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Spatial fidelity of skeletal remains: elk wintering and calving grounds revealed by bones on the Yellowstone landscape

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Abstract. The spatial distributions of bones on landscape surfaces (death assemblages) may contain high-quality data on species' landscape use. Previous investigations into the spatial fidelity of death assemblages focused on general habitat preferences of the source community. Using well-studied elk populations of Yellowstone National Park, I test the geographic sensitivity of death assemblages by assessing the fidelity of shed elk antlers to the distribution of bull elk in late winter (documented through aerial surveys). I also test the geographic fidelity of newborn calf bones to known calving areas. The spatial distribution of antlers is highly faithful to bull elk landscape use, describing the decadal averaged distribution of wintering grounds as well or better than individual aerial surveys. Discrepancies in geographic distributions between recent wintering patterns and the multi-decadal antler assemblage also suggests differences in winter landscape use between current and historical (wolf-free) populations. Neonatal remains, including those partially consumed by carnivores, were always recovered in known calving areas, and all sampled calving grounds produced neonatal bones. Bone surveys are a new, minimally invasive, low-impact tool for obtaining high-quality historically informed data on species' geographic and habitat requirements. This tool will be particularly useful for managing sensitive species, fragile ecosystems, and poorly studied regions.

Key words: *conservation paleobiology; ecological baselines; landscape use; noninvasive survey methods; taphonomy; Yellowstone National Park.*

INTRODUCTION

Establishing how species and populations utilize their geographic ranges (geographic use) is essential for successful conservation and management (Griffith et al. 2002, Doswald et al. 2009, Geremia et al. 2011). While species' landscape use (including home ranges, birthing grounds, breeding areas) varies across annual, decadal, and longer timescales (Griffith et al. 2002, National Research Council 2005, Geremia et al. 2011), available data on geographic use are often based on few individuals sampled across a restricted number of seasons and generations. Given the common absence of historical multi-season, multi-decadal studies, other methods are needed to obtain extended temporal perspectives.

Accumulations of bones on landscape surfaces (death assemblages) faithfully record species richness, community structure, and population shifts of source communities over many decades, and there is a growing literature on the utility of incorporating such assemblages into the tool kit of field biologists (Behrensmeier 1978, Liebig et al. 2003, Kidwell 2007, Western and

Behrensmeier 2009, Dietl and Flessa 2010, Terry 2010a, b, Miller 2011, Pyenson 2011, Behrensmeier and Miller 2012). In addition, species' habitat preferences and local habitat suitability are also faithfully recorded in patterns of skeletal abundances across a region (Behrensmeier et al. 1979, Kidwell 2007, Western and Behrensmeier 2009, Terry 2010b). However, the capacity of bone accumulations to capture finer-scales of biogeographic data, including geographic preferences within a single habitat and seasonal shifts in landscape use due to species phenologies, has remained untested.

Here I test if the geographic distribution of skeletal remains in Yellowstone National Park, which accumulates over decades to centuries (Miller 2011), can provide high-quality data on elk (*Cervus elaphus*) geographic use. I focus on bones that record season-of-input, including shed elk antlers and newborn skeletal remains. Using these data, I test if concentrations of seasonally pulsed bone inputs correspond to known regions of critical importance for species' survival (e.g., wintering grounds and calving/rearing areas). Using spatial interpolation, I then use bone data to map the distribution of seasonally specific landscape use of elk across Yellowstone and test the congruence of that interpolation to an independent suite of bone survey data. Results illustrate that bone surveys offer a powerful new tool for providing historical perspectives

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on patterns of species' geographic use—data that are currently unavailable for most ecosystems.

Antlers and wintering grounds in Yellowstone

In Yellowstone, bull elk generally winter in bachelor groups on the Northern Range (Fig. 1) and shed their antlers in late winter (March to April; Houston 1982, Feldhamer et al. 2003). Shed antlers have a low probability of long-distance transport because they are heavy, awkward to move, and are of low and only sporadically important nutritional value for carnivores and ungulates large enough to move them (Wika 1982, Wald 2011). Thus, antler concentrations should be locally high in areas where bull elk reside in late winter.

Neonatal remains and calving/rearing grounds

Calving and early rearing of neonatal elk occurs in areas with specific nutritional, environmental, and safety characteristics (Houston 1982, Singer et al. 1997, Feldhamer et al. 2003, Barber-Meyer et al. 2008). Annual mortality of elk calves in Yellowstone can be >70%, with >85% of deaths occurring in the first 30 days and >90% in the first six months (Barber-Meyer et al. 2008), a period that can be identified in skeletal remains using patterns of molar eruption (Klein and Cruz-Urbe 1984, Azorit et al. 2002) and morphology of post-cranial skeletal elements (Appendix A: text 1.0). If neonatal bones survive the rapid weathering and destruction that is characteristic of juvenile skeletal elements (Behrensmeyer 1978), they should accumulate in regions used for calving and early rearing. The small sizes and high organic composition of neonatal bones, however, make them susceptible to consumption and transportation by carnivorous mammals and birds. Thus, in contrast to shed elk antlers, there is some expectation that neonatal bones will be rare or absent, and may be dispersed from the location of death; perhaps beyond the boundaries of calving and early rearing areas. A test of the fidelity of neonatal remains to calving grounds is, thus, also a test of the potential of carnivore-mediated skeletal dispersal to blur fine-scale geographic data contained in death assemblages.

MATERIALS AND METHODS

Collecting skeletal data

Geographic locality data on shed antlers and neonatal bones across Yellowstone's Northern Range were collected using standardized bone surveys. To measure bone concentrations, data from 10 1 km long plots were sampled from each of four habitats; rolling grassland, lake margin, river margin, and conifer forest (40 sample plots total). Samples of each habitat were distributed across the study area. To accommodate differences in habitat geometries, sample plot widths were habitat dependent. All data were standardized by sampled area. Grassland plots were 100 m wide (50 m on either side of the midline), forest plots were 60 m wide, and lake and river margin plots extended 30 m from the water's edge

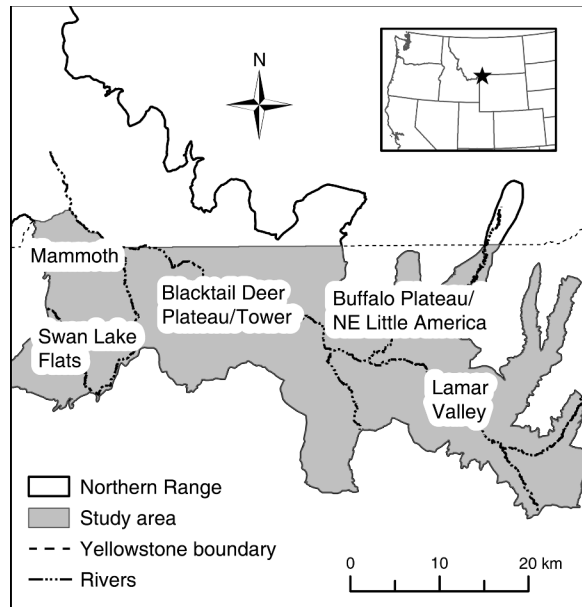


FIG. 1. The Northern Range of Yellowstone National Park showing known calving areas (after Barber-Meyer et al. [2008]). The star in the inset indicates the location of Yellowstone within the United States. Only the Northern Range contained within Yellowstone was examined (shaded region). The Mammoth region includes the Stevens Creek area. The Blacktail Deer Plateau includes Mt. Everts and Tower. The Buffalo Plateau includes Little America and Slough Creek. The Lamar Valley region includes Mt. Norris.

(Behrensmeyer 1978, Miller 2011). Sample plots were spaced a minimum of 1 km apart to reduce the possibility that skeletal elements from one individual would be sampled multiple times due to biological dispersal. This project was part of a more extensive effort to define the ecological fidelity of temperate terrestrial death assemblages (Miller 2011), and no data on the locations of wintering grounds or calving grounds were used to influence sample plot locations. Bone surveys were conducted in the summers of 2005, 2006, and 2007.

To generate data, two field assistants walked back and forth, perpendicular to either side of sample plot midlines (or together along water margins), visually inspecting the entire plot and flagging observed bones, bone fragments, and carnivore feces (each plot typically took a full day to sample). I collected standardized data on each bone, including skeletal element, ontogenetic stage, weathering stage (a proxy for postmortem duration; Behrensmeyer 1978, Miller 2011), and geographic location (eTrex Vista or Rhino II WAS-enabled GPS; Garmin International, Olathe, Kansas, USA).

I used the bone data to (1) test the spatial fidelity of antler accumulations against aerial survey data and (2) interpolate concentrations of antlers and neonatal skeletal remains across the study area using inverse distance-weighting (IDW; Shepard 1968, Longley et al. 2005; see also Appendix A: text 2.0). The spatial

interpolations extend 6 km from all 40 sample plots, though not beyond the study area. The predictive power of the antler interpolation was tested using data from 14 additional sample plots from the same habitats (Appendix A: text 3.0). Predicted values of validation sample plots were defined as the mean value of the interpolated surface sampled by each plot polygon (sampled with a 10 m grid). To calculate confidence estimates around the interpolation, prediction errors for each validation plot (differences between interpolated antlers/km² and sampled values) are expressed relative to the range of interpolated values (i.e., for an interpolation surface that ranges between 0 and 800 antlers/km², a sample plot predicted within 80 antlers/km² is correct within 10% of the interpolation). Sample sizes of newborn bones are small, making validation of the interpolation difficult. In addition, knowledge of the relative importance of Yellowstone calving grounds over time is not as quantitatively developed as bull elk late-winter geographic use, though some data on locations and relative dominance of Yellowstone calving and rearing grounds are available from historical records (Houston 1982) and more recent research on calf mortality (Singer et al. 1997, Barber-Meyer et al. 2008). Thus, the neonatal interpolation is used here as a guide to areas with relatively high and low concentrations of neonatal skeletal remains, and is compared qualitatively with known regions of calving activity and inactivity. Spatial analyses were calculated using ESRI ArcGIS 9.3 software (ESRI, Redlands, California, USA).

Counting skeletal units and standardizations

To compare data among sample plots, antler counts are standardized by sampled area (antlers/km²). Only antlers and antler fragments with the rounded pedicle attachment surface (skull attachment) indicative of shedding are included in these analyses. For neonatal remains, because one calf can contribute multiple bones to a single sample plot, the collection of bones from each plot was summarized into the minimum number of individuals (MNI) using skeletal element abundances, left-sided and right-sided bones, and weathering stages (Behrensmeyer et al. 1979, Badgley 1986, Lyman 2008, Miller 2011, Behrensmeyer and Miller 2012). By coalescing the bone sample down to an estimated number of represented calves, the bone data become more readily comparable to survey results of the living populations. MNI is conservative, however, and it may underestimate true sampled abundances (Lyman 2008). For each sample plot, neonatal MNI are standardized by plot area (MNI/km²).

Available geographic data on bull elk late-winter geographic use

A decade of late-winter elk classifications conducted between 1998 and 2007 (no survey in 2001; Northern Yellowstone Cooperative Wildlife Working Group 1988–2007) serves as the spatial reference for testing

the quality of geographic data from shed antlers (Appendix B). To standardize aerial surveys, the Yellowstone wildlife management community divides the Northern Range into 68 geographic units (elk count units; Appendix C). During late-winter classifications, 10–46 elk units are randomly selected and data are collected on the number, age, and gender (cow, calf, bull) of observed elk. Late-winter surveys are generally conducted in March, near the time of maximum antler shed.

Data transformation

To compare observed bull counts (live data) with area-standardized antler concentrations (dead data), live data were first transformed to the number of observed bulls in each elk unit standardized by elk unit area. For each year, sampled elk units were then ranked by these bull concentrations. The dead data (antler concentrations) were also ranked by the elk units in which they occur. For elk units containing more than one bone survey, antler counts and sample plot areas were pooled to approximate the pooled nature of aerial surveys before calculating antler concentrations (antlers/km²). These rankings provide relative geographic concentrations, by elk unit, for bull elk from aerial surveys (1998–2007) and shed antlers on the landscape.

Comparing aerial (live) and bone (dead) surveys

To test the geographic consistency with which bull elk use the Yellowstone landscape, I used pair-wise Spearman rank-order correlation tests of the elk unit-ranked bull concentrations across all years (live–live comparisons). To test the correlation between individual late-winter surveys and long-term patterns, each late-winter survey is also compared to mean bull concentrations across all other aerial surveys (live_{ave}–live comparisons). To limit autocorrelation, data for the target late-winter survey (live_{*i*}) is not included in the calculation of average live data (live_{ave} excluding *i*). To test the congruence between antler concentrations and annual bull elk distributions (live–dead fidelity), Spearman correlations compared elk units ranked by antler concentrations and individual late-winter surveys (live–dead comparisons). To test live–dead fidelity over longer time scales, Spearman correlations were performed between elk units ranked according to antler concentrations and their long-term average bull concentrations (mean across all sampling years; live_{ave}–dead comparison). Because rivers with margins conducive to bone surveys are spatially biased to the eastern portion of the study area, and half of river margin surveys sampled elk units with limited (two years or less, $n = 3$ surveys) or no late-winter survey data ($n = 1$), or sampled rivers that define borders between elk units ($n = 1$), river margins could not be reasonably included in live–dead comparisons (though they were included in the spatial interpolation). Spearman rho ranges between 1.0 (perfect positive correlation) and –1.0 (perfect negative

correlation; Sokal and Rohlf 2000). Analyses were conducted in the open source statistical platform R version 2.9.2 (R Development Core Team 2009).

RESULTS

The distribution of shed antlers mirrors bull elk geographic use in late winter

All pair-wise comparisons among late-winter aerial surveys (live–live comparisons; Fig. 2a) are generally consistent (median = 0.37, $n = 36$ comparisons), but the overall distribution extends across the full range of Spearman rho, varying from perfectly positive (1.0) to perfectly negative (–1.0). This interannual similarity in geographic use provides the opportunity (but not necessity) for the formation of congruent geographic patterns of shed antler concentrations. Comparisons between individual aerial surveys and bone surveys (live–dead comparisons; Fig. 2b) are more narrowly distributed (median = 0.34, $n = 9$ comparisons), but are not significantly different from live–live comparisons (Mann-Whitney $U = 157$, $P = 0.90$). In both cases, significant rho values are not common; for live–live, $n = 5$ significant values (13% of comparisons), for live–dead, $n = 1$ significant value (11%).

Comparisons of individual late-winter aerial surveys to average bull concentrations (live_{ave}–live; Fig. 2c, boxplot) are positive and the overall range of Spearman values is narrower than live–live comparisons (median = 0.49, $n = 9$ comparisons; $n = 5$ comparisons for $P < 0.05$). Shed antlers were nearly ubiquitous across Yellowstone, with 97% of plots (29 of 30) from lake margins, forests, and grasslands yielding at least one shed antler (antlers were less common on river margins; Appendix D). Correlation between the geographic distribution of shed antler concentrations and mean bull elk concentrations (live_{ave}–dead) is high (Fig. 2c, diamond point; rho = 0.54, $P < 0.05$), approaching the maximum live_{ave}–live correlation (rho = 0.63, $P < 0.01$).

Antler concentrations on the landscape are predictable and map bull elk geographic use

While shed antlers are found across Yellowstone, high concentrations were encountered along the contiguous rolling grasslands and ridges of the Mt. Everts–Blacktail Tower regions (darker regions in the western portion of Fig. 3a) and Mammoth (northwest corner of Yellowstone; see Fig. 1 for geographic reference). One antler-rich site was recorded in the hills north of the Lamar Valley, but antlers were otherwise generally sparse in the eastern portions of the study area. To test the predictive power of the IDW interpolation, predicted antler concentrations for the validation sample plots were compared to their empirical values (circles in Fig. 3a; Appendix E). Half of validation sample plots (7 of 14; open circles with cross-hairs in Fig. 3a) were predicted within 78 antlers/km² (i.e., 10% of the interpolation's total range), and over 85% of sample plots (12 of 14; open circles with vertical lines) were correctly predicted

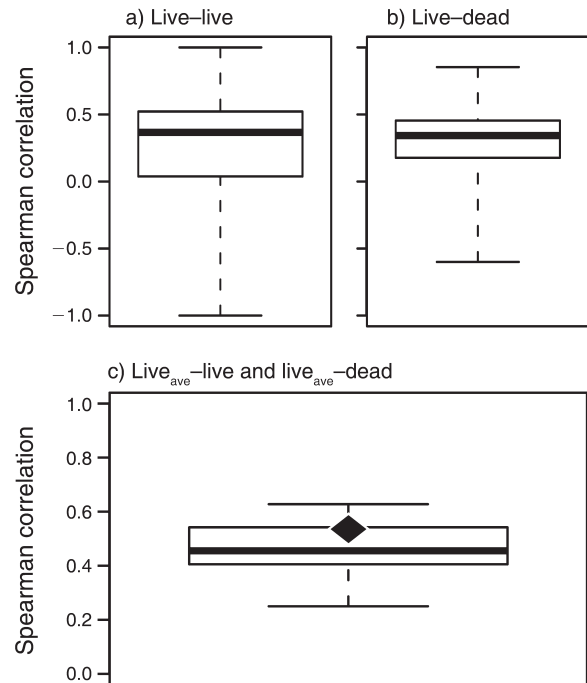


FIG. 2. Geographic consistency (a) among bull elk concentrations from individual late-winter aerial surveys (live–live comparisons), (b) among individual aerial surveys and antler accumulations (live–dead), and (c) between decadal averaged aerial survey data and both individual aerial surveys (live_{ave}–live, boxplot) and antler accumulations (live_{ave}–dead, diamond). Boxplots of Spearman correlations display median and interquartile, whiskers show overall range. Live–live comparisons in panel (a) show modest agreement in the distribution of bull concentrations across Yellowstone. The distribution of live–dead comparisons in panel (b) is not significantly different from live–live comparisons (Mann-Whitney U test, $P = 0.90$), but it spans a narrower range of values, illustrating dampened variability characteristic of extended sampling intervals (also seen in live_{ave}–live comparisons). Antler surveys describe annual bull elk distributions with the same fidelity as aerial surveys and have higher fidelity to decadal averaged aerial survey data (panel [c]; live_{ave}–dead comparison) than most individual surveys of the living.

within 156 antler/km² (20% of the interpolation surface). While small-scale geographic heterogeneities are evident (two validation plots are more poorly predicted), antler concentrations across Yellowstone can be largely modeled using the simple IDW function.

Neonatal remains faithfully document calving and early rearing areas

Calf remains were found in roughly half of all sample plots (22 of 40; solid shapes in Fig. 3b; Appendix F) and were geographically widespread. While the presence of neonatal skeletal remains was more pervasive than expected, sample sizes of neonatal MNI in individual plots were generally small with over half of neonatal-positive plots yielding a single calf (59%; 15 of 22). However, of the seven plots yielding more than one calf, five are within the Blacktail Deer Plateau Region

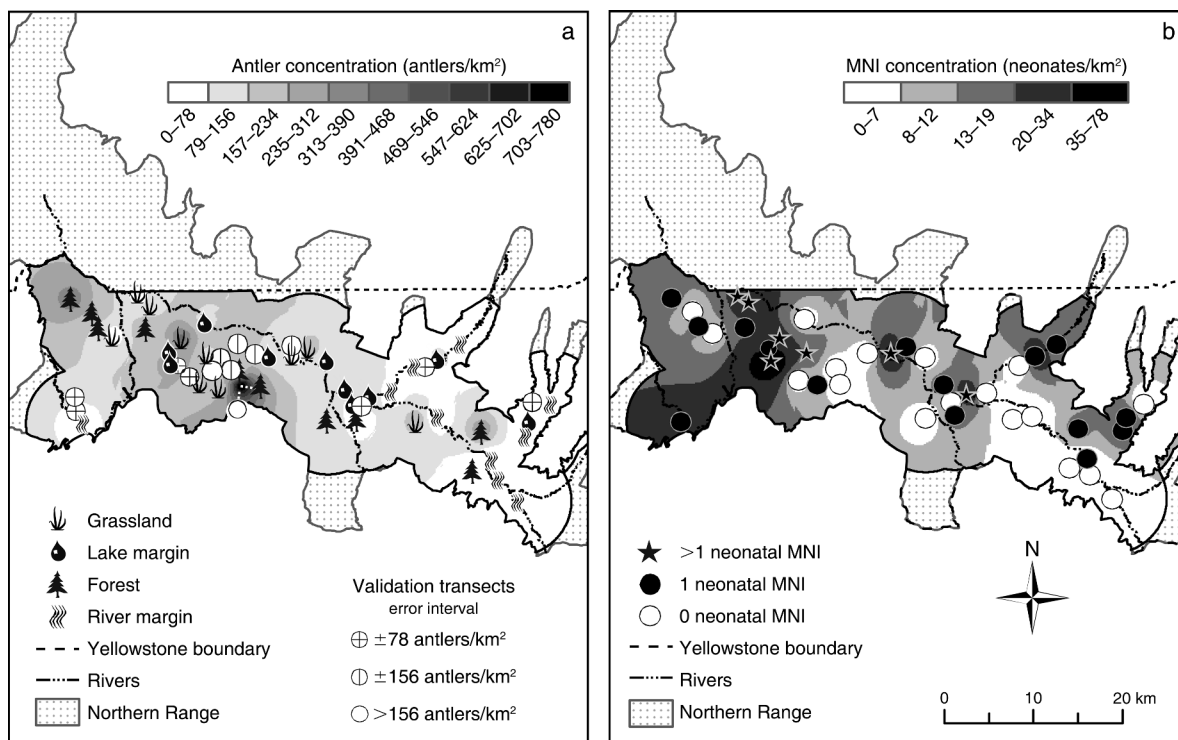


FIG. 3. Inverse distance-weighted interpolation of (a) antler concentrations and (b) neonatal minimum number of individuals (MNI) concentrations on the Northern Range as sampled by 40 plots in grasslands, forests, lake margins, and river margins. For antler concentrations in panel (a), 14 validation sample plots (circles) are also shown (see Appendices D and E). Over 85% of the validation sample plots (12 of 14) are predicted within 20% of the interpolation surface (± 156 antlers/km²). Dashed white lines show placement of sample plots when moved for map clarity. For neonatal remains in panel (b), relatively high concentrations are located on the Blacktail Deer Plateau with spottier concentrations along the Buffalo Plateau. Calf remains are only found within known calving areas. Model output for neonatal MNI concentrations was binned using Jenks natural breaks optimization.

(including Mt. Everts and nearby areas). Spottier concentrations were found in Little America and the Buffalo Plateau Region (including Slough Creek).

Remains of neonatal elk map well onto known calving grounds. Studies of calving in Yellowstone show that many regions of the Northern Range can be used for calving, and preferences among areas appear to shift across decadal timescales (Houston 1982, Barber-Meyer et al. 2008). In the early 2000s, calving was observed at Mammoth, Swan Lake Flats, the Blacktail Deer Plateau (including Mt. Everts and Tower), and the Lamar Valley–Mount Norris area (Barber-Meyer et al. 2008). Calving was also documented on the Buffalo Plateau Region, but in smaller numbers (Barber-Meyer et al. 2008). Calving was also broadly distributed in the 1980s (Singer et al. 1997, Barber-Meyer et al. 2008), but most often observed near Swan Lake Flats and the Lamar Valley. Importantly, every locality in which skeletal calf MNI were observed corresponds to a region that supports the calving and rearing of young elk. Furthermore, the reverse is also true; the death assemblages of all sampled areas known to support calving contained skeletal neonatal individuals. Although much of Yellowstone's Northern Range is conducive to calving (Houston 1982, Barber-Meyer et al. 2008), sampled regions

that are inhospitable did not produce neonatal remains. These regions include burned forests with thick carpets of downed trees that are passable by adult elk (and predatory birds) but presumably less hospitable to calves, as well as regions distal to known-calving areas. The absence of neonatal remains beyond calving and rearing areas seems meaningful, but further sampling in regions with more quantitative spatial understanding of calving ground preferences will provide a more rigorous test of this finding.

DISCUSSION

Bone accumulations provide long-term perspectives on geographic use

Death assemblages accumulate over multiple generations, offering more expansive temporal perspectives than other sources of ecological data retrievable from modern ecosystems (Kidwell 2007, Western and Behrensmeier 2009, Terry 2010a, b, Miller 2011). Bones in Yellowstone, for example, can survive on the landscape across centennial timescales (Miller 2011). The capacity of these data to reveal patterns of landscape-use is illustrated here; the spatial distribution of antlers obtained in a few summers describes decadal

averaged late-winter landscape use of Yellowstone bull elk with *higher* fidelity than most individual aerial surveys (Fig. 2c). In addition, while individual aerial surveys will capture stochastic biological events and high-frequency ecological variability (wide ranging Spearman values of Fig. 2a), multi-generational records (including dead data) provide landscape use data that incorporate, but are not overwhelmed by, the ecological variability inherent to biological systems (Fig. 2b, c).

Antlers provide insight into bull elk resource partitioning in late winter

Pooling antler data among habitats (lake margin, open grassland, forest) provides a general geographic overview and illustrates the high fidelity with which antler accumulations capture bull elk geographic use in late winter (Fig. 2b and c). The variability of this fidelity can be tested using habitat-specific live_{ave}-dead comparisons. These comparisons show that antler accumulations of grasslands ($\rho = 0.64$, $P = 0.096$) and forests ($\rho = 0.74$, $P < 0.05$) have remarkably high geographic fidelity to decadal averaged survey data (both higher than all live_{ave}-live comparisons; Fig. 4a and b), while lake margins show reduced fidelity (Fig. 4c, $\rho = 0.383$, $P = 0.31$). Winter habitat partitioning of bull elk likely plays a role in this discrepancy. Because the sampled lakes are largely frozen at the time of antler shed, they and surrounding snow-buried vegetation offer minimal nutritional value and may not be used as an aquatic escape from predators. There is no indication of bias against bones around lake margins, as they yield among the highest bone concentrations on the Yellowstone landscape and offer ecological data that is highly faithful to ungulate species richness and community structure (Miller 2009, 2011). Thus, in winters, bulls may spend more time in open grasslands and forests (as observed elsewhere: Boyce et al. 2003, Mao et al. 2005) with reduced and less consistent use of lake margins. For grassland and forest bone accumulations, either separately (Fig. 4a and b) or combined (Fig. 4d, $\rho = 0.54$, $P < 0.05$), the available spatial data have comparatively high (or higher) affinity to decadal averaged survey records than individual aerial surveys.

Predation and scavenging do not degrade regional geographic signals

The capacity of neonatal remains to identify calving areas is particularly significant because carnivores have likely transported many of these individuals from sites of death. Over 80% of neonatal MNI (28 of 34; Appendix F) show evidence of carnivore consumption (tooth scrapes and/or punctures). Even with this high transport potential, the geographic distribution of neonatal bones faithfully identifies areas used for calving and early rearing.

The robustness of the skeletal signals of calving grounds may be due, at least in part, to the wide expanses of these important areas (Houston 1982,

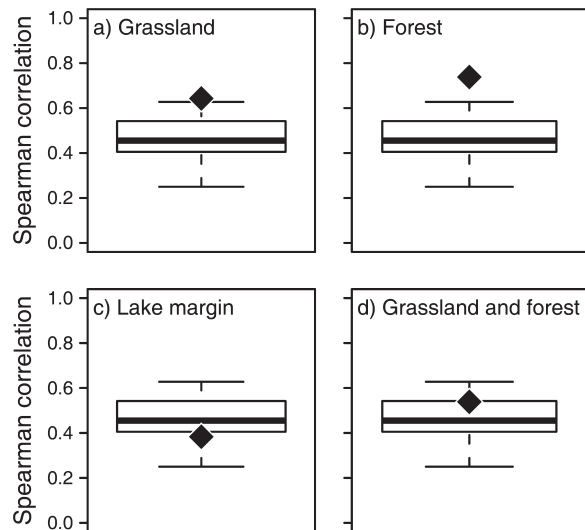


FIG. 4. Live_{ave}-dead comparisons (diamonds) for individual habitats compared to all live_{ave}-live comparisons (boxplots, as in Fig. 2c; $n = 9$, $n = 5$, respectively, for $P < 0.05$). Antler accumulations in (a) grassland and (b) forest habitats show higher fidelity to decadal averaged late-winter aerial surveys than individual constituent surveys (live_{ave}-dead grassland $\rho = 0.64$, $P = 0.096$; live_{ave}-dead forest $\rho = 0.74$, $P < 0.05$). (c) The fidelity of lake margin death assemblages to living surveys is reduced (live_{ave}-dead lake margin $\rho = 0.383$, $P = 0.31$), which may correspond to more limited use of these areas by bull elk in winter. The death assemblage of well-utilized habitats (grassland and forest) when analyzed either individually [panels (a) and (b)] or combined (d; live_{ave}-dead grassland + forest $\rho = 0.54$, $P < 0.05$), show high or superior agreement to decadal averaged aerial survey data than individual surveys themselves.

Barber-Meyer et al. 2008). In fact, similar critical geographic regions for many species (e.g., calving, wintering, and breeding grounds) encompass wide geographic areas (Duff and Singer 1982, Griffith et al. 2002, Healy 2003) that are generally larger than a mammalian (or even avian) predator is likely to carry a meal. Thus, as is evident in the Yellowstone death assemblage, predatory and scavenging activity may only rarely result in the movement of skeletal material beyond the borders of calving grounds. This clarity of geographic signal for readily scavenged, highly transportable skeletal remains indicates that modern and fossil bone accumulations of all ontogenetic stages may have broad potential for mapping geographic patterns of their source communities.

Bones provide new perspectives on the Yellowstone ecosystem

Death assemblages permit new questions to be asked of historical populations. Even for the well-studied Yellowstone ecosystem, there are limited historical data that can be quantitatively integrated with modern studies. For example, long-term quantitative assessments of calving ground use, and changes in intensity of use through time, have not been explicitly tracked over

decadal timescales. Calving regions identified by standardized bone sampling, however, are directly comparable and deviations among areas (e.g., high concentration of calf remains in the Blacktail Region) suggest new historically integrated insight. While a straight spatial reading of relative abundance patterns is tempting, and may be correct, further testing of how neonatal records are affected by spatially differentiated predation intensity and dominant predator (e.g., wolf, bear) will improve understanding of the available spatial data and their potential biases.

Knowledge of late-winter landscape use by Yellowstone bull elk is similarly temporally limited. Because the bone assemblage incorporates data from many decades prior to the initiation of late-winter aerial surveys (Miller 2011), much of the incongruence between aerial survey data and bone records (Figs. 2c and 4) is likely due to differences in sampling duration. Additionally, restructuring of abundances and habitat use among Yellowstone ungulates has occurred since the inception of late-winter surveys, much of which has been at least indirectly attributed to the reintroduction of wolves in 1995, following their extirpation in the 1920s (Smith et al. 2003, White and Garrott 2005). Thus, it may be an oversimplification to characterize comparisons between a decade of aerial surveys and the multigenerational antler record as a simple fidelity test. These comparisons may also be characterized as tests of how late-winter landscape use of a wolf-influenced bull elk population compares to a measure of geographic use that incorporates the previous seventy years of a wolf-free ecosystem. While $live_{ave}$ -dead comparisons are highly and significantly positive, deviations may reflect changes in bull elk wintering landscape use; including greater historical use of the Mammoth and Blacktail Deer Plateau regions.

Death assemblages are readily available sources of low-impact historical ecological data

The use of historically integrated (time-averaged) death assemblages (including accumulations of bones, teeth, shells, and plant materials) to expand the observational window with which ecosystems are studied is underway in a wide range of biotic systems. From marine invertebrates and corals to terrestrial mammals and plants, death assemblages can provide meaningful historical ecological insights, such as quantifying preferred avian (owl) hunting grounds (Terry 2010b), revealing changes in ungulate habitat use over time (Behrensmeier et al. 1979), establishing anthropogenic impacts on habitat suitability of marine mollusks (Kidwell 2007), defining community baselines prior to human influence (Aronson et al. 2007, van Leeuwen et al. 2008), and resolving species' responses to past climate change that offers expectations and management strategies relevant to contemporary populations (Terry et al. 2011, Faith 2012). Death assemblages also offer a powerful source of baseline data on historical ecological variability resulting from past climatic and/or ecological

drivers against which to assess recent changes in populations, community structure, and biogeography (Dietl and Flessa 2009, 2010). Furthermore, because data on skeletal accumulations can be collected using low-impact methods and when living members of target species are absent, death assemblages provide a valuable and minimally invasive means of studying sensitive species and fragile ecosystems.

For mammalian communities, while the extended temporal perspectives provided by bone accumulations will be valuable across many climate settings and habitats, death assemblages in arctic regions, where durations of bone survival can extend to millennial timescales (Meldgaard 1986, Sutcliff and Blake 2000), are a clear target for future study. A particularly germane study species with broad political, economic, and social significance across the Northern Hemisphere is caribou (*Rangifer tarandus*), whose unique physiology and ecology make this northern cervid ideally suited for studying many aspects of life history and landscape use through bone accumulations. Female caribou, like males, annually grow and discard antlers. However, while male caribou shed antlers shortly after breeding, pregnant females retain their antlers until casting them within days of calving (Espmark 1971, Whitten 1995). As caribou commonly aggregate during calving (Griffith et al. 2002, Feldhamer et al. 2003), regions used as calving grounds have the opportunity to develop concentrations of shed female antlers and the bones of newborn fatalities. Similarly, breeding areas can develop accumulations of shed male antlers (Miller and Barry 1992). Thus, changes in landscape use across broad timescales may be directly investigated using death assemblages, placing current biological patterns in a broader temporal context. The caribou example is particularly salient as rapid warming and pressure for mineral and petroleum extraction are increasing in key calving areas in many arctic regions (including the Arctic National Wildlife Refuge, Alaska). The historical insights offered by skeletal remains can help us establish the long-term biological value of such areas and assess the ecological impacts of their loss or degradation.

CONCLUSIONS

Skeletal elements can provide high-quality multi-decadal patterns of landscape use. Surface accumulations of shed elk antlers and neonatal bones in Yellowstone National Park delineate elk wintering and calving grounds and contribute to a more thorough understanding of local herds' geographic requirements. Analysis of spatial data contained in bone accumulations, including modern and possibly some fossil assemblages, enables rapid acquisition of seasonal and species-specific patterns of landscape use across a broad observational window.

For regions that lack historical ecological data or remain poorly studied, bone surveys represent a critical new, low-impact tool for establishing historical variabil-

ity of geographic use. For well-studied regions, bone surveys can augment traditional monitoring efforts and address questions that are logistically difficult or have otherwise been historically ignored. This accessible historical data will permit wildlife management and conservation efforts to quickly identify regions of critical biological importance and provide extended perspectives for identifying recent patterns of geographic use that are abnormal to long-term baselines.

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SUPPLEMENTAL MATERIAL

Appendix A

Supplemental descriptions of sampling and analytical methods (*Ecological Archives* E093-232-A1).

Appendix B

Late-winter elk classification data from the Northern Yellowstone Cooperative Wildlife Working Group (1988–2007) (*Ecological Archives* E093-232-A2).

Appendix C

Map of Elk Count Units and bone survey locations on the Northern Range of Yellowstone National Park (*Ecological Archives* E093-232-A3).

Appendix D

Shed antler results from Yellowstone bone surveys (*Ecological Archives* E093-232-A4).

Appendix E

Shed antler results, expected antler concentrations, and error intervals for Validation Sample Plots (*Ecological Archives* E093-232-A5).

Appendix F

Neonatal results from Yellowstone bone surveys (*Ecological Archives* E093-232-A6).