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Original Research

Comparison of Beaver Density Estimates from Aerial Surveys of Waterways Versus Transects

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Abstract

Historic beaver-sign (*Castor canadensis*) survey flights were often conducted over waterways to maximize beaver detections. However, densities determined from strip transect surveys are more useful to compare across and within study areas than waterway indices based on observations per distance flown because transects are more representative of the wider landscape. Yet, it is unknown if, and to what extent, aerial waterway surveys are reflective of transect densities. I conducted aerial surveys for active beaver signs each fall during 2015–2018 over 2 waterway routes and 2 corresponding strip-transect routes. The simple linear regression of transect densities on waterway densities (n=8) yielded a reasonable (R^2=0.79) preliminary equation for converting historic waterway data to transect densities. Additionally, visual inspection indicated that converted waterway densities reasonably reflected the trend in transect densities in an area where the wider habitat was similar in terms of beaver harvest, land use, and proportion of water features. Although trend was well-reflected, individual waterway densities in this area were only 57-75% of transect densities. In other areas, where water features were limited, visual inspection suggested the trend of waterway densities was less reflective of transect density trend and individual waterway densities overestimated transect densities (up to 309%). Nevertheless, while transect densities are better for comparisons within and across study areas, waterway surveys are still important for timely and specific within-study area insights. This research provides useful benchmark examples of reliability regarding waterway observation indices converted to densities for conservation, research, and management of beavers and their ecosystems. Because these conclusions are based on a small sample, additional research is recommended to better define this relationship especially in areas with differing habitats, beaver harvests, and land use patterns.

Key Words: Aerial Survey, Beaver, *Castor canadensis*, Density, Food Cache, Indices, Trend, Waterway Surveys

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INTRODUCTION

Beavers (*Castor canadensis*) are considered important ecosystem engineers altering wetland topography, forest vegetation, and biogeochemical features of landscapes (Johnston 1994; Naiman *et al.* 1994). Recently, beavers have also been discovered to be more important to grey wolf (*Canis lupus*) diet than previously surmised (Gable *et al.* 2016; Gable and Windels 2018). Further, beaver availability as prey may help in part to explain long-term wolf pack size and persistence (Barber-Meyer *et al.* 2016). Because of the lack of detailed information on wolf-beaver dynamics (Mech *et al.* 2015; Gable *et al.* 2018), I began conducting aerial surveys of beaver presence as part of a long-term wolf study in Minnesota, USA (Mech 2009; see below).

Specifically, I was interested in using strip-transect surveys (STSs) to compare beaver densities in the northeastern and southwestern parts of the study area because these areas differ in habitat, beaver harvest, land use, and large ungulate composition. I also was interested in conducting waterway survey routes (WSRs) in these areas to follow historic methodological precedent, with results based on an index of observations per distance flown on waterway routes (waterway survey indices, WSI).

Historic beaver survey flights were often conducted using WSRs (rather than STSs) to maximize beaver detections (Swank and Glover 1948; Swenson *et al.* 1983). However, to compare across and within study areas, densities (from STSs that are more representative of the wider landscape) are more ideal than WSIs. The ability to convert historic beaver WSIs (colonies/km flown on WSRs) into beaver densities (colonies/km^2) on the wider landscape would allow for density comparisons to contemporary studies and across study areas. But for that conversion to be valid, assumptions about how much area an observer surveyed when flying a WSR and how representative WSRs are of the wider landscape are required. WSRs were intended to focus on areas ideal for detecting beaver presence, rather than sampling the wider landscape, so it is unknown how reliable these conversions are.

I used beaver survey data from 4 consecutive years, that included 2 WSRs and 2 corresponding STSs flown each year, to determine how conversions of WSR data into density data would compare to densities calculated using STSs in areas of varied habitat and beaver-harvest pressure.

MATERIAL AND METHODS

Study Area

I conducted aerial beaver-sign surveys in the context of a long-term wolf research project (Mech 2009). The U.S. Geological Survey Minnesota Wolf and Deer Project study area (hereafter "study area") includes 2,060-km^2 of both non-wilderness and wilderness (Boundary Waters Canoe Area Wilderness, BWCAW) in the Superior National Forest, Minnesota, USA (48° N, 92° W; see Nelson and Mech 1981 for a detailed description). Topography comprises rocky ridges, swamps, numerous lakes, and uneven upland ranging from 325 to 700 m above sea level (Heinselmann 1996). Average monthly temperatures range from approximately -18 to 2°C during November – April and approximately 4 to 18°C during May – October (Heinselman 1996). From mid-November through mid-April, snowfall averages 150 cm (Nelson and Mech 2006). The area is in a transition zone between the southern boreal forest of neighboring Ontario, Canada and the hardwood forests typical of areas farther south in Minnesota (Pastor and Mladenoff 1992). Forest overstory is predominately conifers, e.g., white pine (*Pinus strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), interspersed with quaking aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) (Heinselman 1996). Generally, in the northeastern portion of the study area, the primary large ungulate (wolf prey) is moose (*Alces americanus*) and in the southwestern portion, white-tailed deer (*Odocoileus virginianus*) (Frenzel 1974; Mech 2009). During 2015–2018, mean resident-pack wolf (not including transients or lone wolves) density was ~16/1,000 km^2 (Mech and Barber-Meyer, unpublished data). Beaver and snowshoe hare (*Lepus americanus*) were also prey for resident medium and large carnivores (O'Donoghue *et al.* 1997; Barber-Meyer and Mech 2016). Beavers in the non-wilderness area were legally harvested whereas beavers in the core of the wilderness area did not face significant harvest pressure.

Observation flights

During 17 October – 4 November in 2015-2018, 2 WSRs (northern and southern) and 2 corresponding STSs (northeast and southwest) were flown each year in the study area (Figure 1) to assess active beaver signs, presence, relative abundance and densities (Brown and Parsons 1982; Swenson *et al.* 1983). The northern WSR and northeastern STS were in an area with more water features and wilderness, lower beaver harvest, and reduced or absent logging compared to the southern WSR and southwestern STS (Table 1), and the large ungulate composition (major wolf-prey) included more moose than deer.

Table 1. Wilderness and water features of the strip transect surveys (STSs) and waterway survey routes (WSRs) aerially surveyed for beaver signs during fall 2015-2018 in the Superior National Forest, Minnesota, USA. Area calculations included an 800-m (~0.5-mi) buffer along the flight path.

Name	Distance (km)	Total area (km^2)	% wilderness	% water
Northeast transect	79	123	100	15
North waterway	211	320	77	29
Southwest transect	79	123	0	5
South waterway	161	238	11	5

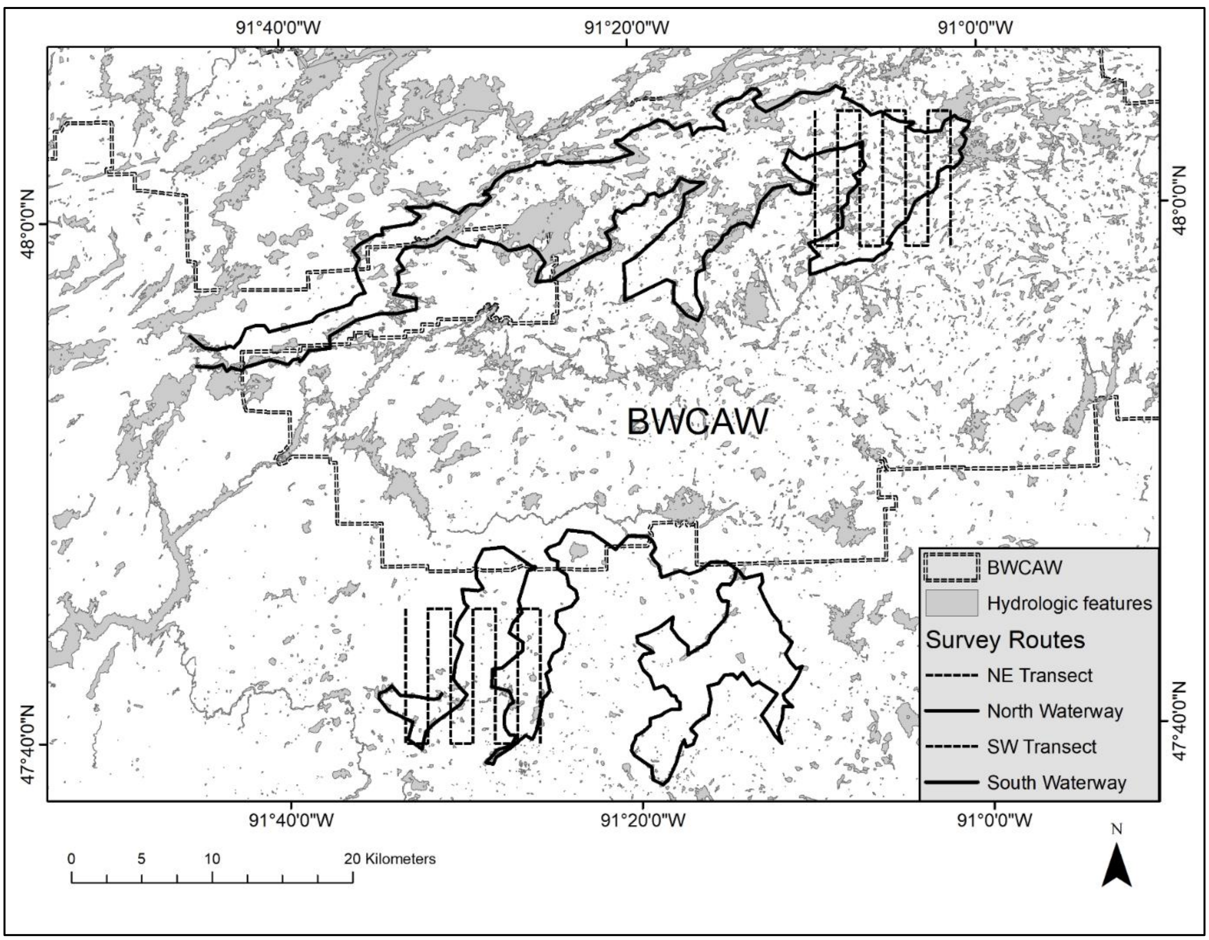

Figure 1. Map showing aerial beaver-sign strip transect surveys (STSs) and waterway survey routes (WSRs) conducted during fall 2015-2018 in the Superior National Forest (SNF), Minnesota, USA. Hydrologic features and the Boundary Waters Canoe Area Wilderness (BWCAW), also part of the SNF, are delineated as well.

Flights were conducted in a DHC-2 DeHavilland Beaver (Payne 1981; Romanski 2010) at approximately 152 m (500 ft) above ground level and approximately 161 km/hr (100 mph) air speed (see Payne 1981 and Romanski 2010 *re* the potential for differing aircraft to influence survey results). Ideally, surveys were conducted after the majority or all of deciduous leaf-fall had occurred (but before snow covered the ground or ice covered the lakes) (Hay 1958; Payne 1981) and on days when there was sufficient cloud cover or between 10:30-13:30, when glare from the sun was minimized. I also only conducted flights during calm or no winds and no precipitation to minimize surface water disturbances that can influence sightability of beaver food caches. I generally aimed to conduct all survey flights in 1 day (or as close together as possible depending on pilot and flight availability) to minimize differences in leaf fall and beaver activity across the STSs and WSRs.

I sat up front next to the pilot as an observer and recorder of data, and the pilot was the second observer. We attempted to record beaver presence within 800 m (approximately 0.5 mi) of the aircraft on both sides. We determined beaver presence by a lodge with mud or freshly chewed or peeled logs on it, canals, or a food cache in the water near the lodge (Hay 1958; Payne 1981; Johnston and Windels 2015). We also recorded active beaver presence in cases where we did not see a lodge but we noted either a functioning dam with fresh mud or freshly-chewed logs on it, or an area that was obviously recently inundated with water and beaver canals were present (Hay 1958; Brown and Parsons 1982; Swenson *et al.* 1983). We undoubtedly missed some active beaver signs. At times, tall trees obstructed our view of near-shores; other times, glare from the sun briefly obscured our view; and it was occasionally difficult to determine if a lodge was active or recently abandoned (this is more of a problem in early fall). Sometimes, even though vegetation was growing on lodges, we could determine that they were active if we were close enough to see fresh mud on some portions of the lodges, and if there were some freshly chewed or stripped-of-bark logs in the area (Romanski 2010). However, it is also possible that we erred in considering lodges active when in fact they were recently abandoned. We generally tried to record each active lodge; in rare cases where there was more than 1 significant active lodge in a large pond or lake, we counted the number we considered active (this was a factor in very few cases, i.e., <10 situations out of over 400 sightings). Sometimes, there was a main lodge and some significantly smaller active "mini-lodges" very near the main one – in those cases, where it was a small water body – we generally considered this a single colony and only counted the main lodge.

I held a standard GPS with the routes pre-programmed, and I marked a GPS point on our flight path (not precisely where the beaver sign was estimated to be located) whenever either observer called out evidence of an active beaver colony. We did not circle back to check our observations.

Analysis

For each year and each WSR or STS, I calculated a relative abundance index by dividing the number of points (active beaver sign) per km flown. For STSs, I also calculated density by dividing the number of points by 123 km^2 assuming observability to 800 m (~0.5 mi) on each side of the plane. I assessed general trends over the 4 years by visual inspection.

I used ArcMap v. 10.5.1 to add an 800-m (~0.5 mi) buffer around the flight path of the WSRs to generate an observable area for each WSR. I divided the number of beaver sign points by this area to calculate WSR density estimates.

I also used ArcMap v. 10.5.1 and geospatial layers from the Minnesota Geographic Data Clearinghouse (http://www.mngeo.state.mn.us/chouse/data.html) to calculate differences among the WSRs and STSs (with a buffer around the flight path of 800 m, ~0.5 mi) in proportions of water and wilderness (BWCAW). I plotted annual densities in Microsoft Excel 2016. I analyzed the simple linear regression of STS versus WSR densities in Statistix v. 10. I assessed the influence of potential statistical outliers (outlier *t* statistic) and cases with Cook's Distance values >0.2 by re-running the regression without those datapoints. I plotted the regression in Microsoft Excel 2016. I considered significance at $\alpha = 0.05$.

RESULTS

I conducted 530 km of aerial surveys for active beaver signs each fall during 2015–2018 (Table 1; Figure 1). Surveys were conducted on 27 October and 3 November, 2015, 2 and 4 November, 2016, 17 October, 2017, and 2 November, 2018. The northeast STS and north WSR included ≥77% wilderness and ≥15% water features, whereas the southwest STS and south WSR included ≤11% and 5%, respectively (Table 1). I recorded 1,350 total beaver sign points with a mean of 337.5 beaver sign points each year (annual counts ranged from 225 to 438) (Table 2). Generally, annual fluctuations in STS densities from 2015-2018 indicated (by visual inspection) an increase from 2015 to 2016 with a return to near 2015 levels by 2018 (Figure 2). Density (active beaver sign points / km^2) was greater each year for the northeastern STS than that calculated from the northern WSR (Figure 2). In contrast, the density for the southwestern STS was lower each year than that calculated from the southern WSR (Figure 2). The linear regression of

Table 2. Results (beaver sign points marked, index = points / km flown, density = points / km^2) from aerial counts of beaver signs conducted via strip transect surveys (STS) and waterway survey routes (WSR) during fall 2015-2018 in the Superior National Forest, Minnesota, USA. Area calculations included an 800-m (~0.5 mi) buffer along the flight path.

Name	2015 points	2016 points	2017 points	2018 points
Northeast transect	67	125	98	90
North waterway	99	204	191	135
Southwest transect	15	34	13	15
South waterway	44	75	80	65
	2015 index	**2016 index**	**2017 index**	**2018 index**
Northeast transect	0.85	1.58	1.24	1.14
North waterway	0.47	0.97	0.91	0.64
Southwest transect	0.19	0.43	0.16	0.19
South waterway	0.27	0.47	0.50	0.40
	2015 density	**2016 density**	**2017 density**	**2018 density**
Northeast transect	0.54	1.02	0.80	0.73
North waterway	0.31	0.64	0.60	0.42
Southwest transect	0.12	0.28	0.11	0.12
South waterway	0.18	0.32	0.34	0.27

transect densities on WSR densities (Figure 3) was based on 8 points (2 per year, 1 from the northern area and 1 from the southern). Nevertheless, the linear regression equation transect density = 1.98*waterway density - 0.2973 had a reasonably high R^2 value (0.79; Figure 3) and was significant ($F_{1,7}$ = 22.2, *P*=0.003). The datapoint with the highest Cook's Distance (0.20) and outlier *P* (0.10) was the 2017 southern waterway-southwestern transect. Removing that point increased the R^2 to 0.86 with the resulting linear equation of transect density = 1.90*waterway density - 0.2291 ($F_{1,6}$ = 29.59, *P*=0.003). There was no *a priori* reason to suggest the 2017 southern counts should be excluded. Thus, because the datapoint was ambiguous regarding Cook's Distance and was not a significant outlier, because this regression was based on a small sample (i.e., removing points may result in overfitting the regression), and because results were similar with and without this point, I retained this point and present the equation and plot of the full regression (Figure 3).

DISCUSSION

Although surveys for beaver signs to determine presence are not as precise in monitoring population trends as are direct counts of beavers in each colony (because of the variation in the number of beavers per colony) (Swenson *et al.* 1983), they are, nevertheless, a relatively efficient and less invasive means of tracking substantial changes as compared to live-trapping and tagging beavers. Thus, interest in the utility of aerial surveys continues. Specifically, comparisons with historic aerial-survey data and between contemporary surveys from different areas are valuable to the conservation, research, and management of beavers and

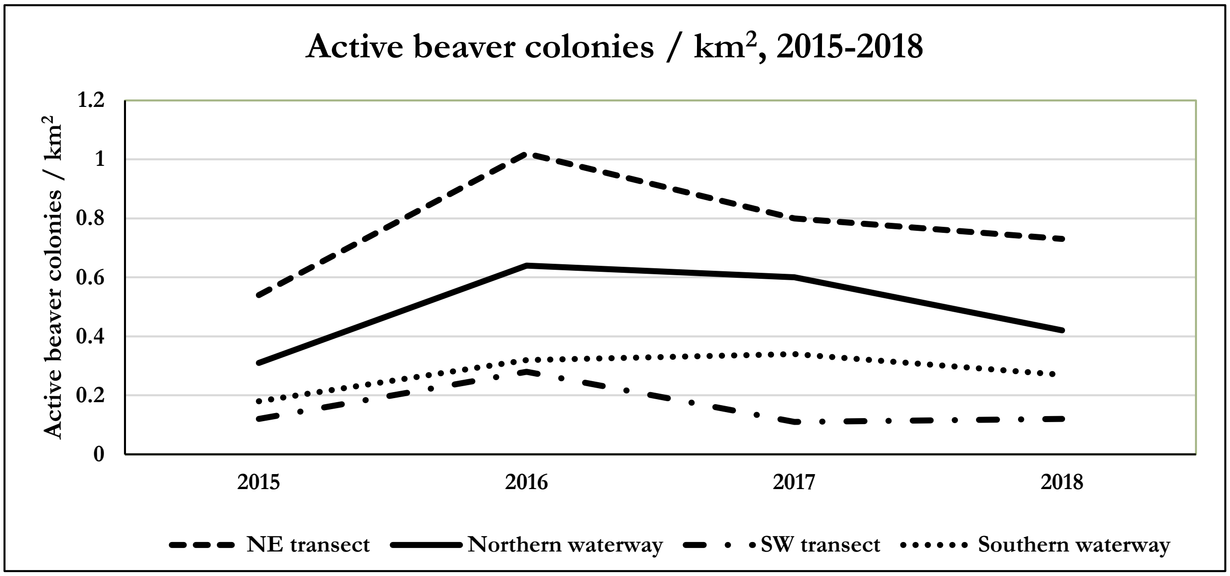

Figure 2. Annual strip transect survey (STS) densities and converted waterway survey route (WSR) densities from aerial surveys of active-beaver sign in the Superior National Forest, Minnesota, USA, during fall 2015-2018.

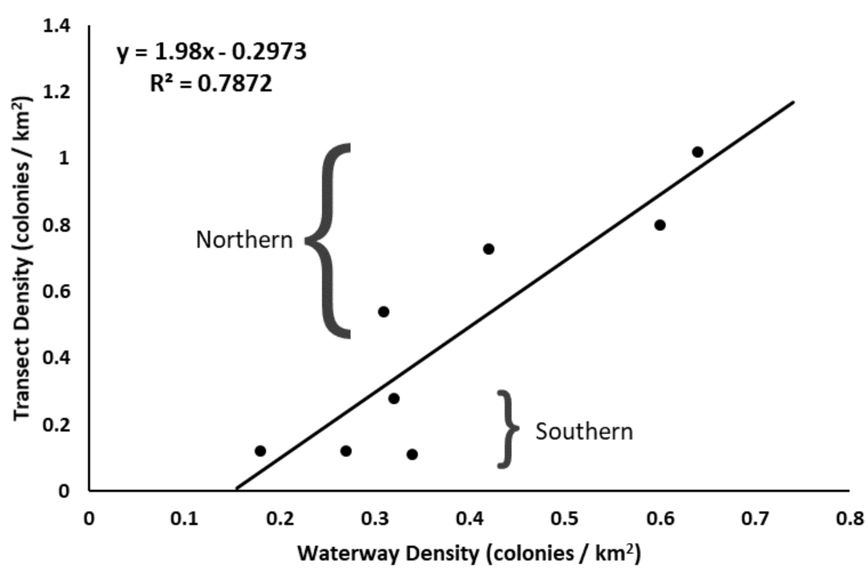

Figure 3. Scatterplot of waterway survey route (WSR) densities (active beaver colonies / km^2) versus strip transect survey (STS) densities (active beaver colonies / km^2) for 2015-2018 in the Superior National Forest, Minnesota, USA. The linear regression trendline of 8 points (2 per year; 1 from the northern area, 1 from the southern) illustrates the relationship (transect density = 1.98*waterway density - 0.2973; R^2=0.79).

the ecosystems they inhabit. Typical WSIs (observations / distance flown) present challenges for comparisons because they do not always represent the wider landscape, but are designed, rather, to maximize beaver detection. STS densities (that are more reflective of the overall landscape) are more readily comparable across landscapes and time.

This research indicated that densities calculated from WSRs can reasonably reflect general trend in STS densities provided the wider habitat is similar in terms of beaver harvest and land use, and also has a high proportion of water features (Figure 1, Table 2). While visual inspection indicated trend was reasonably reflected, converted WSR densities in this area (north and northeast) were only 57-75% of STS densities (Table 2). In areas where water features are limited, converted WSR densities will likely overestimate STS densities (Figure 1; Table 2). For example, results from such an area (the south and southwest) indicated converted WSR densities ranged from 114-309% of STS densities (Table 2), and visual inspection suggested WSR density trend was less reflective of the STS density trend (Figure 2). Nevertheless, the linear regression of transect densities on WSR densities provided a reasonable (Figure 3) preliminary equation for converting historic WSRs to STS densities. Of course, this regression is based on 8 points from only 4 years in 1 study area, so additional research is warranted to better define this relationship, especially for other habitats such as arid or montane regions with lower densities of waterways and, likely, beavers.

These results provide benchmarks for how reliable densities converted from WSIs may be compared to STS densities in varying landscape context. Depending on the habitat (water and vegetation), beaver harvest, and land use, WSR densities may sufficiently reflect STS densities and be useful for comparisons to other study area densities and historic data. However, in cases where the WSR does not approximate the wider landscape, converted WSI densities must be viewed with caution and depending on the specific differences, may systematically overestimate transect densities owing to the inherent oversampling of water features. Notably, these conclusions are based on a small sample size, which could lead to spurious results and interpretations. Thus, it is recommended that this research be conducted elsewhere to determine how robust these findings are to other habitats, varying beaver harvest, and land use patterns.

Nevertheless, when possible, conducting WSRs in addition to STSs is advisable because data from WSRs may more rapidly point to changes in the population in terms of distribution and possibly abundance (especially in areas of sparse water features and less dense beaver populations) because they are designed to optimize beaver sign detection. Further, conducting both STSs and WSRs can help elucidate whether relative differences in beaver abundance are due to simply more water in one area or are also due to differences such as beaver harvest and forestry practices. Thus, while STS densities are better for comparing historical and contemporary observations and for comparing across varying landscapes, WSRs may still be important for timely and specific within-study area insights.

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