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Abstract

Despite Yellowstone National Park's (YNP) long history and well studied large mammals and vegetation, beavers (*Castor canadensis*), an important ecosystem driver, have received relatively little study. We summarize population surveys of beavers that began in 1921 and continued up to the present. The first surveys (1921 and 1923) were from the ground and conducted in a limited area in the northern portion (northern range; NR) of the park. Twenty-five colonies were found and beavers were considered abundant and using aspen (*Populus tremuloides*) and willow (*Salix* spp.) as a food source and building material. A follow up survey in 1953 found 6 NR sites, but none of the earlier sites from the 1920s were active and no aspen use was reported. Some locations were reported from the park interior. A limited ground survey was conducted in 1979-80. In 1988-89 and 1994 two incomplete, mostly ground surveys were conducted and estimated 71 and 44 colonies, respectively, in YNP. In 1996, 1998, 1999, 2001, 2003, 2005, 2007 and 2009 complete, park-wide aerial surveys were conducted and active colonies ranged from 44 (1996) to 127 (2007) with an increasing trend. Therefore, in a period of about 90 years (1920s–2000s) the beaver population in the northern portion of the park appears to have declined then increased probably because of a willow recovery.

Keywords: beavers, *Castor Canadensis*, Yellowstone, willow, aspen

Introduction

Once widely distributed across North America, beavers (*Castor canadensis*) were much reduced during Euro-American settlement of the continent (Baker and Hill 2003). Some have argued that beaver fur, used to make felt for hats in Europe, was the major impetus for exploration of the New World which resulted in European colonization (Innis 1930, Nute 1978). Consequently, beavers were extirpated through human trapping and hunting from vast regions of North America and often there were no or poor records (typically journals only) of their abundance and distribution (Schullery and Whittlesey 1992). Despite Yellowstone National Park's (YNP) early establishment in 1872, essentially during the western fur trade, records of beavers in YNP are similarly opaque coming primarily from journals of trappers and early park administrators (Schullery and Whittlesey 1992). Park records, however, are reflective of region-wide trends suggesting a reduction of beavers in the mid- to late 1800s (Schullery and Whittlesey 1992). After this time, the first survey of beavers conducted in the park was in 1921 (Warren 1926) which found abundant beavers in the Tower Junction area (a region in northern YNP). Starting with this first survey in 1921, our goal was to summarize subsequent efforts searching for beaver colonies (and sign of them) across YNP. These searches were recorded in unpublished park reports and a thesis, which we combined with more recent, rigorous surveys in order to create a population history of beavers in YNP.

Summarizing beaver population records in Yellowstone is important because there are many disparate notes and reports creating a confusing history (Table 1). Ernest Thompson Seton first noted beavers in the late 1890s in the Tower Junction area (cited in Warren 1926). This attention at Tower Junction probably caused Edward Warren (1926) to survey beavers in 1921 and 1923, partially because some worried they would cut down all the aspen (Warren 1926). In the winter of 1930–1931, E. Roy Arnold (1931) unsystematically checked the

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TABLE 1. Surveys for beavers conducted in Yellowstone National Park 1921-2009.

Investigator	Years Surveyed	Method	Area Surveyed[A]	Citation
E. Warren	1921 and 1923	Ground	Tower/Mammoth	Warren 1926
E. Arnold	1931	Ground	Tower Area	Arnold 1931
R. Jonas	1953-1954	Ground	Tower/Mammoth Some Interior	Jonas 1955
S. Fullerton	1979-1980	Ground	Park-wide	Fullerton 1980
Consolo Murphy	1988-1989	Ground	Park-wide	Consolo Murphy and Hanson 1993
Consolo Murphy	1994	Ground	Park-wide	Consolo Murphy and Tatum 1995
Smith	1996, 1998, 1999, 2001, 2003, 2005, 2007, 2009	Aerial	Park-wide	This Study

[A] None of the surveys preceding the aerial surveys conducted by Smith were considered complete and only represent partial coverage of Yellowstone National Park. The Smith 2005 survey also was not complete due to early ice causing cessation of survey effort.

status of some of the Warren colonies around Tower Junction. In 1953 Robert Jonas, a graduate student at Montana State University (MSU), resurveyed the areas reported on by Warren (Jonas 1955) with the objective to evaluate the status of beavers and condition of the habitat since the Warren surveys. Jonas expanded his survey area slightly, mostly through interviews with park rangers, but he did not systematically survey the northern portion of the park (an area now referred to as the 'northern range' (NR) and the wintering area for many Yellowstone ungulates; Houston 1982, Lemke et al. 1997) or the park interior. All of these were ground surveys—the observers walked (or rode horseback) the area of interest. Another ground survey occurred in 1979–1980 that again focused on the NR area of Warren, Arnold, and Jonas, but this too was incomplete, lacked a finished report (Fullerton 1980), and often referred to beaver sign and not colonies.

In 1988–1989 and 1994 National Park Service (NPS) biologist Sue Consolo Murphy expanded the search area for beavers and looked across the park, mostly from the ground like Warren and Jonas, but was the first to use aircraft (Consolo Murphy and Hanson 1993, Consolo Murphy and Tatum 1995). From 1996–2009, the senior author (D.W. Smith) conducted intensive aerial surveys of the entire park searching every other year with the objective of a complete count and to detect population trend (Table 1, Smith and Tyers 2008).

Besides summarizing the beaver population history in YNP, we discuss willow (*Salix* spp.) and aspen (*Populus tremuloides*) abundance and distribution because it is the primary winter food of beavers and a widely published on topic that is intensely debated (Singer et al. 2000, Wagner 2006, Wolf et al. 2007, Kauffman et al. 2010). It is debated because declines in willow and aspen over the past 100 years are attributed to various causes (National Research Council 2002). Some have argued that the NR ecosystem of YNP at the beginning of the 20th century was in a vastly different condition, an ecological state dominated by willow, aspen, and beavers with some elk (*Cervus elaphus*) and more carnivores (e.g., wolves, *Canis lupus*). In the last 100 years carnivore reductions, which allowed ungulates to increase, transitioned the community to a shrub–steppe–grassland dominated by elk (Wolf et al. 2007, Wagner 2006). These authors suggest that beavers may have been critical to maintaining this willow–aspen 'state' through a positive feedback cycle involving beaver pond hydrology. The loss of beavers may have contributed to altering this system.

Others have argued that willow and aspen have always been a minor component of the vegetation on the NR, never occupying more than 10% of the entire area (Houston 1982, Despain et al. 1986, YNP 1997). This argument further states, and despite declines of 50–100% in area occupied by willow/aspen in the last 100 years (Wagner 2006), that little of this vegetative reduction can be attributed to loss of beavers and increases in elk but is mainly due to fire suppression and climate (Houston 1982, Despain et al. 1986). This was one of the most argued of all YNP issues (Houston 1982, Singer et al. 2000, Despain et al. 1986, Kay 1990, YNP 1997, Wagner 2006 to mention only some). Although usually mentioned, discussion concerning beavers is underrepresented compared to ungulates, arguably almost neglected and certainly their role in vegetation changes, or response to them. This is especially interesting now because willow for the first time in decades has begun growing taller (Ripple and Beschta 2004a, Beyer et al. 2007), allowing a resurgence in the beaver population on YNP's NR. This willow release is coincident with mid-1990s wolf reintroduction (Bangs and Fritts 1996), and there is some evidence that approximately 10 years after willow (mid to late 2000s), aspen may also be releasing (Ripple and Beschta 2007; E. Larsen, University of Wisconsin-Stevens Point, personal communication). This willow/aspen resurgence has sparked a new debate as to the cause of the release, one that extends historical arguments centering on elk, climate, and fire (or a combination of these) to now invoking wolves (Beyer et al. 2007, Ripple and Beschta 2004b). We seek to place beavers in this debate as they may be important to any argument.

An already complicated story is made more so because beavers were reintroduced upstream of YNP by Gallatin National Forest (GNF) from 1986–1999. This reintroduction provided the colonizers that contributed to the YNP population increase, but this increase could not have occurred had the habitat not recovered first (Smith and Tyers 2008). Our focus is YNP, but GNF's reintroduction of beavers played a significant role in the recolonization of YNP's NR, so beaver re-occupation of GNF needs to be included in the YNP NR account.

Therefore, given this complicated debate and unreported history, our objectives were to: 1) determine beaver abundance, distribution and population trend in YNP from 1996–2009; 2) summarize early beaver censuses and compare to contemporary ones to reconstruct beaver abundance and areas of use over the last 90 years; and 3) review the willow and aspen literature from the NR of YNP to aid interpretation of beaver population fluctuations.

Study Area

The NR and interior of YNP have been described in numerous publications (e.g., Houston 1982, Despain 1990, Smith and Siegel 2000), but in general these two systems can be contrasted based on elevation, vegetation, and geology (Smith et al. 2004). The NR is lower elevation (1500–2200 m) with primarily shrub–steppe, Douglas-Fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) at higher elevations. Riparian areas, highly linear in nature, have willow, which have declined and been height limited for several decades until the late 1990s release (Beyer et al 2007, Wolf et al. 2007, Bilyeu et al. 2008). Aspen, which occurs over < 2% of the area, and cottonwood (*Populus angustifolia* and *P. trichocarpa*) have both declined since the Warren (1926) and Jonas (1955) studies (Houston 1982, Kay 1990, Beschta 2005, Wagner 2006). Little to no recruitment has been reported for several decades (excepting post-1988 fire affects; Larsen and Ripple 2003, Kauffmann et al. 2010). Like willow, however, but about a decade later, a release of aspen stems may be occurring in some areas (Ripple and Larsen 2000, Ripple and Beschta 2007, E. Larsen, University of Wisconsin-Stevens Point, personal communication). Contrasted with the NR, the YNP interior is a high plateau fringed by mountains on the east and northwest (2200–3000 m) with mostly coniferous vegetation (primarily lodgepole pine but with some Engelmann spruce [*Picea engelmannii*] and subalpine–fir [*Abies lasiocarpa*] and high elevation whitebark pine [*Pinus albicaulis*]) with some exceptions in the southeast, southwest, and northwestern portions of the park where willow is found. Extensive stands of willow exist in areas along the Yellowstone River south of Yellowstone Lake, especially on the river delta as it flows into Yellowstone Lake, and other stands occur but less extensively in the Thorofare, Bechler, and drainages in the northwest region of the park. There is virtually no aspen available to beavers in this interior region. Aspen is present but uncommon and out of reach of beavers due to previous cutting activity. This is especially evident along northwestern drainages (e.g., Maple, Campanula, Gneiss creeks).

In general, stream gradients across the park exceed the slope that beavers can occupy (Baker and Hill 2003, Hay 2010). Some exceptions occur, for example along the Yellowstone River throughout its course across the park, (excepting the Grand Canyon of the Yellowstone) and other rivers like the Gallatin, Lamar, Snake, Firehole, Madison, and Gibbon. Some creeks and streams, especially Slough Creek, also have habitable gradients for beaver settlement. There are extensive low gradient areas along these waterways, however, that do not have vegetation suitable for beavers, so the beaver habitat requirement of low gradient combined with suitable woody vegetation (or aquatics) is limited across most of Yellowstone.

Methods

Previous Beaver Surveys

We reviewed the published, but not peer reviewed, reports of Warren (1926), Jonas (1955), and Consolo Murphy and Hanson (1993) and the unpublished reports of Arnold (1931), Fullerton (1980), and Consolo Murphy and Tatum (1995) for descriptions and locations of beaver colonies throughout YNP. These reports represent six incomplete surveys for beavers across YNP from 1921–1994 (Table 1). We mapped each survey of beavers using an active colony in autumn as a unit of measure with ArcMap 9.3 (Environmental Systems Research Institute, Redlands, CA). An active colony was sometimes not clearly defined by the various authors, many just reported beaver sign, so some interpretation was necessary (see definition below). We also noted what types of woody vegetation was being utilized by beavers, as it was often mentioned in the reports.

We divided the park into two units: the northern range (NR) and the interior. We did this because the areas are often considered as two separate systems (Houston 1982, National Research Council 2002) based upon differences in elevation, vegetation, geology, and wildlife (Despain 1990, Smith and Siegel 2000). Throughout we refer to these different locations, but when discussing the beaver population (Table 2) report on the total for YNP.

Warren (1926) and Jonas (1955) used ground surveys on the NR and did not survey the entire area. Some of Jonas' locations were from the park interior and were identified through interviews with park staff. Fullerton (1980) again used ground surveys and searched for areas of beaver activity and did not attempt to assess active colonies, although they were mentioned. Both Consolo Murphy led surveys searched from the ground across the park, and developed a park staff reporting system to locate areas of beaver activity and report sightings. Each of her surveys augmented the ground effort with one fixed-wing flight which was not systematic but checked areas surveyed from the ground. It was explicitly stated that neither the 1988–89 (Consolo Murphy and Hanson 1993) or 1994 surveys (Consolo Murphy and Tatum 1993) estimated the beaver population or trend. None of the above surveys covered the entire park and most areas were searched in summer to early fall and it is well known that mid- to late-fall is a more appropriate time to count beaver colonies (Hay 1958, Baker and Hill 2003).

Definitions of a beaver colony were not consistent between the observers, and not always clearly reported. Rather, beaver sign or activity was discussed sometimes without concluding that a beaver colony was present, or the activity was found in summer which is not always indicative of colony presence (Smith 1997, Baker and Hill 2003). The colony definition we used was a fresh lodge and/or recent beaver sign with a food cache in October (Shelton 1966, Hodgdon and Lancia 1983, Jenkins and Busher 1979). Fresh lodges are easy to spot from aircraft because recent repair by beavers adds sticks (freshly peeled ones shine bright white) and mud to the structure, while inactive lodges have vegetation growing from them with old, faded pieces of wood. Occasionally a lone beaver or pair will renovate an old lodge, but some signs of use will usually be visible. Critical to the assignment of activity is the presence of a food cache in fall as this almost always indicates presence of a colony (Jenkins and Busher 1979, Hodgdon and Lancia 1983, Baker and Hill 2003).

TABLE 2. Location of beaver colonies in Yellowstone National Park, 1996-2009.

	Number of Active Colonies							
Location	1996	1998	1999	2001	2003	2005	2007	2009
Northern Range								
Glenn Creek	0	0	0	0	1	*	1	0
Slide Lake	1	1	0	0	0	*	0	0
Gardner River	0	0	0	0	0	0	0	0
Yellowstone River	0	0	0	0	0	1	0	0
Elk Creek	0	0	0	0	0	0	1	0
Lamar Valley	0	0	0	1	1	*	3	1
Slough Creek	0	0	1	3	6	9	6	8
Crystal Creek	0	0	0	0	0	0	0	1
Soda Butte	0	0	0	0	0	0	0	1
Round Prairie	0	0	0	0	0	0	0	1
Northwest								
Bacon Rind Creek	0	0	0	0	1	1	3	0
Fan Creek	0	0	0	0	0	2	5	4
Gallatin River	2	2	5	6	1	7	7	9
Grayling Creek	3	0	1	6	5	5	5	4
Panther Creek	0	0	0	0	0	0	0	1
Willow Park	*	2	4	3	4	4	6	4
Campanula/Gneiss/Duck Creek	7	6	7	8	10	15	16	13
Cougar Creek	4	7	11	9	3	4	5	6
Maple Creek[1]		4	6	7	6			
Harlequin Lake	0	1	1	1	1	1	1	1
Madison River	3	3	3	3	1	2	1	0
Southwest								
Bechler River	1	0	3	2	3	3	1	2
Boundary Creek	2	2	1	3	7	0	6	2
Falls River	0	2	3	6	3	2	6	2
Mountain Ash/Proposition Creek	7	6	6	1	0	3	1	1
Other Bechler	0	1	1	0	1	0	2	2
Southeast/Southcentral								
Hayden Valley	0	0	0	1	0	*	0	0
Otter Creek	*	*	*	*	0	0	2	0
Basin Creek	*	*	*	*	0	0	3	3
Grouse Creek	1	0	0	0	1	*	1	0
Outlet Creek	0	1	0	0	0	*	1	1
Heart Lake Area (Surprise/Beaver/Aster Cks)	0	0	0	0	6	*	2	4
Shoshone (Moose/Delacy)	0	1	1	1	0	*	2	2
South Lewis Lake Area	0	0	0	2	2	*	0	0
Snake River	3	2	4	4	3	*	3	0
Yellowstone River Area (Delta)	15	14	23	17	21	*	29	36
Chipmunk Creek	0	0	2	0	0	*	1	1
Total	**49**	**51**	**77**	**77**	**85**	**65**	**127**	**116**

[1]For years 1996-2001, Maple Creek data was tabulated under Campanula/Gneiss/Duck Creek or Cougar Creek.

*Not censused

Often beavers in YNP use bank dens without constructing a lodge, so a fresh food cache along the bank with sign was the definitive measure of an active colony. This definition was applied when interpreting all of the previous literature.

New Beaver Surveys

In 1996, 1998, 1999, 2001, 2003, 2005, 2007, and 2009 we counted beaver colonies across the entire park using fixed-wing aircraft (Supercub PA-18) following standard methods published for aerial beaver surveys (Hay 1958, Swenson et al. 1983). Our objective was a complete count of YNP. Most of the time an active beaver colony was easily identified by the types of sign mentioned in the previous section. In < 5% of the cases > 1 food cache was recorded and attributed to just one colony. Beaver territoriality probably prohibits two colonies being closely located within 50 m (Jenkins and Busher 1979, Hodgdon and Lancia 1983, Baker and Hill 2003), and often two food caches were observed within this distance. In these cases we attributed the two caches to one colony (Baker and Hill 2003). While flying over each colony site, we marked the location with a Garmin GPS unit that was later downloaded into ArcMap so colony locations could be plotted on a map.

The aerial surveys were always conducted in late fall (typically no earlier than mid–October) after the willows and aspens had shed their leaves (which enhanced sightability) and the construction of food caches were well underway and easily observed from aircraft (Baker and Hill 2003, Smith 1997, Hay 2010). In 2005 early onset of ice curtailed the survey so the entire park was not counted that year. Each survey took multiple flights of 3–4 hours each and survey time ranged from 12–16 hours/survey. The same pilot and one of four observers flew each survey, but one observer (D.W. Smith) flew > 80% of the survey routes.

Surveys focused on areas of appropriate habitat and areas of historical beaver occupation. More time was spent flying waterways the first two surveys to ensure that some unlikely areas did not support beavers, later these areas were not surveyed. We also did not survey streams of high gradient (> 6%; Hay 2010) and/or sites with no deciduous or aquatic vegetation.

Results

Previous Beaver Surveys

In 1921 Warren (1926), by our definition, found 25 colonies on the northern range and a partial survey in 1923 of the same area found 9 colonies (Figure 1). He made no attempt at a complete survey of the NR, but rather recorded activity at colony sites that were accessible from the Tower Junction/Mammoth areas (Figure 1). He did not survey the park interior. He noted that most of the colonies were cutting aspen trees.

In 1931, park ranger Arnold stationed at Tower Junction and near where Warren had conducted his surveys, opportunistically surveyed some of the Warren areas (specifically the areas from Geode Creek east to the Lamar–Yellowstone confluence between the park road and the Yellowstone River). He mostly reported beaver activity and sign, and mentioned 'many active colonies', however neither his notes nor map allow a count of how many colonies were present. He also mentioned much old beaver activity in these areas and a 'depleted' food supply at one colony site near Geode Creek and only alder available at Elk Creek. At another site (Crescent Hill) he mentioned ample aspen.

In 1953, Jonas (1955) repeated the Warren's survey. In addition to revisiting the Warren sites, he expanded the survey to other parts of the park including some areas from the park interior. He found no beavers at the Warren colony sites on the NR. He found 8 other northern range sites that were not reported by Warren (Figure 1). He reported little beaver use of aspen and reported on the decline of aspen and beavers on the NR. He reported 13 other sites from the park interior (Figure 1).

In 1979–1980 Fullerton (1980) ground-searched for beaver colonies in the Warren/Jonas sample area and found only one occupied site at Lost Lake. Jonas did not record this site as active. In the Mammoth area she recorded beaver activity in the Gardner River, at the Beaver Ponds, Crevice Lake, and Willow Park. Several areas of beaver activity were recorded along the Lamar River, especially in the area around the confluence with Soda Butte Creek (but none along the creek itself).

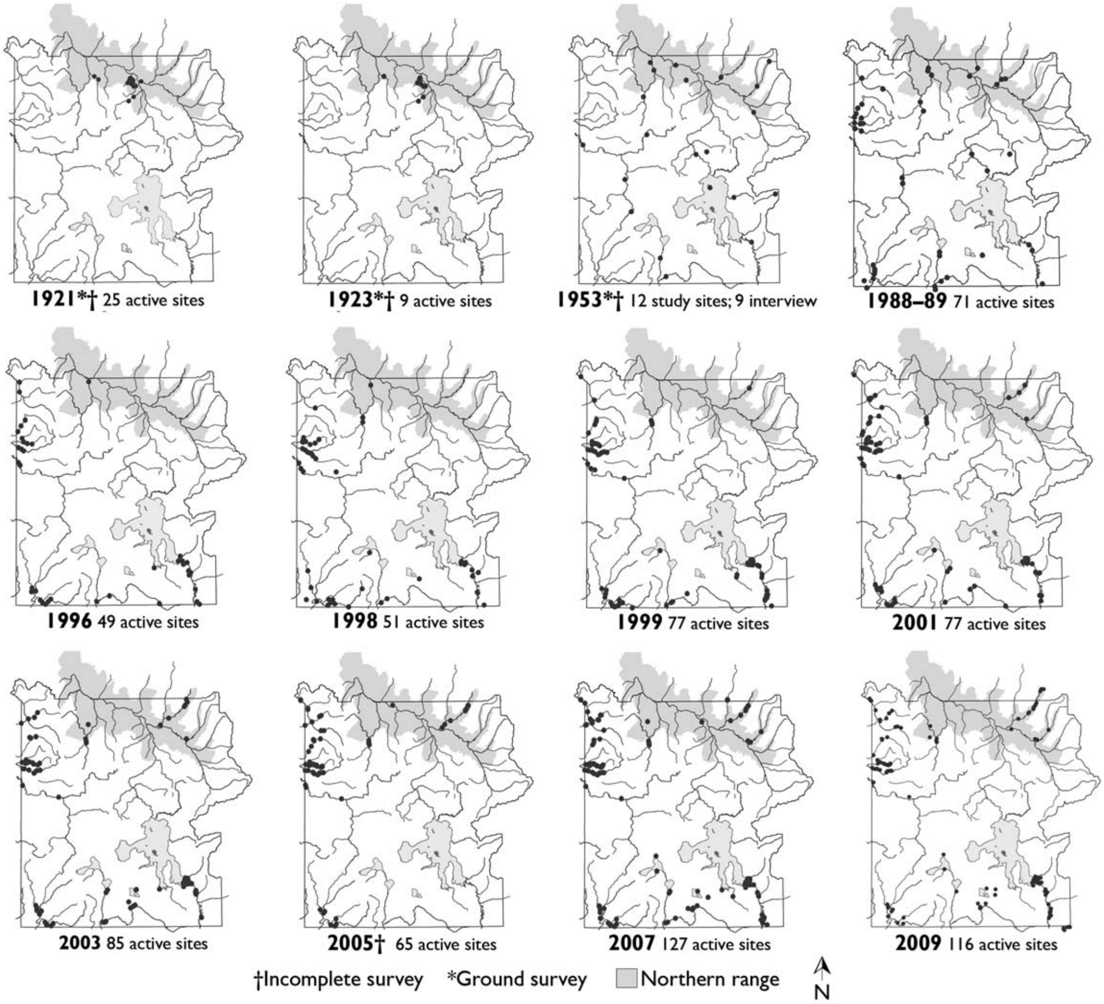

Figure 1. Distribution of beaver colonies in Yellowstone National Park 1921-2009. Surveys are not comparable because some did not cover the entire park or used different methods (i.e., censused via ground vs. with aircraft (see notes under each map). The 2005 survey was complete except for southeast region of the park, so colony count is not actual total, but counts and distribution of other areas is comparable to other years. Definition of a beaver colony was standardized for this paper (presence of a food cache) as not all previous workers had a consistent definition. Shaded region represents the area referred to in the text as the northern range.

Notably, reports on beaver occupation in Slough Creek were inconclusive, but it does not appear that she surveyed the upper (northern) reaches of the creek. She recorded aspen use at only one site (Beaver Ponds) otherwise beavers were feeding on willow (or aquatics, see below). In the interior she found numerous areas of beaver use especially in the southeast, southwest, and northwest regions (as far south as the Madison River where extensive activity was noted), and this was the first survey to identify these areas as dense centers of beaver activity and occupation. Other areas of beaver activity were Pelican Creek, Hayden Valley (Yellowstone River), Canyon area lakes (Cascade, Grebe, Cygnet), and Harlequin Lake. She noted use of aquatics at several sites (Obsidian, Cascade, Grebe, Beaver, Harlequin lakes)

Consolo Murphy and colleagues conducted the most extensive ground survey for beavers to date in 1988 and 1989 (Consolo Murphy and Hanson

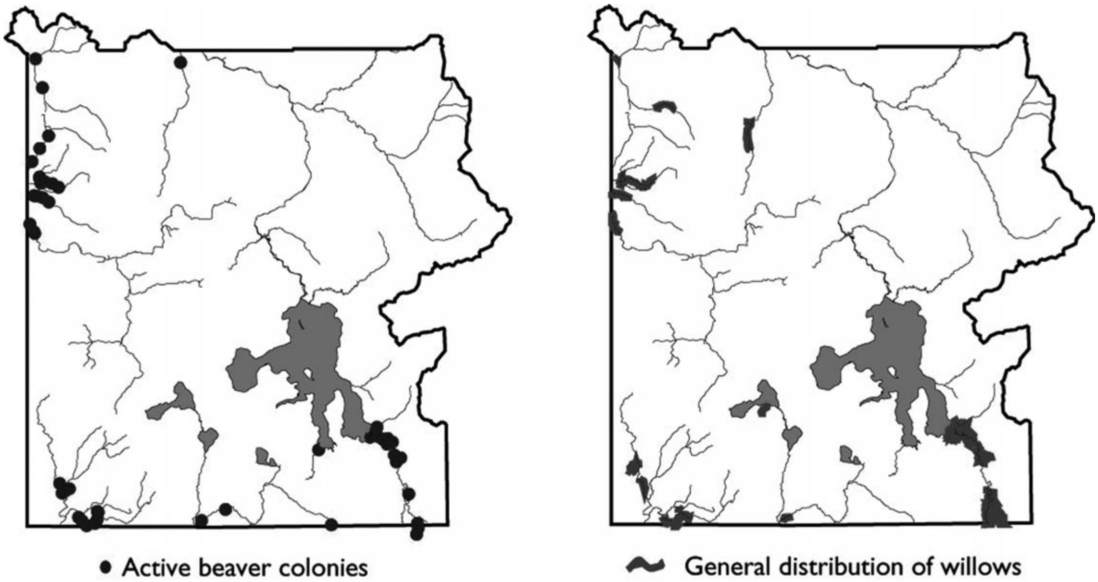

Figure 2. Distribution of beaver colonies and willow stands in Yellowstone National Park in 1996 (Smith and Tyers 2008).

1993) and again in 1994 (Consolo Murphy and Tatum 1995). They found 71 beaver sites (colony or beaver sign) park-wide in 1988–89 (Figure 1) which included a complete count of the NR in the Warren/Jonas areas, but they did not specifically mention the colonies surveyed by them, and they appeared to be inactive from their figure (their Figure 2). They repeated the survey in 1994 (Consolo Murphy and Tatum 1995) and found 44 colony/beaver sites with no occupation in the Warren/Jonas sites. These surveys again found the same three areas as Fullerton (southeast, southwest, and northwest) densely populated by beavers. Beaver activity and sign was associated with aquatics, willow (mostly), and aspen, but they did not provide locations for aspen. These areas were likely from the interior, not the Warren/Jonas colonies.

New Beaver Surveys

In 1996, we began complete park-wide aerial surveys every other year completing 8 surveys by 2009 (Figure 1). In 1996 we found only one beaver colony on the NR (Slide Lake near Mammoth), but after that, colonies began to slowly increase, especially along Slough Creek, and by 2007 ten colonies were found on the NR (Table 2). No colonies were found at the Warren/Jonas sites, except possibly one along lower Elk Creek which was a site discussed by Warren and Jonas, but it was not clearly stated whether or not a colony existed there in the 1920s and 1950s (Warren 1926, Jonas 1955; Figure 1). Warren (1926) mentioned that Ernest Thompson Seton recorded a colony on Elk Creek in the late 1800s, and it may have been in the same area that was found to have beavers intermittently in the 2000s. Several colonies were found in Lamar Valley, another was on the main stem of the Yellowstone River, and another was typically present north of Mammoth Hot Springs varying in location between Slide Lake and the Beaver Ponds hiking trail with activity along the Gardner River, but this colony was not present the last two surveys. In 2009 a colony was located along Crystal Creek from the aerial survey, but later ground reconnaissance found that the beavers did not overwinter at this site. None of the colonies anywhere in the park was found using aspen. A small number (< 5) of cottonwood were observed cut into, but not toppled, in the Lamar Valley, and several (< 5) small cottonwood trees were observed downed along the Gardner River north of Mammoth Hot Springs, otherwise all colony sites were associated with willow (Figure 2).

The aerial counts found, similar to the Fullerton and Consolo Murphy surveys, three areas of high colony density: the delta region along the Yellowstone River extending to Thorofare, the Bechler region, and the northwest corner of the park. The delta region consistently supported the highest colony density in the wide willow plain that characterizes the Yellowstone River delta (Figure 1). Other regions of the interior supporting beaver colonies were Willow Park, Glenn Creek, Snake River, Shoshone Lake, Heart Lake, Lewis Lake area (south), Harlequin Lake, Chipmunk Creek, Grouse Creek, Outlet Creek, and Hayden Valley to name the most prominent and consistent colony locations (Table 2). Most of the stream sites mentioned did not have a beaver colony during each survey occasion, suggesting movement or rotation among sites year–to–year or among surveys. All of the colonies were located in willow stands (Figure 2), except the Harlequin Lake site where lodgepole pine was observed several years in the food cache.

From 1996–2009, colony counts showed an increasing trend (Table 2). In 1996, 49 colonies were located in YNP, by 1999–2001 that number had increased to 77 colonies park-wide, increasing again to 85 in 2003 (Table 2). Early ice-up curtailed completion of the 2005 survey, but colony numbers had increased in 2007 to 127 colonies and were approximately stable between 2007 and 2009 with 116 colonies counted (Table 2).

Tyers from 1986 to 1999 released 129 beavers into drainages north of YNP. Ten (8%) of these beavers were implanted with radio transmitters, and 3 (30%) of this group likely dispersed into YNP, but the exact ultimate location is not known.

Discussion

More beaver colonies were found on the NR in the early 1920s than in the 1950s and 1980s, although the latter survey mostly recorded beaver sign (not colonies), but was still suggestive of a smaller beaver population (Warren 1926, Arnold 1931, Jonas 1955, Fullerton 1980). Evidence of more sign was reported during the 1990s (Consolo Murphy and Hanson 1993, Consolo Murphy and Tatum 1994) and our surveys found an increase in colonies from the late 1990s through 2009 (Figure 1). Therefore, beaver populations on the NR appear to have been abundant in the early 1900s, then the population declined through the 1950s to the early 1990s and then increased from the late 1990s to 2009 (Table 2). It is notable that recolonization did not take place in the same areas, nor did it rely on aspen, which was the primary woody vegetation used by beavers in the early 1900s (Warren 1926); instead recovery relied on willow. Most of the reported beavers in the1920s were in the Tower Junction area (Warren 1926), whereas the recent recovery found most of the beavers in Slough Creek and secondarily in the Lamar River (Table 2), with none in the Tower Junction area (except sporadic sign on Elk Creek with no permanent colony). The loss of aspen appears to be related to the beaver decline between the Warren and Jonas surveys, as emphasized by Jonas (Warren 1926, Jonas 1955). The recent recovery was triggered by the late 1990s release of willow on the NR (Ripple and Beschta 2006, Beyer et al. 2007). It is unknown, but also unlikely, whether the beaver recovery is as extensive or the population size as large as it was in the late 1800s or early 1900s, or prior to the fur trapping of the mid-1800s (Schullery and Whittlesey 1992, Wagner 2006) which raises the question of how significant will be the ecosystem effects of the recent beaver recovery (Wolf et al. 2007).

What caused willows and beavers to increase now after decades of low willow stature and few beavers? Beaver abundance during Warren's (1921 and 1923; Warren 1926) surveys was based on availability of aspen (and willow) created by a surge in aspen recruitment from 1870–90 (Romme et al. 1995, Wagner 2006), but after beavers cut this aspen, it did not regrow, probably because of elk browsing (Larsen and Ripple 2003, Kauffman et al. 2010). Willow growth and stature paralleled those of aspen (Wolf et al. 2007). Hence, the primary woody vegetation that beavers relied on early in the 20th century was gone, causing colony abandonment and a population decline. Competition with elk has been widely cited as a likely cause for reduced woody vegetation (Jonas 1955, Kay 1990, Chadde and Kay 1991, Singer et al. 2000, Wagner 2006, Ripple and Beschta 2006, Beyer et al. 2007, Wolf et al. 2007), but other others suggest an interaction between elk and climate (YNP 1997, Johnston et al. 2011).

Baker et al. (2005) specifically studied this relationship through rigorously controlled experiments in Rocky Mountain National Park, concluding that beaver cutting with intense elk browsing produced low stature willows (biomass and diameter) and "strongly suppressed the standing crop" (p. 110). They also referred to a system where low densities of ungulates (both wild or domestic) caused beavers and willows to flourish and described beaver–willow relationships (especially tall willows) as mutualistic.

In YNP, Bilyeu et al. (2008), tested these relationships finding that loss of beavers and stream incision "retarded willow height recovery" (negative feedback loop) emphasizing the importance of beaver induced hydrology and stated that, "very heavy elk browsing suppresses willows, and that reducing or eliminating browsing promotes willow recovery" (p. 89). Given this relationship, Wolf et al. (2007) hypothesized that the loss of beavers altered the condition of the NR from a 'beaver–willow' state in the 1920s to an 'elk–grassland' state afterward. This elk–grassland state was present into the 1990s when some willows recovered and some beavers returned, but whether a large scale landscape switch back to the previous state (positive feedback loop) will take place is unclear (Wolf et al. 2007). The above scenario appears to be true for both the NR and the northwestern region of the park, although tall willows are much more common in the northwest and more similar to the beaver–willow state described by Wolf et al. (2007).

An alternative hypothesis is that the scenario described above was due to a warming, drying climate (especially during the 1930s), which is part of the long-term climatic cycle in YNP (Persico and Meyer 2009). In responding to this cycle, where fire was suppressed and conditions were unfavorable to willow–aspen growth and establishment, beavers consequently declined (Houston 1982, Despain et al. 1986, YNP 1997). Elk browsing (and wolf presence) is considered of minor or little consequence to vegetation, and if elk affect willow they are only the proximate factor (YNP 1997). If true, then beaver population fluctuations should be independent of elk, but beavers fluctuated inversely with elk supporting the competitive hypothesis, but these correlative data do not imply a cause and effect. Graumlich et al. (2003) found Yellowstone river flows in the 20th century exceeded those for the previous two centuries (therefore, and other than the 1930s, not a drying climate), and more importantly Wolf et al. (2007) found that, "climate is not limiting willow establishment in the study area" (p. 1582). They found that climate-driven hydrologic variables explained only 11% of the variability in willow establishment and that nearly continuous willow establishment in the 20th century is not sensitive to climatic variation. Further they state that substrate, not water availability, limits seedling establishment (Wolf et al. 2007). Of course climate and elk browsing could be interactive (Johnston et al. 2011) and is an expanding area of study not yet fully understood. Other studies have also rejected the climate hypothesis (Chadde and Kay 1991, Beschta 2005, Kauffman et al. 2010).

Besides changes in willow, the GNF beaver reintroduction from 1986 to 1999 (Smith and Tyers 2008) clearly hastened beaver occupation of the NR of YNP, but it did not cause the beaver recolonization. Beavers released north of the park emigrated downstream into YNP speeding up reoccupation. Had GNF not reintroduced beavers, movement of beavers in an upstream direction from the Yellowstone River would have occurred, just at a slower rate. Either way, recolonization of beavers was dependent on recovery of willows their main building material and food source. Consolo Murphy and Hanson's (1993) observations of beaver sign on the NR in the late 1980s and early 1990s without extensive settlement suggests dispersal of beavers into the NR of YNP from the GNF upstream reintroduction prior to full willow recovery. Consolo Murphy and Hanson (1993) describe beaver movement as ephemeral and frequent and hardwood and willow communities as not abundant further indicating beaver habitat was not yet suitable for the GNF releases to settle the park. We also tracked beavers that had been radio marked downstream into YNP, further confirming the source population for beaver settlement on the NR was from released GNF beavers (Tyers, unpublished data).

The population fluctuations of beavers in the interior of YNP is less clear because of less effort, especially during the early surveys (Warren did not work in the interior; Figure 1). It appears beaver numbers have been stable here and subsisting on willow (Figure 2, Fullerton 1980). Willow is less prone than aspen to depletion by beavers (Boyce 1974), and ungulate density is lower in the interior especially in winter when browsing usually takes place (Houston 1982, Wagner 2006), both of which are factors that favor a stable food source and a less cyclical population. Despite variable survey intensity, beavers were found on every survey in the interior, and during the late 1990s and 2000s at high density in some willow stands (Table 2). From 1996 on no beaver colonies in the interior were found utilizing aspen. It is unknown when aspen became unavailable (Consolo Murphy and Hanson 1993), as recent aerial surveys found aspen near beaver drainages but out of reach, and observation of old cut aspen stumps suggested previous use. These observations were all made along northwestern stream drainages and not in the area of extensive willow at the Yellowstone River delta, or in the Thorofare, Bechler, Snake, Willow Park regions which are also areas dominated by willow (Figure 2).

The recent (1996–2009) park-wide increase in beaver colonies was probably due to two factors: 1) improved ability and efficiency of observers and 2) changing environmental conditions favoring beaver expansion. The increase in numbers of colonies found between 1996 and 1999 (Table 1) suggest improvements in the ability of observers to detect colonies, with probably a slight increase in the beaver population. Between 1999 and 2003 colony numbers were approximately stable, then they increased significantly afterward (2005 was an incomplete survey), suggesting an actual increase rather than an improvement in observer/survey efficiency as this had peaked by 1999.

NR population increases have already been attributed to willow recovery, but causes for beaver population increases in the interior are less clear, particularly in the northwest (Figure 1, Table 2), but it is likely willow in the interior reflected well documented willow growth on the NR. It is possible that below normal precipitation during the decade of the 2000s (Beyer et al. 2007, Wolf et al. 2007) created drought conditions that might have favored beaver colonization of higher gradient streams. Typically high water flows in spring remove beaver dams across streams that were built the previous fall when the water was low. Without high flows over an extended period of time in the spring, beavers may have been able to quickly rebuild dams less damaged by reduced peak floods, especially if the period of high flow was reduced. It is known that abundant water improves beaver habitat in low gradient areas (Baker and Hill 2003, Hay 2010), and although we acknowledge speculative, high flows may restrict settlement in mountainous areas because beavers cannot use steeper gradient streams, thus periods of low flow may allow beaver population expansion. Such a scenario may have been a contributing factor to a beaver population increase in the northwestern region of the park, but willow recovery was also a likely factor.

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