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Aspen snag dynamics, cavity-nesting birds, and trophic cascades in Yellowstone's northern range

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Abstract

We examined current and possible future aspen stand dynamics and cavity-nesting bird abundances for Yellowstone's northern ungulate winter range. Our measurements suggest aspen stands located within Yellowstone National Park (YNP) are in a different condition than those located in the Gallatin National Forest (GNF), immediately outside the park. Stands inside YNP were composed of more snags and had fewer small-diameter live stems than stands in GNF. Six of the 11 cavity-nesting bird species we analyzed were more abundant inside YNP where aspen snags were more abundant.

We discuss potential implications of current and future aspen stand dynamics in the context of wolf re-introduction and trophic cascades for cavity-nesting birds. Our results suggest aspen stands within YNP will experience a relatively high abundance of snags in the near future, followed by a period of low snag abundance that will influence the abundance of several cavity-nesting bird species. The relative composition of future aspen stands within YNP will likely differ from historical conditions, and stands outside YNP, for several decades.

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1. Introduction

Aspen (*Populus tremuloides*) has been identified as an important breeding habitat for western North American birds (Flack, 1976; Winternitz, 1980). In addition, aspen is the principal deciduous tree species providing nesting habitat for cavity-nesting birds in the montane western U.S. (Dobkin et al., 1995). The importance of aspen habitat for both primary-excavating and secondary cavity-nesting bird species has been noted by several researchers (Winternitz and Cahn, 1983; Li and Martin, 1991; Dobkin et al., 1995; Martin and Eadie, 1999) as well as its importance as ecological "hot spots" (Hansen and Rotella, 2002). Outside Colorado and northern Utah, aspen habitat typically represents less than 5% of most western landscapes (Despain, 1990; Barnett and Stohlgren, 2001; Barmore, 2003). Thus, its reduction or disappearance may have considerable implications for birds.

Western U.S. aspen typically reproduce asexually. Existing clones produce new ramets (suckers) from an underground root system that grow and recruit into the overstory of an aspen stand consisting of one or more clones. In this way, aspen clones are thought to have persisted in western U.S. landscapes for thousands of years (Jelinski and Cheliak, 1992; Mitton and Grant, 1996). Reproduction by seed is rare in most of the western U.S., occurring only during infrequent "windows of opportunity" (Romme et al., 1997; Stevens et al., 1999) when the timing of disturbance and climate conditions are favorable.

Aspen habitat appears to be in decline in the western U.S. (Kay, 1997; Bartos and Campbell, 1998). Several mechanisms have been proposed to explain this decline, including climate change and competition with exotics, but interrupted disturbance regimes and increased browsing intensity by wild and domestic ungulates appear to be the favored hypotheses (Bartos and Campbell, 1998). Some researchers suggest intense browsing by elk (*Cervus elaphus*) has led to the decline of aspen stands within Yellowstone National Park (YNP) (Kay, 1990; Ripple and Larsen, 2000; National Research Council, 2002). The proposed mechanism involves intense ungulate browsing of young suckers, which kills or suppresses them, subsequently preventing recruitment of new stems into the

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overstory. This hypothesis requires browsing pressure to be greater than historic levels, when aspen recruitment was apparent. The extirpation of wolves (*Canis lupus*), the main predator of elk, in the 1930s, the prohibition of hunting within YNP, and the adoption of the “natural regulation” elk management policy by the National Park Service in 1968 may have led to a larger northern Yellowstone elk herd in recent decades (see Huff and Varley, 1999 and Wagner, 2006 for discussions of changing elk management on Yellowstone’s northern range). Perhaps more importantly, the absence of wolves may have allowed the development of different foraging behavior among herbivores (primarily elk) leading to increased browsing of willows (*Salix* sp.), cottonwood (*Populus* sp.), and aspen suckers (e.g., Ripple and Beschta, 2004; Beyer et al., 2007). Furthermore, it has been suggested that this foraging behavior may be changing with the re-introduction of wolves (Ripple et al., 2001; Smith et al., 2003; Ripple and Beschta, 2004; Creel et al., 2005; Hebblewhite et al., 2005).

North of the YNP boundary, the Gardner District of the Gallatin National Forest is one of the nation’s most popular elk hunting destinations. From 1999 to 2001, an average of 1375 elk/year were harvested in the non-park portion of the northern range (Montana Department of Fish, Wildlife, and Parks 2004). Human hunting of elk on lands outside the park may influence elk abundance and behavior. During early winter 1989–1999, northern range elk densities outside YNP averaged 7.6 elk/km²; average density inside YNP was 12 elk/km² (Larsen and Ripple, 2005). The decline and loss of aspen within the YNP portion of Yellowstone’s northern ungulate range is likely due to an altered trophic cascade involving wolves, native ungulates, and vegetation such as aspen. The loss of a top predator, combined with protection from human predation, apparently allowed changes in the abundance and behavior of ungulate prey populations. Conversely, the re-introduction of wolves in the northern Yellowstone ecosystem in 1996 seems to have stimulated the recovery of some previously impacted vegetation, such as willows and cottonwood. The support for these effects is substantial (e.g., National Research Council, 2002; Ripple and Beschta, 2003, 2005, 2006; Beschta, 2005; Fortin et al., 2005; Hebblewhite et al., 2005; Beyer, 2006; Beyer et al., 2007), but the role of elk in a trophic cascade continues to be debated (Vucetich et al., 2005).

Assuming the existence of top-down structuring of the northern range ecosystem, and holding disturbance constant or absent, we expect an increase in the relative abundance of aspen snags followed by a decrease as stands continue to deteriorate. Following the decrease, assertion of trophic cascades effects should allow relative snag abundance to recover at or near historical levels, depending on the interim loss of impacted, non-regenerating clones. The pattern of snag abundance is assumed to be tracked by abundances of cavity-nesting birds that use aspen snags heavily in this region. Further, we expect the above-mentioned changes in snag and cavity-nester abundances to be diminished or absent outside YNP, where human hunting appears to keep elk browsing pressure lower than inside YNP. It is reasonable to expect cavity nester abundance to track snag abundance. Winternitz and Cahn

(1983) found nesthole trees in Colorado aspen were mostly large (dbh > 20 cm), dead or decadent (infected with heartrot), and old (average age > 100 years). Other studies of cavity-nesting birds in the western U.S. suggest a preference for aspen snags, especially those with broken tops and/or large diameter, which appear highly attractive to cavity-nesters in general (e.g., Harestad and Keisker, 1989; Li and Martin, 1991; Dobkin et al., 1995; Moore, 1995; Caton, 1996). Thus, our overall objective in this study was to evaluate the condition of aspen snags and cavity-nesting birds in the context of a wolf-elk-aspen trophic cascade in Yellowstone’s northern ungulate range. Our specific objective was to describe and compare the relative abundances of large-diameter aspen snags and cavity-nesting birds inside and outside YNP, and further discuss these conditions within a temporally explicit hypothetical framework of aspen dynamics within YNP.

2. Study area

The 153,700 ha northern ungulate winter range of the northern Yellowstone ecosystem extends from Dome Mountain in the Gallatin National Forest (GNF) southeast to the Lamar Valley in Yellowstone National Park (YNP), USA (Fig. 1). Approximately two-thirds of the range is within YNP and the remaining one-third is in the GNF. A few small private holdings occur within the GNF (Lemke et al., 1998).

Elevation ranges from 1560 to 2350 m. Average annual precipitation is 40 cm/year and ranges from 25 to 66 cm/year with increasing elevation (Western Regional Climate Center,

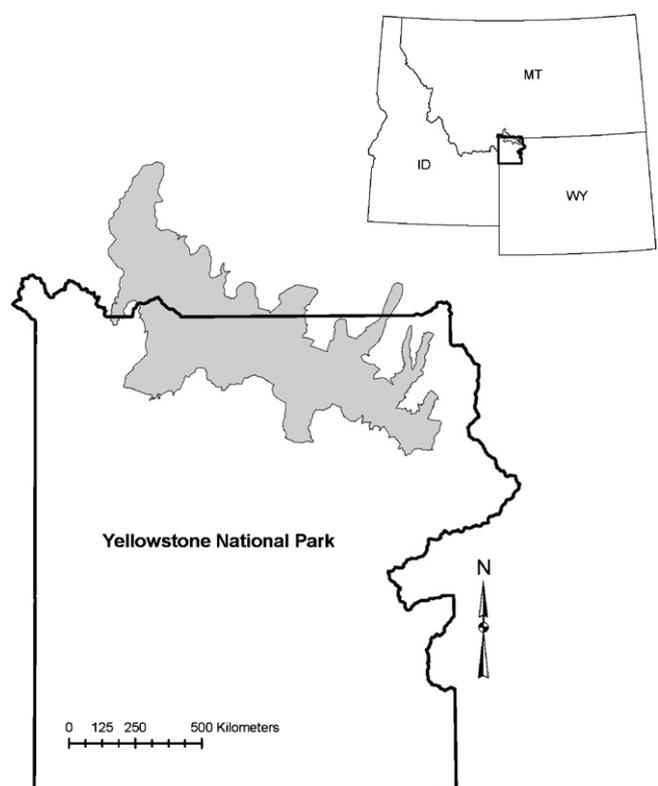


Fig. 1. Location of the northern ungulate winter range (shown in gray) in the greater Yellowstone ecosystem, USA.

2004). Lodgepole Pine (*Pinus contorta*) is the dominant vegetation at higher elevations, particularly in poor soils. Douglas-fir (*Pseudotsuga menziesii*) and Engleman Spruce (*Picea englemanni*) occur where conditions are suitable. Aspen primarily occur in an elevational band at ~2200 m where conifer-dominated forest meets steppe dominated by sagebrush (*Artemisia* sp.) and grasses, including Idaho fescue (*Festuca idahoensis*) and timothy (*Phleum pratense*). Aspen patches are distributed throughout the transition zone and steppe, primarily occurring where moisture conditions are favorable.

YNP is managed as a natural preserve. The GNF portion of the northern range is managed for elk winter range and human recreation (including hunting), with limited resource extraction and livestock grazing (Lemke et al., 1998). Thus, general landscape patterns of vegetation are relatively consistent throughout the study area, but management differs regarding elk hunting between YNP and GNF portions of the range.

3. Methods

3.1. Vegetation data

From an existing map (St. John, 1995) and 1994 aerial photographs (where gaps in map coverage occurred) we randomly selected 32 aspen patches ≥ 100 m from primary roads and ≤ 1 km from a road (primary or secondary) or main trail. We defined aspen patches as contiguous areas of aspen stems with canopy cover $\geq 50\%$ at the time of mapping or photo acquisition, and located ≥ 100 m apart. Thirty aspen patches were selected in 2001 and two more added in 2002. During field sampling we found that conifer invasion and changes in canopy cover had occurred in some patches, but retained these in our sample. Five patches from this initial sample were either misidentified or no longer extant. We chose the nearest extant patches that satisfied location criteria as replacements. One patch was located in the Decker Flats area of GNF, bordering YNP. The very close proximity to YNP and special hunting restrictions for this location were confounding to our hypotheses. Thus we omitted this patch from our analysis. All remaining patches were >1 km from the YNP boundary with 13 patches inside the park and 18 patches outside.

For each patch, we measured basal area of aspen and conifer stems ≥ 1 cm diameter at breast height (dbh) and canopy cover (%) for aspen and conifer separately. We used a five-point sampling pattern, initiated at the patch centroid with four points positioned 25 m in each cardinal direction. We did not sample at points that fell outside the patch. We used variable radius sampling technique with a 5, 10, or 20 basal area factor (BAF) prism to measure tree basal area (Dilworth and Bell, 1985). The BAF that included ~8–12 trees at the patch centroid was used for all subsequent sampling within a given patch. This provided similar sample precision among patches. At each sampling point, tree canopy cover was measured for aspen and conifer separately, using a mirror densitometer (Forestry Suppliers, Inc., Jackson, MS, USA). We measured the dbh of each tree selected by the prism and noted its status as dead (snag) or alive.

As suggested by previous work with cavity-nesting bird species in North America (e.g., Kilham, 1971; Harestad and Keisker, 1989; Dobkin et al., 1995), we considered snags with dbh ≥ 20 cm as large-diameter snags preferred by cavity-nesting birds.

3.2. Bird data

We conducted point counts during the early breeding season each of 3 years (30 May–1 July 2001–2003). Counts were 6 min in duration, using a modified protocol outlined in Ralph et al. (1995). All birds within a 50-m radius were tallied and their species and nesting behavior noted. Species were categorized by migrant status (migratory or resident) (McEneaney, 1996), and nesting habit (open cup canopy, open cup shrub, open cup ground, primary cavity, secondary cavity) (see Ehrlich et al., 1988 for detailed definitions). Detections known to be outside an aspen patch boundary were flagged for omission during analysis. Fly-overs were not counted unless they were considered to be using habitat for foraging (e.g., tree swallow (*Tachycineta bicolor*) or common nighthawk (*Chordeiles minor*) foraging >10 m above canopy). Counts were not conducted during heavy precipitation or windy conditions (>16 km/h), but were not constrained by cloud cover. Despite potential biases associated with unequal detectability of bird species during point count sampling (Boulinier et al., 1998; Moore et al., 2004; Royle et al., 2005), we assumed similar bird detectability among sites (e.g. Finch and Reynolds, 1987; Schieck and Niefeld, 1995) since cavity-nesting species found in the region exhibit similar behavior (e.g., diurnal, vocalize, cavity-nesting, visually and audibly conspicuous during morning hours) and, excepting American kestrel (*Falco sparverius*), do not vary tremendously in size.

Each aspen patch was sampled three times during 2001 and 2002, and twice during 2003. We performed one count at each patch centroid and additional counts in larger patches; one additional count for each 5 ha. These additional counts were positioned 100 m from centroid point along the major geographic axis of the patch. Only two patches were >5 ha. Using the protocol described previously, we collected vegetation data at these additional points and the average values of all points in the patch were used in subsequent analyses. Additionally, for patches with >1 point we used the average of bird count data in our analyses. We sampled spatially clustered groups of three to five aspen patches daily during morning hours (sunrise to 10:30 a.m.); an initial patch was randomly chosen, and each nearest patch sampled consecutively as time permitted. This approach varied the order of sampling and was assumed to reduce time-of-day bias. All bird sampling was done by one observer (JPH).

3.3. Analysis

We used Welch's two-sample *t*-test for samples with unequal variance to assess differences in aspen diameter, canopy cover, snag composition, and the abundance of cavity-nesting birds (species with > 35 detections), inside and outside YNP.

Table 1

Northern range aspen stand characteristics for 13 stands inside (YNP) and 18 stands outside (GNF) Yellowstone National Park, June 2001

	YNP		GNF		<i>t</i>	<i>p</i>
	Mean	S.E.	Mean	S.E.		
Live stem diameter (cm)	37	0.9	27	0.6	9.8	<0.01
Dead stem diameter (cm)	31	1.9	21	1.4	3.6	<0.01
Canopy cover (%)	66	3.7	77	4.2	1.9	0.06
Snags ≥ 20 cm (%)	18	3	10	2	2.3	0.03

Variables: live aspen stem diameter (cm) all stems, dead aspen stem diameter (cm) all stems, overstory aspen canopy cover (%), and large-diameter snags (% of all stems ≥ 20 cm). Comparisons are Welch's *t*-test for samples with unequal variance.

Uniform application of Welch's *t*-test is a conservative approach that is more likely to accept null hypotheses of no difference when variances are similar reducing the possibility of concluding false differences. Additionally, since we were performing multiple comparisons of cavity-nesting birds with simultaneously collected data, we applied the false discovery rate (FDR) procedure described by Benjamini and Hochberg (1995) to these results and adjusted reported differences as indicated by comparison with an estimated *q*-value (Storey and Tibshirani, 2003). Statistical analyses were done in S-Plus statistical software (Insightful, 2001) and differences considered significant at $\alpha = 0.05$ and $q^* = 0.07$. In addition, we constructed 95% confidence intervals for cavity-nesting birds (species with > 35 detections) inside and outside YNP for a visual comparison of abundances. Non-overlapping confidence intervals were interpreted as a significant difference in abundance.

4. Results

4.1. Aspen condition

Several characteristics differed between aspen stands inside YNP and outside the park (GNF) (Table 1, Fig. 2). Mean live and dead aspen stem diameters were on average 10 cm greater inside YNP than outside (GNF). Live aspen canopy cover inside YNP tended to be less than outside the park and the relative abundance of large-diameter snags (≥ 20 cm) was significantly greater in YNP with YNP stands containing $\sim 80\%$ more large-diameter snags (18% versus 10%, respectively). YNP stands were typically more open with almost no small diameter live stems, GNF stands contained smaller diameter trees that were recruiting into the overstory, and more of the large-diameter stems (≥ 20 cm) in YNP stands were snags (Fig. 2).

4.2. Birds

We identified 11 bird species that were detected ≥ 35 times during sampling for inclusion in our analyses (Table 2): American Kestrel (*F. sparverius*), Black-capped Chickadee (*Parus atricapillus*), House Wren (*Troglodytes aedon*), Mountain Bluebird (*Sialia currucoides*), Mountain Chickadee (*Parus gambeli*), Northern Flicker (*Colaptes auratus*), Red-

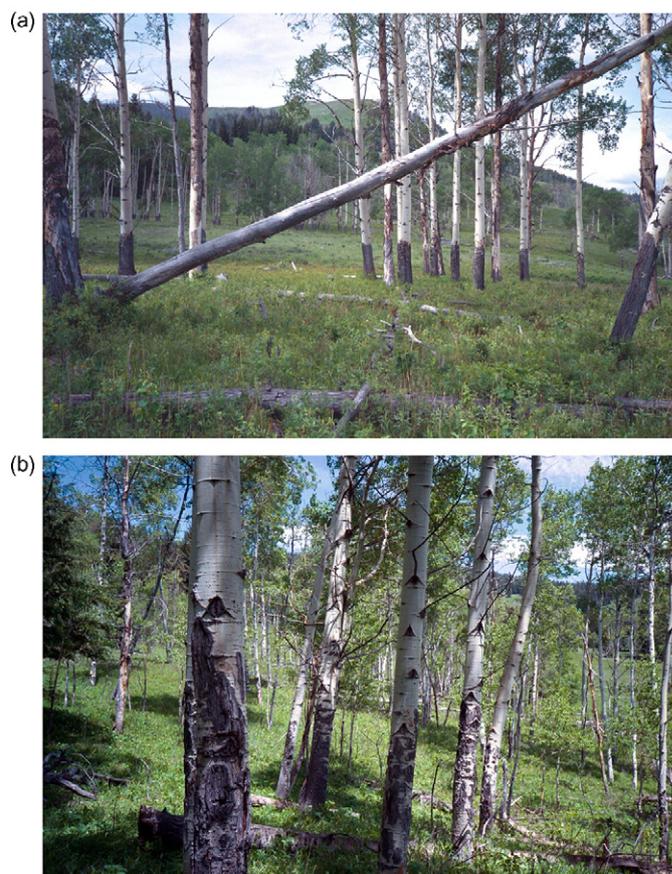


Fig. 2. Typical northern range aspen stands (a) inside and (b) outside YNP during June 2001. Note open stand conditions, abundant snags, and absent small diameter aspen in YNP stand. GNF stand has fewer snags and apparent recruitment of small diameter aspen.

breasted Nuthatch (*Sitta canadensis*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), Starling (*Sturnus vulgaris*), Tree Swallow (*Tachycineta bicolor*), and Violet-green Swallow (*Tachycineta thalassina*). Six of the 11 species were significantly more abundant inside YNP than outside (GNF) (American Kestrel, $t = 2.41$, $p = 0.02$; House Wren, $t = 2.12$, $p = 0.04$; Mountain Bluebird, $t = 2.72$, $p = 0.01$; Northern

Table 2

Cavity-nesting birds detected ≥ 35 times during sampling in the northern ungulate range of the Yellowstone ecosystem during June 2001, 2002, 2003

Species	Migrant	<i>n</i>	YNP	GNF
American Kestrel (<i>Falco sparverius</i>)	Y	37	25	12
Black-capped Chickadee (<i>Parus atricapillus</i>)	N	63	22	41
House Wren (<i>Troglodytes aedon</i>)	Y	163	95	68
Mountain Bluebird (<i>Sialia currucoides</i>)	Y	77	44	33
Mountain Chickadee (<i>Parus gambeli</i>)	N	131	48	83
Northern Flicker (<i>Colaptes auratus</i>)	Y	188	112	76
Red-breasted Nuthatch (<i>Sitta Canadensis</i>)	N	78	43	35
Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>)	Y	58	21	37
Starling (<i>Sturnus vulgaris</i>)	N	77	70	7
Tree Swallow (<i>Tachycineta bicolor</i>)	Y	39	29	10
Violet-green Swallow (<i>Tachycineta thalassina</i>)	Y	70	38	32

Migrant status after McEneaney (1996), YNP: Yellowstone National Park, GNF: Gallatin National Forest.

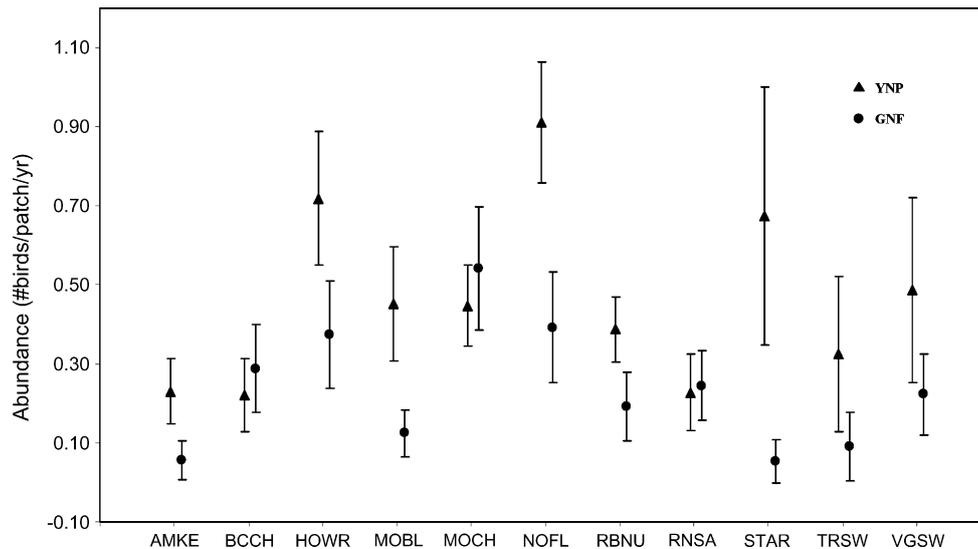


Fig. 3. Mean abundance and 95% confidence intervals of cavity-nesting birds in aspen stands on Yellowstone's northern range inside (YNP) and outside (GNF) Yellowstone National Park. AMKE: American Kestrel, BCCH: Black-capped Chickadee, HOWR: House Wren, MOBL: Mountain Bluebird, MOCH: Mountain Chickadee, NOFL: Northern Flicker, RBNU: Red-breasted Nuthatch, RNSA: Red-naped Sapsucker, STAR: European Starling, TRSW: Tree Swallow, VGSW: Violet-green Swallow.

Flicker, $t = 3.36$, $p < 0.01$; Red-breasted Nuthatch, $t = 2.21$, $p = 0.03$; Starling, $t = 2.39$, $p = 0.02$; confidence intervals shown in Fig. 3). Since the largest significant p -value was less than the estimated q -value (0.04) from the FDR controlling procedure, we retained all differences above as significant. Two species (Tree Swallow and Violet-green Swallow) showed a marginal but non-significant trend toward greater abundance inside YNP (Tree Swallow, $t = 1.41$, $p = 0.17$; Violet-green Swallow, $t = 1.34$, $p = 0.19$; confidence intervals shown in Fig. 3). The remaining 3 species (Black-capped Chickadee, Mountain Chickadee, and Red-naped Sapsucker) showed no difference in abundance between YNP and GNF (Black-capped Chickadee, $t = 0.63$, $p = 0.53$; Mountain Chickadee, $t = 0.70$, $p = 0.48$; Red-naped Sapsucker, $t = 0.18$, $p = 0.86$; confidence intervals shown in Fig. 3).

5. Discussion

5.1. Aspen condition

As expected, we found a sparser canopy among YNP stands as mature trees have converted to snags and have not been replaced by overstory recruitment (i.e., growth of sprouts into tall saplings and trees). In contrast, GNF stands had more apparent recruitment resulting in a denser canopy, stems at multiple heights, and lower relative snag abundance. The smaller mean stem diameter for GNF stands is consistent with an age class distribution that includes recently recruited small-diameter trees. Conversely, the larger mean stem diameter of YNP stands reflects an absence of small-diameter stems. Thus, it appeared GNF stands had recently experienced successful recruitment of new stems, and YNP stands had not. The processes leading to these conditions may have profound implications for the future. Assuming the presence of trophic cascades processes, continued success of wolf re-introduction,

and the absence of major disturbance, we expect northern range aspen stands within YNP to follow a path of deterioration and then recovery over the next several decades. This path should result in an increase in the relative abundance of aspen snags as live trees die and covert to snags, followed by an overall decline as standing snags fall and are not replaced by recruited stems, followed by an eventual recovery as recruitment catches up and once again produces snags at or below historic levels (Fig. 4). Our results suggest a current relative abundance of snags within YNP aspen stands that is being tracked by some cavity-nesting bird species. With the retention of wolves and reduced elk abundance, we expect aspen stands to eventually recover (over the next 150 years) with subsequent effects on cavity-nesting birds (Fig. 4) but it should be noted that aspen clones lost to the present decline cannot be involved in recovery and northern range aspen habitat within YNP may not fully recover to historic levels (i.e., 1900).

5.2. Aspen decline

There is considerable evidence for top-down structuring of the northern Yellowstone ecosystem through a trophic cascade where wolves are the top predator (National Research Council, 2002; Ripple and Beschta, 2004, 2006; Beschta, 2005; Fortin et al., 2005; White and Garrott, 2005; Beyer et al., 2007). In the absence of wolves, intense elk browsing of young aspen suckers has severely impacted aspen stands within YNP by reducing or eliminating recruitment of new stems to replace mature aspen as they die. Fig. 5 shows repeat photographs of a typical aspen stand within YNP during 1986 and 2004 (~10 years prior, and 10 years after wolf re-introduction). Among the foreground trees, reduced live canopy cover, greater snag abundance, numerous fallen aspen stems, and an apparent lack of regeneration and recruitment is visible in the later photograph. The earlier photograph was acquired ~55 years after wolf

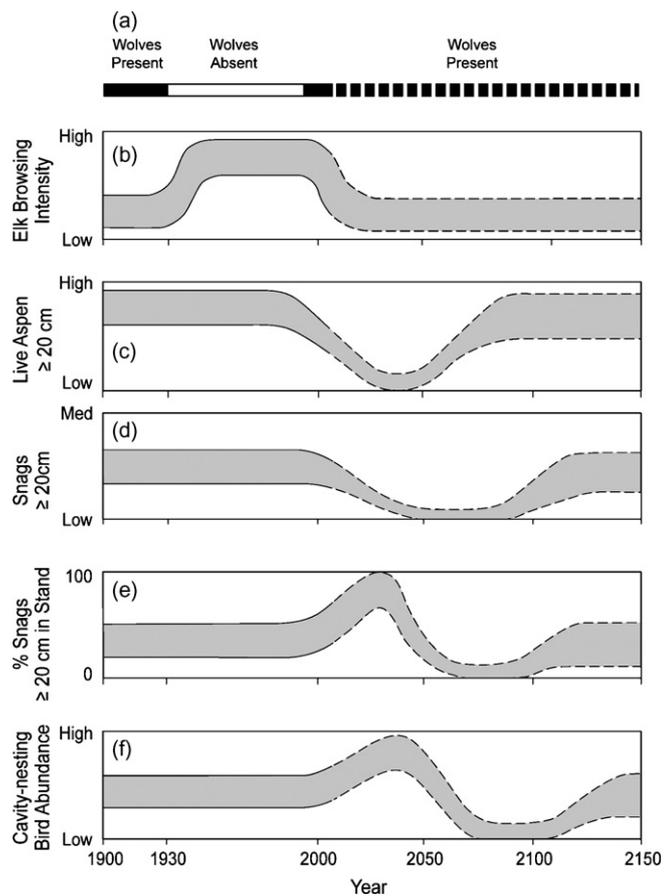


Fig. 4. Hypothesized changes in (a) wolf presence, (b) elk browsing intensity, (c) large live aspen (>20 cm dbh) abundance, (d) large aspen snag (>20 cm dbh) abundance, (e) large snag relative abundance (% of stand), and (f) cavity-nesting bird abundance within YNP over a 250 years interval (19:00–21:50). Gray areas indicate range of condition. Dashed lines indicate projections. Post-reintroduction wolf presence (1996) is assumed to remain constant. Projected elk browsing intensity is assumed to return to historical (pre-wolf extirpation) levels. Projected live aspen and aspen snag dynamics assume an absence of disturbance (e.g. fire). Relative scale is same for large live aspen and aspen snags. Large snags relative abundance (% of stand) calculated from large live aspen and large aspen snag abundances (snag abundance/snag abundance + live abundance). Cavity-nesting birds are assumed to retain preference for aspen snags during scarcity.

extirpation and 25 years after the adoption of the “natural regulation” elk management policy by the National Park Service. In the approximately 20-year period between these photographs, aspen condition has deteriorated rapidly and, although wolves had been present for almost 10 years, the later photograph does not yet show signs of aspen recovery due to trophic cascades effects.

Wolves, especially where combined with other top predators, such as grizzly bear (*Ursus arctos*), appear to reduce ungulate prey populations in most systems where they have been studied (Peterson et al., 2003). Elk numbers on Yellowstone’s northern range declined after wolf re-introduction, likely due to lethal effects of wolf predation, and are expected to continue declining (White and Garrott, 2005). Concurrent limited aspen and substantial willow recovery have been documented (Ripple and Beschta, 2006, 2007; Beyer et al., 2007). As elk numbers continue to decline, and/or elk

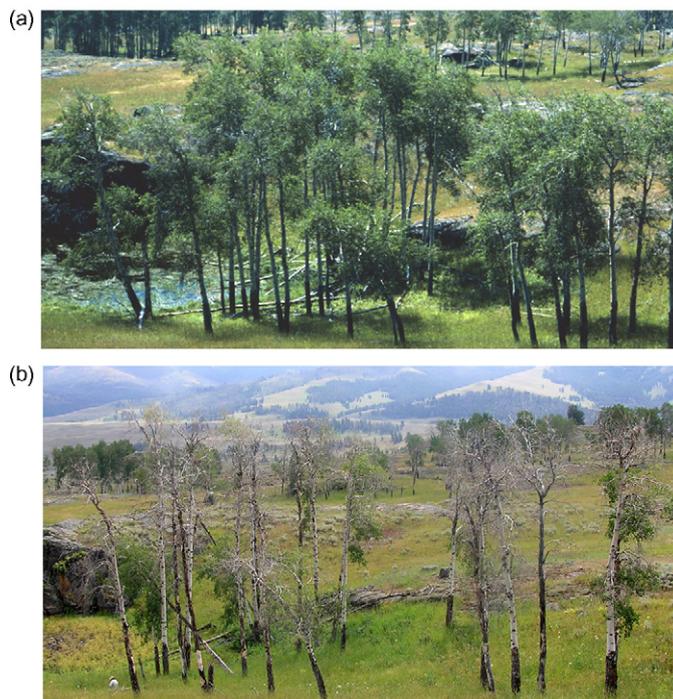


Fig. 5. Repeat photos of an aspen stand on the northern range in YNP. Top photo (a) was taken during August 1986 (Photo by Charles Kay), bottom photo (b) was taken during August 2004.

foraging behavior changes in the presence of wolves (e.g., White et al., 2003), it seems reasonable to expect a more widespread aspen recovery on Yellowstone’s northern range in the future.

5.3. Live aspen and snag dynamics

We found a greater percentage of large-diameter snags in YNP stands that is not mirrored in GNF stands. Photographs of typical stands sampled during this study show greater abundance of standing and recently fallen snags in YNP stands (Fig. 2). Outside YNP, where human hunting may affect elk density and/or foraging behavior, aspen stands have continued to recruit new stems into the overstory; stands within YNP have not. St. John (1995) attributes greater aspen recruitment found within 0.5 km of roads outside YNP (within the northern winter range) to human hunting of elk and suggests predation risk by humans has modified the behavior of elk, and subsequent browsing intensity on aspen. In our samples, all stands outside YNP were recruiting new stems into their overstory and most within YNP were not. For YNP stands, the lack of new stem recruitment combined with the dying off of mature stems appears to result in a greater relative abundance of snags not found outside the park (although this pattern may not persist long term).

Referring to the age-diameter relationship developed by Ripple and Larsen (2000) for aspen on Yellowstone’s northern range, we expect successfully recruiting aspen to reach large diameters (≥ 20 cm dbh) in ~56 years. Consequently, following wolf re-introduction, recruitment of significant numbers of large diameter live aspen is not expected until 2052 at the soonest (~56 years after 1996). The mode of published age

class distributions for northern range aspen (Larsen and Ripple, 2003) and other western U.S. sites (Mueggler, 1989) is ~100 years. Thus, we considered 100-year-old aspen stems as mature, likely to die soon, and become snags. Consequently, stems recruiting shortly after wolf re-introduction (1996–2000) will not convert to large-diameter snags until ~2100. Larsen and Ripple (2003, 2005) found >95% of current living aspen in the YNP portion of the northern ungulate winter range to be >80 years old. We can expect many of these trees to die soon since they are at or near the average lifespan. After death, aspen snags do not persist long. Hart and Hart (2001) report an average period of 10.7 years, standing after death for aspen snags > 15 cm dbh in the Bridger-Teton National Forest, northwest Wyoming. Consequently, most currently live trees and all currently standing snags will fall and become logs before newly recruited stems can reach larger diameters (≥ 20 cm dbh), mature, and die to create new snags. During the period when most current snags have fallen and recruiting stems are maturing, there will be a paucity of large-diameter snags that are preferred as nest sites by many cavity-nesting birds. We estimate the length of this interval to be about 50 years, beginning ~2045 as the remaining large stems mature, die, and fall (see Fig. 4). After this period, we expect the recruitment, maturation, and death of large-diameter stems to continue until relative snag abundance approaches historical (1900) levels. Recovery to conditions resembling those of the historic period (1900–1930) may not occur until ~2150 (see Fig. 4). Note also that the present deterioration of many stands (i.e., the decline and disappearance of clones) within YNP may lead to their permanent disappearance. Subsequently, these stands would not be able to contribute to aspen habitat recovery at the landscape scale. Additionally, the failure of substantial recruitment within surviving clones may lead to a permanent or protracted lack of large-diameter aspen (live and dead) within YNP.

5.4. Cavity-nesting bird dynamics

Six of the 11 cavity-nesting bird species analyzed in this study are significantly more abundant within YNP than outside (GNF). Two species show a non-significant trend toward greater abundance within YNP, and three are equally abundant inside and outside YNP. Northern Flickers, American Kestrels, and Red-breasted Nuthatches appear to be associated with large-diameter aspen snags. Previous work with each of these species suggests strong preference or association with large-diameter snags as nest sites (e.g., Harestad and Keisker, 1989; Li and Martin, 1991; Dobkin et al., 1995; Moore, 1995; Caton, 1996; Steeger and Hitchcock, 1998; Ghalambor and Martin, 1999; Smallwood and Bird, 2002). Consequently, it seems reasonable that the relative abundances of these species would reflect the abundance of large-diameter snags inside or outside YNP. Mountain Bluebirds, House Wrens, and Starlings also appear associated with large-diameter aspen snags. Power and Lombardo (1996) state that relatively little is known about natural nest cavity selection by Mountain Bluebirds. We observed Mountain Bluebirds using cavities in large-diameter snags that were not surrounded by dense cover; a condition

more frequently found inside YNP. House Wrens use natural and abandoned primary-excavator cavities, preferring sites with little or no surrounding foliage (Finch, 1989; Johnson, 1998). In Yellowstone's northern range, House Wrens appear to be associated with deteriorating aspen stands that have abundant snags and sparse understories. Starlings use any suitable cavity for nesting but are very successful competitors for abandoned, and even occupied, primary excavator nest cavities (Ingold, 1989; Dobkin et al., 1995; Moore, 1995). Most Starling nests detected in this study appeared to be Northern Flicker cavities located in aspen snags.

Our data suggest that Tree and Violet-green Swallows are more abundant inside YNP than outside (GNF). However, perhaps due to high variability, the difference was not statistically significant. Swallows are often reported to use existing cavities in snags located in open situations (Rendell and Robertson, 1989; Robertson et al., 1992; Lawler and Edwards, 2002) and aspen stands within YNP are generally more open with sparser canopies.

Of the three species with similar relative abundances inside and outside YNP, one is a primary excavator (Red-naped Sapsucker) that prefers large live aspen stems for nest excavation (Crockett and Hadow, 1975; Dobkin et al., 1995). The remaining two secondary cavity nesters are taxonomically and behaviorally related (Black-capped and Mountain Chickadees). The similar relative abundance of sapsuckers inside and outside YNP suggests similar occurrence of suitable live-aspen nest sites. Black-capped chickadees and mountain chickadees were found in similar numbers inside and outside YNP. Hill and Lein (1989) found similar habitat use by both species in the Rocky Mountains of southwestern Alberta. Both species used conifer habitat extensively with mountain chickadees using areas with large conifers more frequently than black-capped chickadees. Yellowstone's northern range habitats are similar to those found in Hill and Lein's (1989) study. Hill and Lein (1989) also found both species of chickadee using cavities excavated by red-naped sapsuckers. If northern range chickadees prefer sapsucker-excavated cavities, it may account for the similar relative abundances of all 3 species in this study.

It's unknown to what extent cavity nesters that use aspen snags might switch to live aspen or conifers for nest sites as aspen snag abundance declines, but the response is likely to vary by species. Some researchers have found nest-site limitation among western U.S. sites (e.g., Zarnowitz and Manuwal, 1985). Others have found that nest sites are not limiting, but rather foraging opportunity limits cavity nester abundance (e.g. Brawn and Balda, 1988; Welsh and Capen, 1992; Caton, 1996). Low snag abundance in YNP will likely affect species differently. For example, Dobkin et al. (1995) and Crockett and Hadow (1975) found that red-naped sapsuckers used live trees more often than dead trees for nesting in eastern Oregon and southern Colorado, respectively. Daily et al. (1993) found red-naped sapsuckers in Colorado to be significantly associated with aspen that spatially co-occur with willows. Willows are currently more prevalent outside YNP (Jackson, 1992). However, recent studies have documented a release of willows inside YNP attributed to changes in elk herbivory

following wolf re-introduction (Beyer, 2006; Ripple and Beschta, 2006; Beyer et al., 2007). This may influence the future distribution of red-naped sapsuckers.

Assuming YNP aspen stands follow the course presented above (Fig. 4) recruited live aspen will attain large diameters before the end of the low snag abundance interval (return of large live aspen ~2080; return of large snags ~2120). Primary excavators, especially those that prefer live aspen, will likely create cavities in these live aspen. During low snag abundance, these live aspen cavities should see use by all cavity-nesting species regardless of their preference for snags.

Fire disturbance may stimulate aspen regeneration by vigorous suckering leading to canopy recruitment, especially at low ungulate browsing intensity level (White et al., 2003). Fire disturbance also may affect cavity-nesting birds, influencing both nest site availability and high-quality foraging habitat (e.g. Caton, 1996). The presence and timing of fire-killed aspen and conifer snags complicate the ability to predict cavity-nester abundance. A relatively small portion (<30%) of YNP's northern range was involved in the extensive wildfires of 1988 and even less area actually burned. We should note however, that the hypothesized dynamics presented in this study (Fig. 4) assume disturbance, such as fire, is absent. Certainly, the Yellowstone ecosystem experiences disturbances at several scales that would need to be considered when relating the ideas presented here with actual conditions.

6. Conclusions

Current aspen and cavity-nesting bird conditions combined with historical data, recently published data, and an understanding of stand dynamics, leads us to conclude that northern range aspen stands within YNP will experience changes over the next several decades that will likely have consequences for cavity-nesting birds. These changes may provide an opportunity for ecologists to better understand the role of trophic cascade processes in ecosystem structuring over long time scales.

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