Title: Sampling bias exaggerates a textbook example of a trophic cascade

Authors: Elaine M. Brice¹, Eric J. Larsen², Daniel R. MacNulty¹

Affiliations

¹Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT 84322, USA

²Department of Geography and Geology, University of Wisconsin – Stevens Point, Stevens Point, WI 54481, USA

*Correspondence to: elbrice92@gmail.com

Abstract:

Understanding how wildland ecosystems respond to the loss and recovery of large predators is vital to decipher the forces that structure food webs and to guide the practice of ecosystem conservation, restoration, and rewilding. This is a major scientific challenge, however, because these large-scale, uncontrolled systems are difficult (or impossible) to sample properly. We show how a tradition of nonrandom sampling has confounded this understanding in a textbook system (Yellowstone National Park) where carnivore [wolf (*Canis lupus*)] recovery is often associated with a trophic cascade involving changes in herbivore [elk (*Cervus canadensis*)] behavior and density that promote plant regeneration. Long-term data indicate that a customary practice of sampling only the tallest young plants overestimated regeneration of aspen (*Populus tremuloides*) by a factor of 3-44 compared to random sampling. Our results demonstrate how seemingly minor departures from principled sampling can generate substantial misunderstandings about the strength of trophic cascades caused by large terrestrial predators.

Main Text

Much of the empirical information about trophic cascades (indirect effects of predators on plants and abiotic processes) derives from tractable systems that are variously small scale, aquatic, invertebrate, and captive^{1,2}. Substantially less is known about trophic cascades in free-living vertebrate communities that span vast landscapes. One reason for this gap is that it is difficult and costly to measure such large, complex, and uncontrolled systems in accordance with fundamental principles of sampling design, including randomization, replication, and control of variation³⁻⁵. This challenge also means that inference about trophic cascades in large terrestrial ecosystems may be particularly prone to bias.

Concern about sampling bias is a core issue in the longstanding debate about the cascading effects of wolves reintroduced to Yellowstone National Park⁵⁻¹⁰. In this system, the trophic cascade hypothesis is that wolves (*Canis lupus*) scared away and (or) killed enough elk (*Cervus canadensis*) to allow various woody deciduous plants (*Populus* spp., *Salix* spp.) to recover from decades of unchecked herbivory. A primary support for this hypothesis is time series data showing annual decreases in herbivory and annual increases in plant height following the 1995-1997 wolf reintroduction¹⁰⁻²¹. An inverse relationship between herbivory and plant height is considered critical evidence of a wolf-elk-aspen trophic cascade because it demonstrates the mechanism connecting the lower two trophic levels: reduced herbivory increases plant growth, leading to escape from herbivory if plants grow tall^{17,19}. The standard, though untested, assumption is that plants taller than 200 cm escape the reach of elk and survive to join the overstory. A persistent concern is that reports of decreased herbivory and increased plant height after wolf reintroduction are based on sampling designs that deviate from fundamental principles⁷⁻¹⁰.

Nonrandom sampling, for example, underpins nearly every annual trend in herbivory and height of young aspen (*Populus tremuloides*) in Yellowstone National Park that has been credited to a cascading effect of wolves (Extended Data Table 1)^{10–20}. In this case, nonrandom sampling involves measuring the three or five tallest young aspen within a stand. The rationale is that the tallest young aspen are “consistently identified”, the first to “experience a reduction in browsing pressure”, and a “leading edge indication of a broader shift in plant community dynamics”¹⁹. An underappreciated problem, however, is that selective sampling of the tallest young aspen may misrepresent trends in the population of young aspen at large. Specifically, nonrandom sampling may have overestimated changes in herbivory and plant height¹⁰, and thus exaggerated a globally-significant example of a trophic cascade featured in many textbooks^{22,23} and popular media^{24,25}.

We assessed the scope of this potential bias and its implications for understanding trophic cascades in large terrestrial ecosystems with data from a long-term study of young aspen in 113 plots distributed across 995-km² of northern Yellowstone National Park (Fig. 1). Each plot was a 1 m × 20 m belt transect situated randomly within an aspen stand that was itself randomly selected from an inventory of aspen stands. Herbivory (browsed or unbrowsed) and height of the leader stem (the tallest stem) of every aspen ≤ 600 cm were measured at the end of the growing season. Herbivory and height of the five tallest stems ≤ 600 cm growing anywhere within each sampled stand were also measured. Although most plots were measured nearly every year since 1999²⁶, we focused on data from 10 years (2007–2014, 2016–2017) in which sampled stands included measurements of stems in randomly selected plots (‘random stems’) and of stems that were the five tallest (‘5T stems’).

Frequency distributions of herbivory levels and heights of 5T stems did not match those of random stems (Fig. 2), confirming that characteristics of the tallest young aspen did not represent those of the general population. Low herbivory levels ($\leq 20\%$ stems browsed) and tall heights (>100 cm) were more frequent among 5T stems in 2007 (Fig. 2, A and B), and even more so in 2017 (Fig. 2, C and D). Assuming the population of random stems was representative of the population of young aspen at large, disparities between the distributions of random and 5T stems indicate that sampling of 5T stems yielded biased estimates of average herbivory and stem height.

To test if 5T sampling overestimated annual changes in herbivory and stem height, we pooled measurements of all stems across all years and tested if and how the effect of year on herbivory and stem height varied according to sampling method. We treated the individual stem as the unit of analysis, used generalized linear mixed models (GLMMs) with a binomial error distribution to analyze herbivory as the probability that a stem was browsed, and used linear mixed models with a normal error distribution to analyze log-transformed stem height. All models included random effects for stand identity and year to control for repeated measurements, unmeasured stand-related effects, and stand-specific variation in annual rates of change. To determine the extent that annual changes in herbivory and stem height differed between sampling methods, we tested for an interaction between year and a dummy variable for sampling method.

Models with a year $\times$ sampling method interaction fit the data significantly better than did models with only main effects for these variables (herbivory: $\chi^2_1 = 134.60$, $P < 0.001$; height: $\chi^2_1 = 49.42$, $P < 0.001$). The interaction term indicated that annual changes estimated via 5T sampling were 1.3-3.0 times greater than annual changes estimated via random sampling. Specifically, herbivory decreased $23\% \cdot \text{year}^{-1}$ for 5T stems [95% CI = (18%, 27%), $P < 0.001$] versus

7%·year⁻¹ for random stems [95% CI = (2%, 13%), $P = 0.007$; Fig. 3A], and stem height increased 8.6%·year⁻¹ for 5T stems [95% CI = (7.4%, 9.8%), $P < 0.001$] versus 6.7%·year⁻¹ for random stems [95% CI = (5.6%, 7.9%), $P < 0.001$; Fig. 3B).

One reason for these discrepancies was that the sample of 5T stems was dominated by stems that exceeded critical height thresholds beyond which herbivory *decreased* as stems grew taller; stems below these thresholds were subject to higher levels of herbivory that *increased* as stems grew taller (Fig. 3C). A confidence set of GLMMs ($\Delta AIC_c < 2$) indicated the height threshold was 127-140 cm for 5T stems and 118-129 cm for random stems (Extended Data Tables, 2, 3). The most parsimonious models in the set indicated that 5T stems had a threshold at 132 cm and random stems at 122 cm, and that each 1-cm increase beyond these thresholds decreased herbivory of 5T stems by 2.6% (95% CI = 2.4%, 2.9%; $P < 0.001$) and of random stems by 2.2% (95% CI = 2.1%, 2.4%; $P < 0.001$). Below these thresholds, each 1-cm increase in height increased herbivory of random stems by 0.3% (95% CI = 0.1%, 0.4%; $P = 0.005$), and of 5T stems by 0.2% (95% CI = -0.2%, 0.7%; $P = 0.27$). Stems exceeding the critical height thresholds were 1.6-5.1 times more prevalent in the 5T sample than in the random sample (Fig. 3D).

Another reason 5T sampling estimated a faster rate of height increase compared to random sampling was that 5T stems responded more strongly to reduced herbivory than did random stems. This was evident from a linear mixed model of log-transformed stem height fitted to data pooled across the two sampling methods. A model with an interaction between dummy variables for browsing and sampling method outperformed a similar model with only main effects ($\chi^2_1 = 106.69$, $P < 0.001$). The interaction indicated that the absence of browsing increased height of 5T stems by 33% [95% CI = (29%, 36%), $P < 0.001$] and of random stems by 14%

[95% CI = (13%, 16%), $P < 0.001$; Fig. 3E). Correlations between annual point estimates of average browse probability (Fig. 3A) and stem height (Fig. 3B) likewise indicated that the inverse relationship between herbivory and stem height was stronger for 5T stems ($R^2 = 0.92$) than it was for random stems ($R^2 = 0.34$; Fig. 3F). The tallest stems may have grown taller in the absence of herbivory because they occurred where growing conditions were especially favorable (abundant light, adequate moisture, and more basic soils^{27,28}). Additionally, because tall stems were browsed less (Fig. 3C), they may have also allocated relatively fewer resources to defense chemistry expression²⁹, which would have further accelerated height growth³⁰.

If we define the cascading effect of wolves on young aspen as the annual percentage of stands with mean stem height exceeding the reach of elk^{15,16,18,20}, 5T sampling combined with a lenient assumption about browse escape height (>200 cm) estimated an effect 3-44 times greater than that estimated by random sampling with a similar or stricter assumption about browse escape height (>300 cm; Fig. 4). Browse probability of stems >200 cm was as high as 0.44 (95% CI = 0.38, 0.51) for 5T stems and 0.32 (95% CI = 0.24, 0.41) for random stems, whereas browse probability of all stems >300 cm was nearly zero (≤ 0.05 ; Fig. 3C).

Although 5T sampling grossly overestimated the average increase in aspen regeneration following wolf reintroduction, it correctly showed that an increase was underway. Nevertheless, even the more modest increase shown by random sampling cannot be attributed to wolves alone. This is because wolves were not the sole cause of the elk population decline^{10,31}, and there is scant evidence that they frightened elk away from aspen or any other habitat^{32,33}. A weak cascading effect of wolves is consistent with theory that predicts little or no such effect in food webs like northern Yellowstone that feature resource limitation, reticulation (trophic levels with multiple species with similar resource requirements), and environmental heterogeneity (4).

Understanding how predators shape large terrestrial ecosystems is a challenge made
urgent by the rapid pace of global environmental change, including the extirpation and recovery
of large carnivorous land mammals^{34,35}. Our results demonstrate how deviations from basic
sampling principles can distort this understanding. Nonrandom sampling overestimated the
strength of a hypothesized trophic cascade in the system we studied, but it may underestimate
cascading effects in other systems. In observational studies of large terrestrial ecosystems that
lack control, randomization is an essential guard against unreliable inferences and the misguided
policy and management decisions they may spawn. Fidelity to principled sampling is also vital to
address growing concern about the reliability of many scientific findings^{36,37}.

References

1. Piovia-Scott, J., Yang, L. H. & Wright, A. N. Temporal variation in trophic cascades. *Annual Review of Ecology, Evolution, and Systematics* **48**, 281–300 (2017).
2. Alston, J. M. *et al.* Reciprocity in restoration ecology: When might large carnivore reintroduction restore ecosystems? *Biological Conservation* **234**, 82–89 (2019).
3. Ford, A. T. & Goheen, J. R. Trophic cascades by large carnivores: A case for strong inference and mechanism. *Trends in Ecology & Evolution* **30**, 725–735 (2015).
4. Allen, B. L. *et al.* Can we save large carnivores without losing large carnivore science? *Food Webs* **12**, 64–75 (2017).
5. Hayward, M. W., Edwards, S., Fancourt, B. A., Linnell, J. D. C. & Nilsen, E. B. Top-down control of ecosystems and the case for rewilding: does it all add up? in *Rewilding* (eds. Pettorelli, N., Durant, S. M. & du Toit, J. T.) 325–354 (Cambridge University Press, 2019).
6. Bilyeu, D. M., Cooper, D. J. & Hobbs, N. T. Water tables constrain height recovery of willow on Yellowstone’s northern range. *Ecological Applications* **18**, 80–92 (2008).
7. Kauffman, M. J., Brodie, J. F. & Jules, E. S. Are wolves saving Yellowstone’s aspen? A landscape-level test of a behaviorally mediated trophic cascade: reply. *Ecology* **94**, 1425–1431 (2013).
8. Winnie, J. Predation risk, elk, and aspen: reply. *Ecology* **95**, 2671–2674 (2014).
9. Fleming, P. J. S. They might be right, but Beschta *et al.* (2018) give no strong evidence that “trophic cascades shape recovery of young aspen in Yellowstone National Park”: A fundamental critique of methods. *Forest Ecology and Management* **454**, 117283 (2019).

10. Peterson, R. O., Vucetich, J. A., Bump, J. M. & Smith, D. W. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics* **45**, 325–345 (2014).
11. Ripple, W. J. & Beschta, R. L. Restoring Yellowstone’s aspen with wolves. *Biological Conservation* **138**, 514–519 (2007).
12. Halofsky, J. S., Ripple, W. J. & Beschta, R. L. Recoupling fire and aspen recruitment after wolf reintroduction in Yellowstone National Park, USA. *Forest Ecology and Management* **256**, 1004–1008 (2008).
13. Beschta, R. L. & Ripple, W. J. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* **142**, 2401–2414 (2009).
14. Ripple, W. J. & Beschta, R. L. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation* **145**, 205–213 (2012).
15. Painter, L. E., Beschta, R. L., Larsen, E. J. & Ripple, W. J. After long-term decline, are aspen recovering in northern Yellowstone? *Forest Ecology and Management* **329**, 108–117 (2014).
16. Painter, L. E., Beschta, R. L., Larsen, E. J. & Ripple, W. J. Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology* **96**, 252–263 (2015).
17. Beschta, R. L. & Ripple, W. J. Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. *Biological Conservation* **198**, 93–103 (2016).
18. Beschta, R. L., Painter, L. E., Levi, T. & Ripple, W. J. Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone National Park. *Canadian Journal of Forest Research* **46**, 548–556 (2016).

19. Beschta, R. L., Painter, L. E. & Ripple, W. J. Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. *Forest Ecology and Management* **413**, 62–69 (2018).
20. Painter, L. E., Beschta, R. L., Larsen, E. J. & Ripple, W. J. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. *Ecosphere* **9**, e02376 (2018).
21. Runyon, M. J., Tyers, D. B., Sowell, B. F. & Gower, C. N. Aspen restoration using beaver on the northern Yellowstone winter range under reduced ungulate herbivory. *Restoration Ecology* **22**, 555–561 (2014).
22. Boyce, M. S., Merrill, E. H. & Sinclair, A. R. E. Wildlife Management. in *The Princeton Guide to Ecology* (eds. Levin, S. A., Carpenter, S. R. & Godfray, H. C. J.) (Princeton University Press, 2012).
23. Chapin, F. S., Matson, P. A. & Vitousek, P. M. *Principles of Terrestrial Ecosystem Ecology*. (Springer, 2011).
24. Monbiot, G. *How wolves change rivers*. (2014).
25. Morell, V. Aspens return to Yellowstone, with help from some wolves. *Science* **317**, 438–439 (2007).
26. Ripple, W. J., Larsen, E. J., Renkin, R. A. & Smith, D. W. Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. *Biological conservation* **102**, 227–234 (2001).
27. Brown, K., Hansen, A. J., Keane, R. E. & Graumlich, L. J. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. *Landscape Ecology* **21**, 933–951 (2006).

28. Hansen, W. D., Romme, W. H., Ba, A. & Turner, M. G. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. *Forest Ecology and Management* **362**, 218–230 (2016).
29. Rhodes, A. C., Anderson, V. & St Clair, S. B. Ungulate herbivory alters leaf functional traits and recruitment of regenerating aspen. *Tree Physiol* **37**, 402–413 (2017).
30. Lindroth, R. L. & St. Clair, S. B. Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. *Forest Ecology and Management* **299**, 14–21 (2013).
31. Vucetich, J. A., Smith, D. W. & Stahler, D. R. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* **111**, 259–270 (2005).
32. Kohl, M. T. *et al.* Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* **88**, 638–652 (2018).
33. Cusack, J. J. *et al.* Weak spatiotemporal response of prey to predation risk in a freely interacting system. *Journal of Animal Ecology* **89**, 120–131 (2019).
34. Ripple, W. J. *et al.* Status and ecological effects of the world’s largest carnivores. *Science* **343**, 1241484 (2014).
35. Atkins, J. L. *et al.* Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**, 173–177 (2019).
36. Forstmeier, W., Wagenmakers, E.-J. & Parker, T. H. Detecting and avoiding likely false-positive findings – a practical guide. *Biological Reviews* **92**, 1941–1968 (2017).
37. Fraser, H., Parker, T., Nakagawa, S., Barnett, A. & Fidler, F. Questionable research practices in ecology and evolution. *PLOS ONE* **13**, e0200303 (2018).

Fig. 1. Location of sampled aspen stands. The northern Yellowstone elk winter range is the maximum distribution of the northern Yellowstone elk population during winter when elk often browse young aspen.

Fig. 2. Selective sampling of the five tallest young aspen describe distributions of herbivory levels and stems heights that differ from distributions estimated by random sampling. Low herbivory levels (A and C) and tall heights (B and D) were more characteristic of the five tallest young aspen throughout the study from 2007 (A and B) to 2017 (C and D).

Fig 3. Effects of nonrandom sampling on estimates of herbivory and height of young aspen.

(A) Relative to a random sample, a nonrandom sample of the five tallest stems estimated a faster decrease in herbivory, and a (B) faster increase in stem height that were explained by how (C) stems exceeding critical height thresholds beyond which herbivory decreased were (D) more prevalent in the nonrandom sample (N=317-518 per year) than in the random sample (N=1027-1748 per year), and by how (E and F) stems in the nonrandom sample responded more strongly to reduced herbivory than did those in the random sample. Results in (A)-(C) and (E)-(F) are population-averaged fitted values with 95% confidence intervals from best-fit models.

Fig. 4. Effect of nonrandom sampling on estimates of regeneration of overstory aspen

stems. Bars indicate the annual percentage of sampled aspen stands in which the mean height of the five tallest stems and randomly sampled stems exceeded a presumed browse-escape height of 200-cm or 300-cm. No stands had a mean height of random stems >300-cm in 2007, 2008, and 2011.

Methods

Study area

We measured aspen within the portion of the northern Yellowstone elk winter range that lies within Yellowstone National Park (Fig. 1). This 995-km² area is defined by the 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. Sagebrush steppe (mainly big sagebrush [*Artemisia tridentata*]), Idaho fescue [*Festuca idahoensis*], and blue-bunch wheatgrass [*Pseudoroegneria spicata*]) is the dominant plant community at lower elevations, with conifer forests (mainly Douglas fir [*Pseudotsuga menziesii*] and lodgepole pine [*Pinus contorta*]) at higher elevations. Aspen (*Populus tremuloides*) are scattered in discrete stands on relatively moist mid-elevation benches, near streams, and along conifer forest/shrub steppe ecotones³⁸.

Low elevations in the study area create the warmest and driest conditions in the Park, providing important winter range for ungulates, including elk (*Cervus canadensis*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). Elk have been the most abundant ungulate species in the study area for most of the time since Park establishment in 1872³⁸, reaching an estimated 17,740 individuals during winter 1994-1995³⁹. Subsequent decreases in elk numbers and increases in bison numbers led bison to overtake elk as the most numerous ungulate in the study area beginning winter 2011-2012. From winter 1995-1996 to winter 2014-2015, elk numbers decreased from 15,913 to 1,853, whereas bison numbers increased from 681 to 2,164. During this same period, estimated numbers of elk in the winter range outside the Park varied between 2,449 and 5,147, and annually exceeded those inside the Park beginning winter 2011-2012³⁹. Approximate numbers of elk and bison

wintering in the study area during each year of our study (2007-2017) ranged from 1,200-6,000 elk and 1,400-3,200 bison.

Wolves were reintroduced to Yellowstone National Park in 1995-1997⁴⁰ and their annual distribution has been concentrated in the study area⁴¹. Other large carnivores in the study area included cougar (*Puma concolor*), brown bear (*Ursus arctos*), and black bear (*Ursus americanus*). All four predators preyed on elk, with bears killing mainly calves⁴², and cougars and wolves killing calves and adults^{43,44}. Elk that moved beyond the study area into adjacent areas of Montana were also subject to predation from human hunters regulated by Montana Fish, Wildlife, and Parks⁴⁵. Humans were the only significant predator of bison, and this included management removals at the Park boundary, as well as regulated hunting in adjacent areas of Montana⁴⁶.

Study population

Aspen is the most widely distributed native tree species in North America and one of the few upland deciduous tree species in Yellowstone National Park. It is a clonal species that mainly regenerates by root sprouting with occasional seedling establishment after fire and other disturbances. Root sprouting produces genetically identical trees from a common root system that may be substantially older than the age of the oldest tree, which is rarely more than 150 years. Aspen requires moist soils and occurs mostly in areas with at least 38 cm of annual precipitation⁴⁷; the study area is near this lower limit⁴⁸. Although aspen is a minor cover type in the arid portions of its range, it is a major source of biological diversity, providing habitat for numerous plants and animals^{49,50}. Various ungulate species, for example, eat the leaders and twigs of young aspen stems, especially during winter. Persistent herbivory of a stem's leader

prevents its growth to tree height, a process that has contributed to loss of overstory aspen in parts of western North America, including the study area^{51,52}.

Historic landscape photographs suggest that overstory aspen covered approximately 4-6% of the study area during 1880-1900^{38,53}. Aerial photographs indicate that aspen coverage decreased to 2-3% in the 1970s³⁸ and to as little as 1% in the 1990s⁵⁴. Poor regeneration of tree-sized aspen was noted in the study area as early as the 1920s and attributed to herbivory from beaver⁵⁵ and elk^{56,57}. As beaver abundance declined⁵⁸ and elk abundance remained high³⁸, subsequent observers emphasized the role of elk herbivory in preventing aspen regeneration, with some considering it a proximal factor, secondary to fire suppression and climate variation^{38,59,60}, and others judging it an ultimate factor^{51,61,62}. Romme et al.⁶³ concluded that the dearth of aspen regeneration was not the work of any single factor, but involved the combined action of multiple factors including fire suppression, drying climate, and high levels of elk herbivory possibly linked to the extirpation of wolves.

Studies conducted in advance of wolf reintroduction did not predict any cascading effects of wolves on aspen or other plant species⁵⁹. Nevertheless, subsequent research proposed that regeneration of tree-sized aspen is a necessary function of wolves reducing elk herbivory^{64,65}. Consistent with this hypothesis, the first evidence of substantial numbers of unprotected aspen reaching tree height since the early- to mid-20th century^{7,48} occurred about a decade after wolf reintroduction¹¹. Although this pattern favors future increases in overstory aspen, climate warming is expected to reduce suitable habitat for aspen in the study area within the next 40-80 years⁶⁶.

Data collection

We measured herbivory and height of young aspen in 113 plots distributed randomly across the study area (Fig. 1). Each plot was a 1 m × 20 m belt transect set randomly within an aspen stand that was itself randomly selected from an inventory of aspen stands. The inventory was a list of 992 landscape grid cells (240 m × 360 m) across the study area that contained at least one aspen stand. A “stand” was a group of tree-size aspen in which each tree was ≤ 30 m from every other tree. Aspen stands were identified from 83 color infrared aerial photographs (1:24,000) taken in October 1988. To identify stands, a 1.0 cm × 1.5 cm grid of 96 cells (240 m × 360 m ground dimensions) was overlain on each photograph, and a scanning stereoscope was used to identify all cells containing at least one aspen stand. In these aerial photographs, aspen were identifiable as white crowns, whereas conifers appeared as red crowns⁴⁸. One hundred and thirteen grid cells were randomly selected from the inventory (11% of 992 cells), one aspen stand was randomly selected from each cell, and one plot was established in each stand, with the start point and transect direction randomly determined²⁶.

We measured aspen at the end of the growing season from late July to September, focusing on plants that were ≤ 600 cm tall, which we term “young aspen”. For each aspen stand, we measured every young aspen rooted within a *plot* (‘random stems’), as well as each of the five tallest young aspen rooted within the *stand* (‘5T stems’). For each type of young aspen, we measured herbivory (browsed or unbrowsed) and height of the leader stem (the tallest stem). A leader was considered ‘browsed’ if its growth from the previous growing season had been eaten.

Statistics

First, we examined frequency distributions of herbivory levels and heights of random stems and 5T stems for the first and last years of the study (2007, 2017) to visualize the extent that

characteristics of the tallest young aspen represented those of the general population. To do so, we calculated probability densities of herbivory levels and stem heights using kernel density estimation with a Gaussian distribution scaled to integrate to one. Separate probability densities were calculated for random stems and 5T stems for each year. Individual stands and plots were the units of analysis in the probability densities of herbivory, with stands pertaining to 5T stems and plots pertaining to random stems. Herbivory of 5T stems equaled the percentage of the five tallest stems within a stand that were browsed, providing one of six possible values: 0%, 20%, 40%, 60%, 80%, and 100%. Herbivory of random stems was the percentage of young stems within a plot that were browsed, and we rounded these values to the nearest of the preceding percentages to enable comparison with 5T stems (Fig. 2, A and C; 2007: $N_{5T} = 64$ stands, $N_{Random} = 97$ plots; 2017: $N_{5T} = 75$ stands, $N_{Random} = 66$ plots). Sample sizes were less than 113 in these data because some stands/plots were not sampled or contained no young stems. The individual stem was the unit of analysis in the probability densities of height, with individual heights pooled across stands and plots for each year (Fig. 2, B and D; 2007: $N_{random} = 369$, $N_{5T} = 315$; 2017: $N_{random} = 1027$, $N_{5T} = 1540$).

Second, we used mixed-effects models to analyze how selective sampling of 5T stems influenced estimates of annual changes in herbivory (stem-level probability of browsing) and stem height. To do so, we combined measurements of 5T stems and random stems into a single dataset of all stems ($N = 18,623$) across all years ($N = 10$ years; 2007-2014, 2016-2017), and tested how the effect of year on herbivory and height of individual stems differed by sampling method. Specifically, we treated the individual stem as the unit of analysis and tested for an interactive effect of year and sampling method on (a) whether a stem was browsed, and (b) height of the stem. 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). We analyzed models with year specified as a continuous or categorical variable.

Models included a random intercept for stand identity and a random slope for year, which permitted stand-specific trends in herbivory and stem height. The random intercept also controlled for correlation among measurements of the same stand in multiple years and unmeasured stand-related effects including soil, water, and light conditions. We used logistic regression to analyze the probability a stem was browsed (1 = browsed; 0 = not browsed), and linear regression to analyze stem height (cm). We log-transformed stem heights prior to analysis to ensure that model residuals approximated a normal distribution. Fitted values from models of stem height were back-transformed to the linear scale to facilitate interpretation.

To test how 5T sampling affected estimates of annual changes in herbivory and stem height, we used likelihood ratio tests to compare models with and without a year $\times$ sampling method interaction. Models including this interaction outperformed those that did not regardless of whether the effect of year was treated as continuous (herbivory: $\chi^2_1 = 134.60$, $P < 0.001$; height: $\chi^2_1 = 49.42$, $P < 0.001$) or categorical (herbivory: $\chi^2_9 = 170.03$, $P < 0.001$; height: $\chi^2_9 = 144.12$, $P < 0.001$). We calculated population-averaged fitted values of herbivory (Fig. 3A) and stem height (Fig. 3B) from the interaction models by deriving marginal expectations of the responses averaged over the random effects but conditional on the observed variables. We used models including the continuous year $\times$ sampling method interaction to calculate and compare annual changes estimated via 5T sampling and random sampling. Annual decrease in herbivory equaled one minus the odds ratio for the effect of year on the probability of browsing, conditional on the sampling method. Annual increase in stem height equaled $[(e^\beta) - 1] \times 100$

where β was the coefficient estimate for the continuous effect of year on stem height conditional on sampling method.

Third, we quantified the influence of stem height on browse probability to identify the height at which stems escaped herbivory. Using mixed-effects logistic regression models, we analyzed stem heights on a linear scale and estimated separate models for 5T stems (N = 4,265) and random stems (N = 14,358). Models specified stand identity and year as crossed random intercepts, such that the random intercept for stand i was shared across all years for a given stand i , whereas the random intercept for year j was shared by all stands in a given year j . This random effects structure accounted for correlation between measurements taken on the same stand in multiple years and on multiple stands in the same year. It also accounted for unmeasured stand- and year-related effects.

We used piecewise linear splines to identify the threshold stem height beyond which the probability of browsing decreased. To determine the presence and position of height-specific thresholds, we evaluated separate sets of competing models for 5T and random stems. Each model set included models with a single knot placed from 10-200 cm at 1 cm or 10 cm intervals, a model with no knot representing the hypothesis of no threshold in browsing, and an intercept-only model representing the null hypothesis that stem height had no effect on browsing (Extended Data Tables 2, 3). A knot was the join point between two linear splines. We selected knots *a priori* based on the standard assumption that aspen stems taller than 200 cm escape herbivory and join the overstory⁶¹. Our placement of knots was consistent with guidelines for the efficient use of knots^{67,68}. By definition, knots selected *a priori* are fixed (i.e., not random variables) and are therefore not estimated as parameters in models. We constructed variables

containing a linear spline for stem height so that the estimated coefficients measure the slopes of the segments before and after a given knot.

We evaluated competing models using information-theoretic statistics⁶⁹. Our scope of inference concerned the population, so we performed model selection using marginal likelihoods. The most parsimonious model was the one with the lowest Akaike Information Criterion (adjusted for small sample, AIC_c) and smallest ΔAIC_c . ΔAIC_c equals the AIC_c for the model of interest minus the smallest AIC_c for the set of models being considered. The best model has a ΔAIC_c of zero, and models with $\Delta AIC_c < 2$ are plausibly the best. To assess uncertainty about the best model, we identified models with $\Delta AIC_c < 2$ as the confidence set of models (analogous to a confidence interval for a mean estimate⁶⁹; Extended Data Tables 2, 3). We used odds ratios from the best models to estimate how the probability of browsing changed with increasing stem height, and calculated population-averaged fitted values from these models (Fig. 3C) as described above. We also calculated the proportion of stems in each annual sample of 5T and random stems that exceeded the height thresholds identified in the best models (Fig. 3D).

Fourth, we analyzed how selective sampling of 5T stems influenced estimates of the effect of herbivory on stem height. Recall that a strong negative effect of herbivory on stem height is considered critical evidence of a wolf-elk-aspen trophic cascade because it demonstrates the mechanism connecting the lower two trophic levels^{17,19}. This analysis had two parts. First, we used the combined dataset of all stems to test how the effect of herbivory on height of individual stems differed by sampling method. Specifically, we tested for an interactive effect of herbivory (1 = browsed; 0 = not browsed) and sampling method on log-transformed stem height using mixed-effects linear regression models. We specified stand identity and year as crossed random intercepts, used likelihood ratio tests to compare models with and without an

herbivory $\times$ sampling method interaction, computed population-averaged fitted values from the model including the herbivory $\times$ sampling method interaction (Fig. 3E), and used this model to calculate differences in the effect of herbivory on stem height between 5T stems and random stems. Second, we examined how the relationship between annual estimates of average stem height and browse probability differed between 5T stems and random stems (Fig. 3E). These annual estimates were the fitted values of mixed-effect models of herbivory and stem height that specified year as a categorical variable (Fig. 3, A and B). We used simple linear regression to compute the coefficient of determination for each relationship.

Finally, we assessed how selective sampling of 5T stems together with different assumptions about browse escape height influenced estimates of regeneration of overstory aspen stems. Following previous studies^{15,16,18,20}, we measured regeneration of overstory stems as the percentage of sampled aspen stands that showed evidence of stems taller than the presumed reach of elk. Specifically, we measured the annual percentage of sampled aspen stands in which the mean height of 5T stems and randomly sampled stems exceeded a presumed browse-escape height of 200-cm or 300-cm (Fig. 4).

Data Availability: Data are archived in Dryad (##).

Methods References

38. Houston, D. G. *The northern Yellowstone elk: ecology and management*. (Macmillan, 1982).
39. Tallian, A. *et al.* Predator foraging response to a resurgent dangerous prey. *Functional Ecology* **31**, 1418–1429 (2017).

40. Bangs, E. E. & Fritts, S. H. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* **24**, 402–413 (1996).
41. Stahler, E. E., Smith, D. W. & Stahler, D. R. Wolf turf: A glimpse at 20 years of wolf spatial ecology in Yellowstone. *Yellowstone Science* **24**, 50–54 (2016).
42. Barber-Meyer, S. M., Mech, L. D. & White, P. J. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* **169**, 1–30 (2008).
43. Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R. & Peterson, R. O. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park: Seasonal wolf predation in Yellowstone. *Journal of Animal Ecology* **81**, 553–563 (2012).
44. Ruth, T., Buotte, P. & Hornocker, M. *Yellowstone Cougars: Ecology Before And During Wolf Restoration*. (University Press of Colorado, 2019). doi:10.5876/9781607328292.
45. MacNulty, D. R., Stahler, D. R., Wyman, C. T., Ruprecht, J. & Smith, D. W. The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. *Yellowstone Science* **24**, 25–33 (2016).
46. White, E. P. J., Wallen, R. L. & Hallac, D. E. *Yellowstone Bison: Conserving an American Icon in Modern Society*. (Yellowstone Association, 2015).
47. Jones, J. R. & DeByle, N. V. Climates. in *Aspen: Ecology and management in the western United States*. *USDA Forest Service general technical report RM-119* (eds. DeByle, N. V. & Winokur, R. P.) 294 (Rocky Mountain Forest Range Experiment Station, 1985).
48. Larsen, E. J. & Ripple, W. J. Aspen age structure in the northern Yellowstone ecosystem: USA. *Forest Ecology and Management* **179**, 469–482 (2003).

49. Mueggler, W. F. Vegetation associations. in *Aspen: Ecology and management in the western United States*. USDA Forest Service general technical report RM-119 (eds. DeByle, N. V. & Winokur, R. P.) 294 (Rocky Mountain Forest Range Experiment Station, 1985).
50. DeByle, N. V. Wildlife. in *Aspen: Ecology and management in the western United States*. USDA Forest Service general technical report RM-119 (eds. DeByle, N. V. & Winokur, R. P.) 294 (Rocky Mountain Forest Range Experiment Station, 1985).
51. National Research Council. *Ecological Dynamics on Yellowstone's Northern Range*. (The National Academies Press, 2002).
52. Seager, S. T., Eisenberg, C. & St. Clair, S. B. Patterns and consequences of ungulate herbivory on aspen in western North America. *Forest Ecology and Management* **299**, 81–90 (2013).
53. Meagher, M. & Houston, D. B. *Yellowstone and the Biology of Time: Photographs across a Century*. (University of Oklahoma Press, 1999).
54. Larsen, E. J. & Ripple, W. J. Aspen stand conditions on elk winter ranges in the northern Yellowstone, USA. *Natural Areas Journal* **25**, 326 (2005).
55. Warren, E. R. *A study of beaver in the Yancey region of Yellowstone National Park*. (The Station, 1926).
56. Rush, W. M. *Northern Yellowstone Elk Study*. (Montana Fish and Game Commission, 1932).
57. Grimm, R. L. Northern Yellowstone winter range studies. *The Journal of Wildlife Management* **3**, 295–306 (1939).
58. Smith, D. W. & Tyers, D. B. The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Science* **86**, 276 (2012).

59. Yellowstone National Park. *Yellowstone's northern range : complexity & change in a wildland ecosystem*. 164 (1997).
60. Singer, F. J., Swift, D. M., Coughenour, M. B. & Varley, J. D. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968-1993. *Wildlife Society Bulletin* **26**, 17 (1998).
61. Kay, C. Yellowstone's Northern elk herd: a critical evaluation of the 'natural regulation' paradigm. (Utah State University Logan, 1990).
62. Wagner, F. H. *Yellowstone's Destabilized Ecosystem: Elk Effects, Science, and Policy Conflict*. (Oxford University Press, 2006).
63. Romme, W. H., Turner, M. G., Wallace, L. L. & Walker, J. S. Aspen, elk, and fire in northern Yellowstone Park. *Ecology* **76**, 2097–2106 (1995).
64. White, C. A., Olmsted, C. E. & Kay, C. E. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* **26**, 449–462 (1998).
65. Ripple, W. J. & Larsen, E. J. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* **95**, 361–370 (2000).
66. Piekielek, N. B., Hansen, A. J. & Chang, T. Using custom scientific workflow software and GIS to inform protected area climate adaptation planning in the Greater Yellowstone Ecosystem. *Ecological Informatics* **30**, 40–48 (2015).
67. Eubank, R. L. Approximate regression models and splines. *Communications in Statistics - Theory and Methods* **13**, 433–484 (1984).
68. Seber, G. A. F. & Wild, C. J. *Nonlinear regression*. (John Wiley and Sons, 2003).
doi:10.1002/0471725315.fmatter.

- 500 69. Burnham, K. P. & Anderson, D. R. *Model Selection and Multi-model Inference: A Practical*
501 *Information-Theoretic Approach*. (Springer, 2002).

502 **Acknowledgements:** We thank R. Renkin and J. Klaptosky for administrative and field
 503 assistance. We acknowledge support from the U.S. National Science Foundation (DGE-
 504 1633756), University of Wyoming-National Park Service Small Grant Program (1003867-USU),
 505 Yellowstone National Park, and Utah State University.

506 **Author contributions:** E.M.B., E.J.L., D.R.M. conceived and designed the study; E.J.L.
 507 collected most of the data; E.M.B. and D.R.M. analyzed the data and wrote the manuscript with
 508 input from E.J.L.

509 **Competing interests:** The authors declare no competing interests.

510 **Additional Information:**

511 **Extended Data** is available for this paper.

512 **Supplementary Information** is available for this paper.

513 **Correspondence and requests for materials** should be addressed to E.M.B.

514 (elbrice92@gmail.com).

Extended Data

Extended Data Table 1. Refereed articles showing annual trends in height and (or) herbivory of young aspen in Yellowstone National Park attributed to the cascading effects of wolves. Number of the article cited in the main text (Ref.), number of the relevant data figure in the cited article (Fig.), source of data shown in relevant data figure (Data Source), timespan covered by the data (Data Years), type of data collected (Height, Herbivory), and method of data collection (selective sampling of the five tallest young aspen [Five Tallest] or random sampling of all young aspen [Random]) are given for each article. Checkmarks indicate which data were collected and with which sampling method. Shaded cells indicate articles that reproduced data originating from Ripple and Beschta (2007), and dashed-outlined cells indicate articles that reproduced data originating from Painter et al. (2014). Underlined data in Peterson et al. (2014) were unpublished data from E. Larsen, some of which were the subject of the current analysis.

Authors (Year)	Ref.	Fig.	Data Source	Data Years	Data Type		Sampling Method	
					Height	Herbivory	Five Tallest	Random
Ripple & Beschta (2007)	11	1c-d	Original data (98 stands)	1998-2006	✓	✓	✓	
Beschta & Ripple (2009)	13	8b	Ripple & Beschta (2007)	1999-2005	✓	✓	✓	
Ripple & Beschta (2012)	14	1c-d	Ripple & Beschta (2007) Original data (resampled 98 stands)	1998-2006 2010	✓	✓	✓	
Beschta & Ripple (2016)	17	3g	Ripple & Beschta (2007, 2012)	1998-2006, 2010	✓		✓	
Beschta et al. (2018)	19	2b-c	Ripple & Beschta (2007, 2012) Original data (60 additional stands)	1999-2006, 2010 2005-2015	✓	✓	✓	

Extended Data Table 1 continued

Authors (Year)	Ref.	Fig.	Data Source	Data Years	Data Type		Sampling Method	
					Height	Herbivory	Five Tallest	Random
Painter et al. (2014) ¹	15	7a	Original data (87 stands)	2003-2012	✓	✓	✓	
Peterson et al. (2014)	10	1c	Painter et al. (2014) <u>Original data (113 stands)</u>	2003-2012 1999-2013 ²	✓		✓	✓
Painter et al. (2015) ¹	16	2a	Painter et al. (2014)	2003-2012	✓		✓	
Beschta et al. (2016)	18	5c	Painter et al. (2014)	2002 ³ -2012		✓	✓	
Painter et al. (2018) ¹	20	3a	Ripple & Beschta (2007, 2012) Painter et al. (2014)	1999-2006, 2010 2005-2012		✓	✓	
Halofsky et al. (2008) ⁴	12	3a-b	Original data (44 stands)	1995-2004	✓	✓	✓	

¹ Included data from a random sample of young aspen in Yellowstone National Park 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 herbivory during 1997-1998 and 2011-2012 reported in Painter et al. (2014, 2015).

² No data for 2000 and 2003

³ Source of 2002 data was not specified.

⁴ Sampled the three tallest young aspen within a stand.

Extended Data Table 2. Model selection results for GLMMs describing the effect of stem height (ht) on the probability that a “five tallest” young aspen was browsed in northern Yellowstone National Park. Variables ht1 and ht2 contain a linear spline at the indicated knot (cm). The intercept and simple linear models included no knot. All models included random effects for stand identity and year. Log-likelihood (LL), number of parameters (K), AIC_c , differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (W) are given for each model. The best model ($\Delta AIC_c = 0.00$) is in boldface and competitive models ($\Delta AIC_c < 2.00$) are shaded.

Model	Knot (cm)	LL	K	AIC_c	ΔAIC_c	W
intercept	-	-2166.41	3	4339.04	749.59	0.00
ht	-	-1845.00	4	3698.36	108.92	0.00
ht1, ht2	10	-1845.00	5	3700.55	111.11	0.00
ht1, ht2	20	-1839.17	5	3688.90	99.46	0.00
ht1, ht2	30	-1830.38	5	3671.32	81.87	0.00
ht1, ht2	40	-1822.30	5	3655.16	65.72	0.00
ht1, ht2	50	-1817.03	5	3644.62	55.17	0.00
ht1, ht2	60	-1813.72	5	3638.01	48.56	0.00
ht1, ht2	70	-1810.72	5	3632.01	42.57	0.00
ht1, ht2	80	-1808.52	5	3627.60	38.16	0.00
ht1, ht2	90	-1802.95	5	3616.47	27.03	0.00
ht1, ht2	100	-1797.70	5	3605.96	16.52	0.00
ht1, ht2	110	-1793.95	5	3598.46	9.01	0.00
ht1, ht2	111	-1793.71	5	3597.98	8.54	0.00
ht1, ht2	112	-1793.46	5	3597.48	8.04	0.00
ht1, ht2	113	-1793.19	5	3596.94	7.49	0.00
ht1, ht2	114	-1792.95	5	3596.47	7.03	0.00
ht1, ht2	115	-1792.75	5	3596.07	6.62	0.00

Extended Data Table 2 continued

Model	Knot (cm)	LL	K	AIC _c	Δ AIC _c	W
ht1, ht2	116	-1792.61	5	3595.78	6.34	0.00
ht1, ht2	117	-1792.47	5	3595.51	6.07	0.00
ht1, ht2	118	-1792.36	5	3595.27	5.83	0.00
ht1, ht2	119	-1792.17	5	3594.91	5.47	0.01
ht1, ht2	120	-1792.02	5	3594.59	5.15	0.01
ht1, ht2	121	-1791.77	5	3594.11	4.67	0.01
ht1, ht2	122	-1791.53	5	3593.62	4.18	0.01
ht1, ht2	123	-1791.28	5	3593.12	3.67	0.01
ht1, ht2	124	-1791.06	5	3592.68	3.24	0.02
ht1, ht2	125	-1790.89	5	3592.33	2.89	0.02
ht1, ht2	126	-1790.57	5	3591.69	2.25	0.03
ht1, ht2	127	-1790.27	5	3591.10	1.66	0.03
ht1, ht2	128	-1789.96	5	3590.49	1.04	0.05
ht1, ht2	129	-1789.70	5	3589.97	0.52	0.06
ht1, ht2	130	-1789.53	5	3589.63	0.18	0.07
ht1, ht2	131	-1789.47	5	3589.51	0.06	0.07
ht1, ht2	132	-1789.44	5	3589.44	0.00	0.08
ht1, ht2	133	-1789.48	5	3589.51	0.07	0.07
ht1, ht2	134	-1789.52	5	3589.61	0.16	0.07
ht1, ht2	135	-1789.61	5	3589.77	0.33	0.07
ht1, ht2	136	-1789.65	5	3589.86	0.41	0.06
ht1, ht2	137	-1789.75	5	3590.06	0.61	0.06
ht1, ht2	138	-1789.89	5	3590.35	0.90	0.05
ht1, ht2	139	-1790.07	5	3590.71	1.26	0.04
ht1, ht2	140	-1790.33	5	3591.23	1.79	0.03
ht1, ht2	141	-1790.66	5	3591.88	2.44	0.02
ht1, ht2	142	-1791.00	5	3592.56	3.11	0.02

Extended Data Table 2 continued

542

Model	Knot (cm)	LL	K	AIC _c	ΔAIC _c	$\mathcal{W}$
ht1, ht2	143	-1791.37	5	3593.31	3.86	0.01
ht1, ht2	144	-1791.85	5	3594.25	4.81	0.01
ht1, ht2	145	-1792.34	5	3595.23	5.79	0.00
ht1, ht2	146	-1792.80	5	3596.15	6.71	0.00
ht1, ht2	147	-1793.25	5	3597.06	7.62	0.00
ht1, ht2	148	-1793.70	5	3597.97	8.53	0.00
ht1, ht2	149	-1794.21	5	3598.98	9.54	0.00
ht1, ht2	150	-1794.70	5	3599.97	10.53	0.00
ht1, ht2	160	-1799.25	5	3609.06	19.62	0.00
ht1, ht2	170	-1803.13	5	3616.83	27.39	0.00
ht1, ht2	180	-1807.42	5	3625.39	35.95	0.00
ht1, ht2	190	-1811.10	5	3632.77	43.33	0.00
ht1, ht2	200	-1813.79	5	3638.13	48.69	0.00

Extended Data Table 3. Model selection results for GLMMs describing the effect of stem height (ht) on the probability that a randomly sampled young aspen was browsed in northern Yellowstone National Park. Variables ht1 and ht2 contain a linear spline at the indicated knot (cm). The intercept and simple linear models included no knot. All models included random effects for stand identity and year. Log-likelihood (LL), number of parameters (K), AIC_c , differences in AIC_c compared to the best scoring model (ΔAIC_c), and AIC_c weights (W) are given for each model. The best model ($\Delta AIC_c = 0.00$) is in boldface and competitive models ($\Delta AIC_c < 2.00$) are shaded.

Model	Knot (cm)	LL	K	AIC_c	ΔAIC_c	W
intercept	-	-8238.90	3	16484.05	1028.55	0.00
ht	-	-7886.08	4	15780.57	325.08	0.00
ht1, ht2	10	-7885.74	5	15782.08	326.59	0.00
ht1, ht2	20	-7886.00	5	15782.60	327.11	0.00
ht1, ht2	30	-7883.24	5	15777.08	321.58	0.00
ht1, ht2	40	-7877.04	5	15764.69	309.20	0.00
ht1, ht2	50	-7859.22	5	15729.05	273.56	0.00
ht1, ht2	60	-7835.44	5	15681.48	225.99	0.00
ht1, ht2	70	-7803.77	5	15618.14	162.65	0.00
ht1, ht2	80	-7776.04	5	15562.69	107.19	0.00
ht1, ht2	90	-7755.96	5	15522.53	67.04	0.00
ht1, ht2	100	-7738.23	5	15487.07	31.58	0.00
ht1, ht2	110	-7726.73	5	15464.07	8.58	0.00
ht1, ht2	111	-7726.10	5	15462.81	7.32	0.00
ht1, ht2	112	-7725.49	5	15461.59	6.10	0.00
ht1, ht2	113	-7724.91	5	15460.43	4.94	0.01
ht1, ht2	114	-7724.41	5	15459.43	3.94	0.01
ht1, ht2	115	-7724.08	5	15458.78	3.28	0.02

Extended Data Table 3 continued

Model	Knot (cm)	LL	K	AIC _c	Δ AIC _c	W
ht1, ht2	116	-7723.73	5	15458.07	2.58	0.03
ht1, ht2	117	-7723.49	5	15457.58	2.08	0.03
ht1, ht2	118	-7723.15	5	15456.91	1.42	0.05
ht1, ht2	119	-7722.91	5	15456.43	0.94	0.06
ht1, ht2	120	-7722.62	5	15455.85	0.35	0.08
ht1, ht2	121	-7722.51	5	15455.63	0.14	0.09
ht1, ht2	122	-7722.44	5	15455.49	0.00	0.09
ht1, ht2	123	-7722.47	5	15455.54	0.05	0.09
ht1, ht2	124	-7722.55	5	15455.70	0.20	0.08
ht1, ht2	125	-7722.68	5	15455.97	0.47	0.07
ht1, ht2	126	-7722.81	5	15456.22	0.73	0.06
ht1, ht2	127	-7722.99	5	15456.58	1.09	0.05
ht1, ht2	128	-7723.19	5	15456.98	1.49	0.04
ht1, ht2	129	-7723.39	5	15457.39	1.90	0.04
ht1, ht2	130	-7723.66	5	15457.92	2.42	0.03
ht1, ht2	131	-7723.99	5	15458.60	3.10	0.02
ht1, ht2	132	-7724.36	5	15459.33	3.84	0.01
ht1, ht2	133	-7724.81	5	15460.24	4.74	0.01
ht1, ht2	134	-7725.26	5	15461.12	5.63	0.01
ht1, ht2	135	-7725.81	5	15462.22	6.72	0.00
ht1, ht2	136	-7726.37	5	15463.35	7.86	0.00
ht1, ht2	137	-7727.03	5	15464.66	9.17	0.00
ht1, ht2	138	-7727.75	5	15466.11	10.62	0.00
ht1, ht2	139	-7728.53	5	15467.68	12.18	0.00
ht1, ht2	140	-7729.36	5	15469.33	13.84	0.00
ht1, ht2	141	-7730.18	5	15470.96	15.47	0.00
ht1, ht2	142	-7731.08	5	15472.76	17.27	0.00

Extended Data Table 3 continued

551

Model	Knot (cm)	LL	K	AIC _c	Δ AIC _c	551
ht1, ht2	143	-7732.01	5	15474.64	19.14	0.00
ht1, ht2	144	-7733.11	5	15476.82	21.33	0.00
ht1, ht2	145	-7734.31	5	15479.23	23.74	0.00
ht1, ht2	146	-7735.54	5	15481.68	26.19	0.00
ht1, ht2	147	-7736.72	5	15484.05	28.56	0.00
ht1, ht2	148	-7737.86	5	15486.32	30.83	0.00
ht1, ht2	149	-7739.02	5	15488.64	33.15	0.00
ht1, ht2	150	-7740.22	5	15491.05	35.56	0.00
ht1, ht2	160	-7749.68	5	15509.98	54.48	0.00
ht1, ht2	170	-7760.17	5	15530.95	75.46	0.00
ht1, ht2	180	-7771.68	5	15553.96	98.47	0.00
ht1, ht2	190	-7781.88	5	15574.36	118.86	0.00
ht1, ht2	200	-7793.35	5	15597.31	141.82	0.00