$; $p < 0.001$). Stems exceeding the PBH were 1.6–5.1 times (mean \pm SE = 2.8 ± 0.40) more prevalent in the sample of 5T stems than in the sample of random stems (Figure 4b). The best-fit GLMMs indicate that browsing of stems >200 cm was as high as 0.45 (95% CI = $0.40, 0.51$) for 5T stems and 0.35 (95% CI = $0.28, 0.42$) for random stems. Browsing was negligible (<0.07) only after stems exceeded ~ 300 cm (Figure 4a).

Overstory recruitment

GLMMs of the probability that a stem exceeded 200 or 300 cm with a year \times method interaction fit the data better than did those with only main effects for these variables (200 cm: $\chi^2_1 = 53.3$, $p < 0.001$; 300 cm: $\chi^2_1 = 75.8$, $p < 0.001$). The positive sign of the interaction (200 cm: $\beta = 0.24$; 95% CI = $0.17, 0.31$; $p < 0.001$; 300 cm: $\beta = 0.40$; 95% CI = $0.30, 0.49$; $p < 0.001$) indicates that 5T sampling estimated a faster increase in recruitment compared to random sampling (Figure 5a,b). Recruitment of stems >200 cm increased 5.6 percentage points \cdot year $^{-1}$ (95% CI = $5.2, 6.0$)

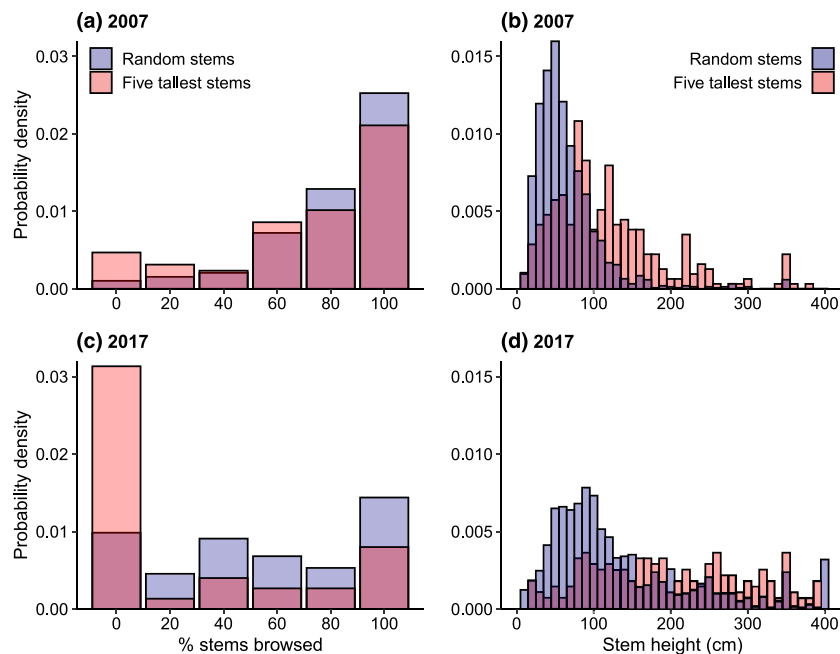
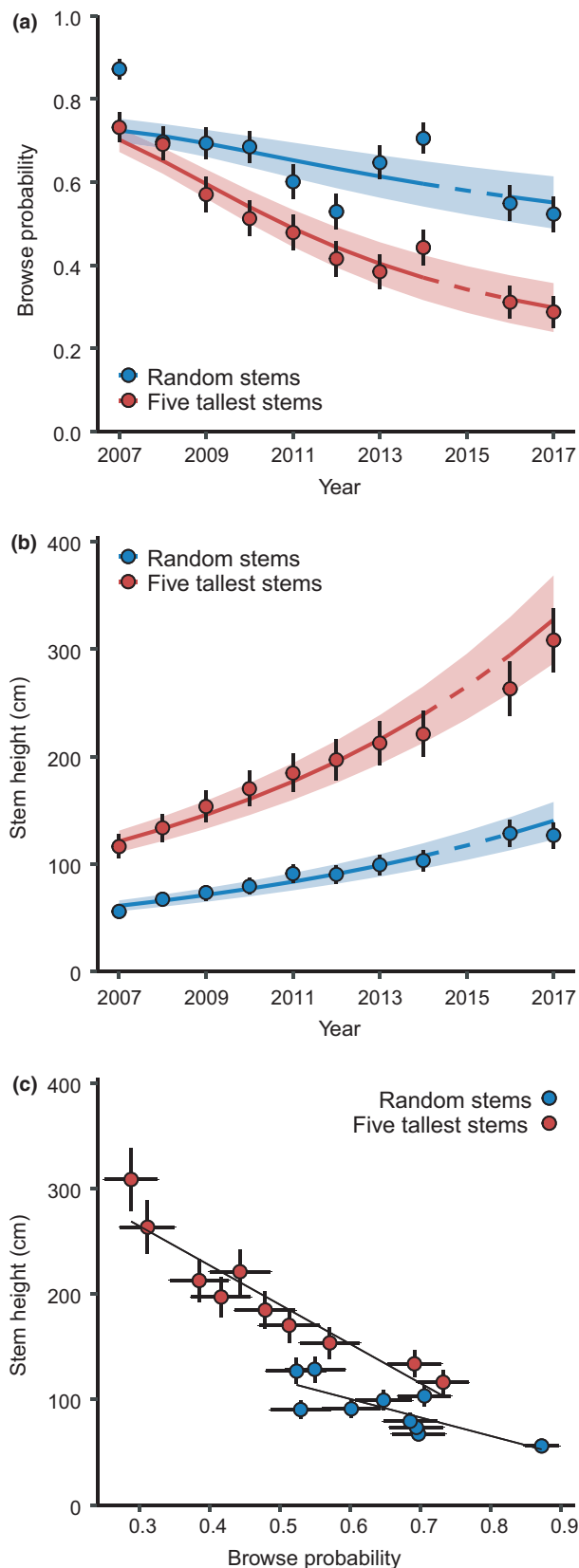


FIGURE 2 Probability densities of browsing (a, c) and height (b, d) of the five tallest young aspen and randomly sampled young aspen in northern Yellowstone National Park during the first and last years of the study (2007, 2017). Dark red shading indicates overlapping probability densities. Low browsing levels and tall heights were more characteristic of the five tallest young aspen throughout the study from 2007 (a, b) to 2017 (c, d). Probability densities for each year of the study are provided in Figure S3



for 5T stems versus 2.1 percentage points-year⁻¹ (95% CI = 1.5, 2.8) for random stems ($z = -7.0$, $p < 0.001$), and recruitment of stems >300 cm increased 4.8 percentage points-year⁻¹ (95% CI = 4.0, 5.6) for 5T stems versus 1.0

FIGURE 3 Effects of sampling method on estimated annual trends in browsing and height of young aspen in northern Yellowstone National Park, 2007–2017. Relative to a random sample, a nonrandom sample of the five tallest stems estimated a faster annual decrease in browsing (a), faster annual increase in stem height (b) and stronger negative correlation between browsing and stem height (c). Results in (a) and (b) are population-averaged fitted values and associated 95% confidence intervals from best-fit GLMMs of the interactive effect of year and sampling method on browse probability and stem height with year modeled as a continuous (lines) or categorical (points) effect. Results in (c) are the relationships between the categorical fitted values in (a) and (b), with lines estimated from simple linear regressions. No data were collected in 2015

percentage point-year⁻¹ (95% CI = 0.40, 1.6) for random stems ($z = -8.3$, $p < 0.001$).

Stand-level assessments indicate that 5T sampling estimated a total increase in overstory recruitment from 2007 to 2017 that was 4–7 times greater than that estimated by random sampling. The annual percentage of stands with a median stem height greater than 200 cm (300 cm) increased from 13% to 68% (5%–49%) for 5T sampling versus 1% to 15% (0%–6%) for random sampling, and in any given year, the percentage estimated from 5T sampling was 4–26 times (5–31 times) greater than that estimated by random sampling (Figure 5c,d). Random sampling revealed that young aspen were annually absent in 2%–9% of stands and 11%–19% of plots within stands (Figures S5 and S6). Every stand produced young aspen during at least 1 year of the study, whereas 7% of plots consistently produced no young aspen.

DISCUSSION

To the extent that annual decreases in browsing and annual increases in height of woody deciduous plants in northern YNP (e.g. Figure 3) reflect the cascading effects of reintroduced wolves (Beschta et al., 2018; Beschta & Ripple, 2016; Beyer et al., 2007), our results indicate the existence of a trophic cascade that was weaker than is often claimed. We show that a practice of non-random sampling—one featured in a dozen peer-reviewed publications over more than a decade (Table 1)—exaggerated the aspen population response to wolf reintroduction. Sampling only the five tallest young aspen within a stand estimated annual changes in browsing, stem height and overstory recruitment that were significantly faster than those estimated by random sampling of all young aspen within a stand (Figures 3a,b and 5). We suggest that 5T sampling exaggerated the aspen response for the following three reasons.

First, 5T sampling favoured stems that were taller than the PBH of elk (Figure 4). Stems taller than the PBH likely grew faster than stems shorter than the PBH because the former were browsed at a decreasingly low rate as they grew taller, whereas the latter were browsed at an increasingly high rate as they grew taller (Figure 4a). Stems taller than the PBH may have also allocated relatively fewer resources to defence chemistry expression as browsing decreased

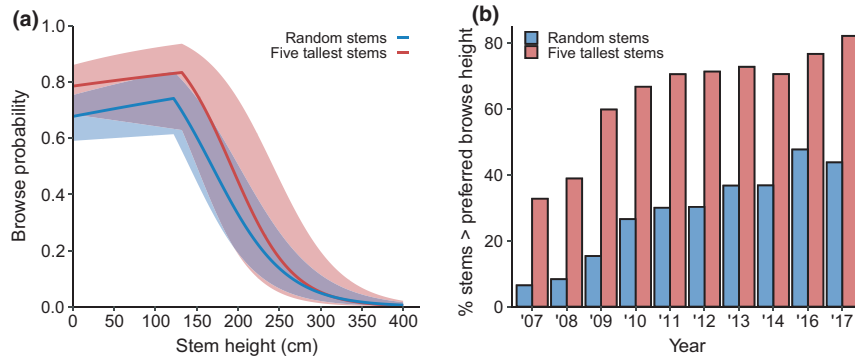


FIGURE 4 Effects of stem height on the probability a young aspen stem was browsed (a), and the annual percentage of stems in the sample of young aspen that exceeded the preferred browsing height of 132 cm (five tallest stems) or 122 cm (random stems) (b) in northern Yellowstone National Park, 2007–2017. Lines in (a) are population-averaged fitted values and associated 95% confidence intervals from best-fit GLMMs estimated separately for five tallest stems (Table S1) and random stems (Table S2). Bars in (b) are percentages of the total annual sample size – pooled across plots – of five tallest stems ($N = 317$ –518 stems-year⁻¹) and random stems ($N = 1027$ –1748 stems-year⁻¹). No data were collected in 2015

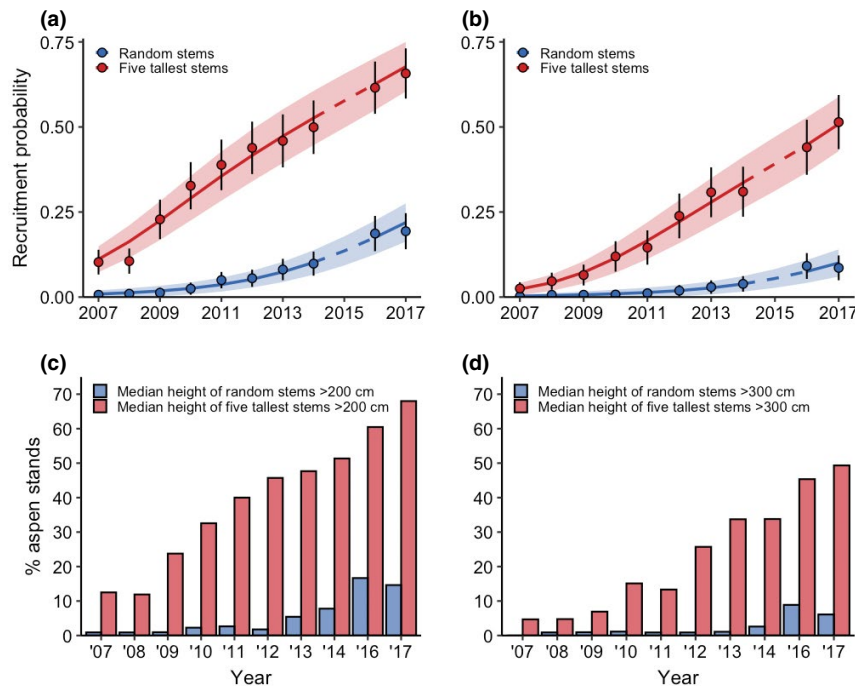


FIGURE 5 Effects of sampling method and browse-escape height assumption on stem-level (a, b) and stand-level (c, d) estimates of annual trends in overstory aspen recruitment in northern Yellowstone National Park, 2007–2017. Sampling the five tallest aspen under the assumption that stems taller than 200 cm escaped browsing and joined the overstory estimated rapid annual increases in overstory recruitment (a, c), whereas randomly sampling all young aspen under the assumption that stems taller than 300 cm escaped browsing and joined the overstory estimated relatively slow annual increases in overstory recruitment (b, d). Results in (a) and (b) are population-averaged fitted values and associated 95% confidence intervals from best-fit GLMMs of the interactive effect of year and sampling method on the probability that a stem exceeded 200 cm (a) or 300 cm (b) with year modeled as a continuous (lines) or categorical (points) effect. Bars in (c) and (d) are percentages of the total annual sample of aspen stands in which the median height of the five tallest stems and randomly sampled stems exceeded a presumed browse-escape height of 200 or 300 cm. No stands had a median height of random stems >300 cm in 2007 and no data were collected in 2015

(Rhodes et al., 2017), which would have further accelerated their height growth (Lindroth & St. Clair, 2013).

The PBH that we estimated (122–132 cm) is similar to the PBH of elk and comparable cervids (*Cervus elaphus*) in other systems (Konôpka et al., 2018; Motta, 2003; Renaud et al., 2003; Rounds, 1979). Experiments indicate that the PBH equals ungulate shoulder height, and that

ungulates prefer to browse at this height because it minimises neck angle which in turn maximises foraging efficiency. Camera trap photos of elk browsing aspen in our plots are consistent with the hypothesis that elk prefer to browse at the level of their shoulder height (Figure S7).

Our PBH estimate is also similar to (or less than) previous estimates of mean height of the tallest young

aspen (Table 1), which implies that these studies also measured a large number of stems taller than the PBH. These estimates refer to the 1–2 years in which field sampling occurred as well as to preceding years that lacked field sampling. Estimates for the latter were retrospectively inferred using plant architecture methods. Although such methods might not be useful when browsing is intense (Ripple & Beschta, 2007), the prevailing assumption is that such estimates are accurate indicators of browsing and stem height across decadal time scales. To the extent that this assumption is valid, our results suggest that reported trends in browsing and stem height based on the tallest young aspen (Table 1) do not represent trends in the aspen population at large because they too were biased toward stems that were taller than the PBH.

A challenge highlighted by the PBH is that stem height is both a cause and an effect of reduced browsing. Thus, the negative correlation between browsing and stem height (e.g. Figure 3c) that some consider critical evidence of a trophic cascade (Beschta et al., 2018; Beschta & Ripple, 2016; Beyer et al., 2007) is not an exclusive indicator of browsing suppressing stem height (Peterson et al., 2014). Rather, the negative correlation also indicates that stem height suppresses browsing, which reflects previous findings that factors besides browsing control stem height (Romme et al., 1995). This relationship helps explain why the negative correlation between browsing and stem height was stronger for 5T stems compared to random stems (Figure 3c): the stronger negative correlation was consistent with the strong negative effect of stem height on browsing that most 5T stems experienced given most were taller than the PBH. Similarly, the weaker negative correlation for random stems was at least partially due to the countervailing positive effect of stem height on browsing that most of these stems experienced since most were shorter than the PBH (Figure 4). These results suggest that a negative correlation between browsing and stem height is not reliable evidence of a trophic cascade because it does not represent an unambiguous causal link between reduced browsing and increased stem height.

Second, the tallest young aspen were most likely exposed to the best growing conditions. Tall stature is itself an indicator of a locally productive resource environment because only stems exposed to sufficient sunlight, moisture and soil quality have the capacity to grow tall (Brown et al., 2006; Hansen et al., 2016). Thus, more productive resource conditions may have contributed to the faster annual height growth and overstory recruitment of 5T stems (Figures 3b and 5). Faster height growth could have in turn contributed to the faster decrease in browsing (Figure 3a). It is also possible that better resource conditions permitted 5T stems to respond more rapidly to a reduction in browsing (Figure 3c).

Third, 5T sampling overlooked the absence of aspen regeneration. By definition, 5T sampling measures only

stands and locations within stands that produce young aspen. It does not measure stands or locations within stands where young aspen have failed to regenerate (e.g. Figure S6a–f). During each year of our study, we noted an absence of regeneration in 2%–9% of stands and 11%–19% of plots within stands (Figure S5). Overlooking these absence data likely inflates stand-level estimates of overstory recruitment calculated as the percentage of sampled stands with stems taller than the presumed reach of elk (e.g. fig. 7b in Painter et al., 2014, fig. 2b in Painter et al., 2015; fig. 5d in Beschta et al., 2016). Overestimating recruitment because the absence of regeneration is undocumented in poorly recruiting stands represents a form of visibility bias that has received little attention in discussions about the cascading effects of wolves on aspen.

A separate source of bias that further inflates stand- and stem-level estimates of overstory recruitment is the traditional assumption that stems taller than 200 cm escape browsing. Our analysis indicates that escape from browsing is not certain until stems exceed approximately 400 cm (Figure 4a). This suggests that previous estimates of overstory recruitment that assume a BEH of 200 cm (Beschta et al., 2016; Painter et al., 2014, 2015, 2018) are best interpreted as maximum estimates.

Our results do not support the hypothesis that the tallest young aspen represent a ‘leading edge’ indicator of a ‘broader shift in plant community dynamics for northern [YNP] aspen stands’ (Beschta et al., 2018). Contrary to the expectation that characteristics of the average young aspen should resemble those of the tallest young aspen over time (Peterson et al., 2020), we found that mean levels of browsing, height and recruitment of random stems increasingly differed from those of 5T stems (Figures 3a,b and 5). Trends in the height distributions of 5T stems relative to those of random stems indicate that this widening gap was because 5T stems represented a minority of young aspen that substantially outperformed the majority of young aspen. Specifically, height increase of 5T stems tracked the height increase of the 85–90th percentile of random stems, which was substantially faster than the height increase of more than half of random stems (Figure S4). Assuming our sample of random stems was representative of the population at large, our results suggest that the dynamics of 5T stems represent those of the top-performing ~10%–15% of young aspen in stands that have survived to the 20th and 21st centuries.

Our study highlights how deviations from basic sampling principles can bias knowledge about trophic cascades in terrestrial wildlife systems. Had we sampled only the tallest young aspen, we would have concluded, incorrectly, that wolf reintroduction had a strong indirect effect on aspen. Instead, our random sampling design, which included a more representative sample of aspen stands and stems, indicated that wolf reintroduction had a weaker indirect effect (Figures 3 and 5)

that did not reverse the deterioration of all aspen stands (e.g. Figures S6 and S8). A weaker aspen response is consistent with (i) documented losses of other aspen stands in the study area since wolf reintroduction (Figure S8; Beschta et al., 2020), (ii) evidence that wolves had weak and/or inconsistent effects on elk foraging behaviour (Childress & Lung, 2003; Laundré et al., 2001; Wolff & Van Horn, 2003) and habitat selection (Cusack et al., 2020; Kohl et al., 2018, 2019), and weak to moderate effects on elk population density (MacNulty et al., 2020; Peterson et al., 2014; Vucetich et al., 2005), and (iii) theory that predicts weak cascading effects in food webs like Yellowstone that are resource-limited, spatially heterogeneous and reticulated (Ford & Goheen, 2015). Climate change may have also contributed to a weaker aspen response given that many of our plots occurred in or adjacent to areas projected to become unsuitable for aspen due to anthropogenic climate forcing (Piekielek et al., 2015; Figure S9). Among studies of other woody deciduous plants (e.g. *Salix* spp.) in YNP, those that randomly sampled all plants (e.g. Bilyeu et al., 2008; Marshall et al., 2013) described an indirect effect of wolves that was also weaker than that described by studies that sampled only the tallest plants (e.g. Beschta & Ripple, 2007; Ripple & Beschta, 2006).

Understanding how ecosystems respond to the loss and/or addition of large predators is vital to resolving broader debates about the forces that structure food webs, determine species abundance and deliver ecosystem services (Atkins et al., 2019; Dobson, 2014; Estes et al., 2011; Ripple et al., 2014). Our study, which focused on a textbook example of large predator extirpation and reintroduction, demonstrates how deviations from basic sampling principles can distort this understanding. Non-random sampling overestimated the strength of a trophic cascade in the system we studied, but it may underestimate cascading effects in other systems. In observational studies that lack control and replication, randomisation is one of the few available protections against unreliable inferences and the misguided policy and management decisions they may inspire. Growing concerns about the reliability of research findings in ecology (e.g. Fidler et al., 2017; Fraser et al., 2018; O'Grady, 2020) emphasise the vital importance of basic sampling principles for studies of trophic cascades and other ecological phenomena.

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AUTHOR CONTRIBUTIONS

E.M.B., E.J.L., D.R.M. conceived and designed the study; E.J.L. collected most of the data; E.M.B. and D.R.M. analysed the data and wrote the manuscript with input from E.J.L.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13915>.

OPEN RESEARCH BADGES




This article has earned Open Data and Open Materials badges. Data and materials are available at: <https://doi.org/10.5061/dryad.2z34tmpnj>; https://datadryad.org/stash/share/hUtcog9mVp60lyw-j__pcNAHeR-4PpI9NgQ8R3y_MkA

DATA AVAILABILITY STATEMENT

Data and code are archived in Dryad (<https://doi.org/10.5061/dryad.2z34tmpnj>).

ORCID

Elaine M. Brice  <https://orcid.org/0000-0001-6034-4065>

Daniel R. MacNulty  <https://orcid.org/0000-0002-9173-8910>

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