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Author(s): JOSEPH L. GANEY, GARY C. WHITE, JEFFREY S. JENNESS and SCOTT C. VOJTA
Source: *The Journal of Wildlife Management*, Vol. 79, No. 8 (November 2015), pp. 1369-1377
Published by: Wiley on behalf of the Wildlife Society
Stable URL: https://www.jstor.org/stable/24764394
Accessed: 24-08-2018 21:20 UTC

The Journal of Wildlife Management 79(8):1369–1377; 2015; DOI: 10.1002/jwmg.947

Research Article

Mark–Recapture Estimation of Snag Standing Rates in Northern Arizona Mixed-Conifer and Ponderosa Pine Forests

JOSEPH L. GANEY,[1] *U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, AZ 86001, USA*
GARY C. WHITE, *Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Fort Collins, CO, USA*
JEFFREY S. JENNESS, *Jenness Enterprises, Flagstaff, AZ 86001, USA*
SCOTT C. VOJTA, *U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, AZ 86001, USA*

ABSTRACT Snags (standing dead trees) are important components of forests that provide resources for numerous species of wildlife and contribute to decay dynamics and other ecological processes. Managers charged with managing populations of snags need information about standing rates of snags and factors influencing those rates, yet such data are limited for ponderosa pine (*Pinus ponderosa*) and especially mixed-conifer forests in the southwestern United States. We monitored standing rates of snags in 1-ha plots in Arizona mixed-conifer ($n = 53$ plots) and ponderosa pine ($n = 60$ plots) forests from 1997 through 2012. We used the Burnham live–dead, mark–resight model in Program MARK and multimodel inference to estimate standing rates during 5-year intervals while accounting for imperfect detection. Because snag standing rates may be influenced by plot characteristics, we used plots rather than snags as sampling units and conducted bootstrap analyses (500 iterations per model) to resample plots and estimate standing rates and associated parameters. We modeled standing rates in 3 discrete steps. First, we selected a parsimonious base model from a set of models including snag species, and then we evaluated models created by adding snag and plot covariates to the base model in steps 2 and 3, respectively. Snag standing rates differed among snag species and 5-year sampling intervals. Standing rates were positively related to snag diameter, negatively related to snag height, and were lower for snags with intact tops than for broken-topped snags. Standing rates also were positively related to topographic roughness, elevation, tree density, and an index of northness, and negatively related to slope and relative topographic exposure. Our results provide comparative data on standing rates of multiple species of snags based on a large and spatially extensive sample and rigorous analysis, and quantify the relative importance of several snag and plot characteristics on those rates. They indicate that modeling snag dynamics is complicated by both spatial and temporal variation in standing rates and identify areas where further work is needed to facilitate such modeling. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS aspen, dead trees, Douglas-fir, Gambel oak, *Pinus ponderosa*, snag dynamics, snag longevity, white fir.

Snags (standing dead trees) are important components of forests that provide resources for numerous species of wildlife and contribute to decay dynamics and other ecological processes (Thomas et al. 1979, Harmon et al. 1986, Bull et al. 1997, McComb and Lindenmayer 1999, Laudenslayer et al. 2002). Because of their importance as wildlife habitat, managers have focused special attention on snag populations (Thomas et al. 1979, Bull et al. 1997, Laudenslayer et al. 2002). Managing snag populations to provide a sustainable supply of important wildlife habitat components requires an understanding of the underlying dynamics of snag populations, including standing rates and factors that influence those rates (Mellen et al. 2002, Garber et al. 2005, Russell et al. 2006, Marcot et al. 2010). Previous studies indicated that snag standing rates were influenced by snag characteristics, with standing rates varying among snag species and generally greater for large diameter than for small diameter snags (Morrison and Raphael 1993; Chambers and Mast 2005, 2014; Russell et al. 2006; Parish et al. 2010). Snag standing rates also were influenced by characteristics of the areas in which those snags were located in some studies (Chambers and Mast 2005, 2014; Garber et al. 2005; Russell et al. 2006), whereas other studies showed no such site effect (Lee 1998, Parish et al. 2010). Standing rates also may differ based on the tree mortality agents that created the snags in question (Dahms 1949; Keen 1955; Laudenslayer 2002; Chambers and Mast 2005, 2014).

Received: 19 August 2014; Accepted: 6 July 2015
Published: 19 August 2015

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[1] *E-mail: jganey@fs.fed.us*

We know little about snag standing rates and factors influencing those rates in most southwestern forest types. Several studies have quantified standing rates of ponderosa pine (*Pinus ponderosa*) snags in ponderosa pine forest (Cunningham et al. 1980; Chambers and Mast 2005, 2014; Ganey and Vojta 2005; Passovoy and Fulé 2006), but only Ganey and Vojta (2005) did so (over a limited time frame) for southwestern mixed-conifer forests. Information is available from other geographic areas and/or forest types, but it is unclear whether results from these studies extrapolate well to southwestern mixed-conifer and ponderosa pine forests. Inference based on most studies also is limited. Many studies of standing rates in these or similar forest types focused on single or at best a few study sites, and most followed a single cohort of snags, often of a single snag species, created by a single cause of tree mortality such as wildfire (Dahms 1926, Chambers and Mast 2005, Russell et al. 2006), prescribed fire (Harrington 1996, Laudenslayer 2002), or bark beetles (Keen 1955, Schmid et al. 1985, Chambers and Mast 2014). These studies provided valuable information about snags (especially ponderosa pine snags) in particular sites created by particular mortality agents, but that information cannot be extrapolated to managing snag populations including multiple species of snags, of various ages, created by multiple mortality agents across variable landscapes. Managing these populations requires knowledge of standing rates for multiple species of snags, as well as the extent of spatial and temporal variability in those rates and factors underlying that variability.

We studied snag dynamics from 1997 to 2012 at multiple sites in mixed-conifer and ponderosa pine forests in northern Arizona (Ganey and Vojta 2014). We used a mark–recapture framework to model standing rates of snags in these forest types while accounting for imperfect detection of snags. Our primary objectives were to estimate standing rates of snags, identify factors influencing those standing rates, and estimate relative importance of those factors. Our study differed from most previous studies in 6 important ways. First, it incorporated multiple species of snags from the same study plots, allowing us to separate differences in standing rates among species from apparent differences caused by studying different species in geographically distant study areas. Second, it was based on a spatially extensive and spatially variable sample, rather than on 1 or a few study sites, allowing for estimation of standing rates across that variable landscape and the importance of selected landscape factors influencing that variability. Third, it explicitly evaluated temporal variability in standing rates. Fourth, it included snags of varying age rather than following the fate of a single cohort of snags, included snags created by all mortality agents operating in these forests rather than focusing on snags created by a single mortality agent, and accounted for imperfect detection of snags. Fifth, it allowed characteristics of individual snags to vary among sampling intervals rather than modeling standing rates based on values of snag covariates at the beginning of the study. Finally, it explicitly accounted for the potential lack of statistical independence among snags within a plot in the modeling process.

STUDY AREA

We sampled snags within an area covering 73,000 ha across the Coconino and Kaibab National Forests, north-central Arizona (Fig. 1). Within this area, study plots were randomly located in mixed-conifer and ponderosa pine forests (plot selection described in Ganey 1999). Mixed-conifer forests were dominated by ponderosa pine, white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*), which together accounted for approximately 90 percent of total trees in this forest type (Ganey and Vojta 2011). Other common species included Gambel oak (*Quercus gambelii*), quaking aspen (*Populus tremuloides*), and limber pine (*P. flexilis*), in that order of frequency. Ponderosa pine accounted for over 90% of trees in ponderosa pine forest (Ganey and Vojta 2011). Gambel oak also was relatively common (approx. 8% of total trees by frequency), and alligator juniper (*Juniperus deppeana*), Douglas-fir, quaking aspen, limber pine, pinyon pine (*P. edulis*), and other species of juniper were present in small numbers in some stands.

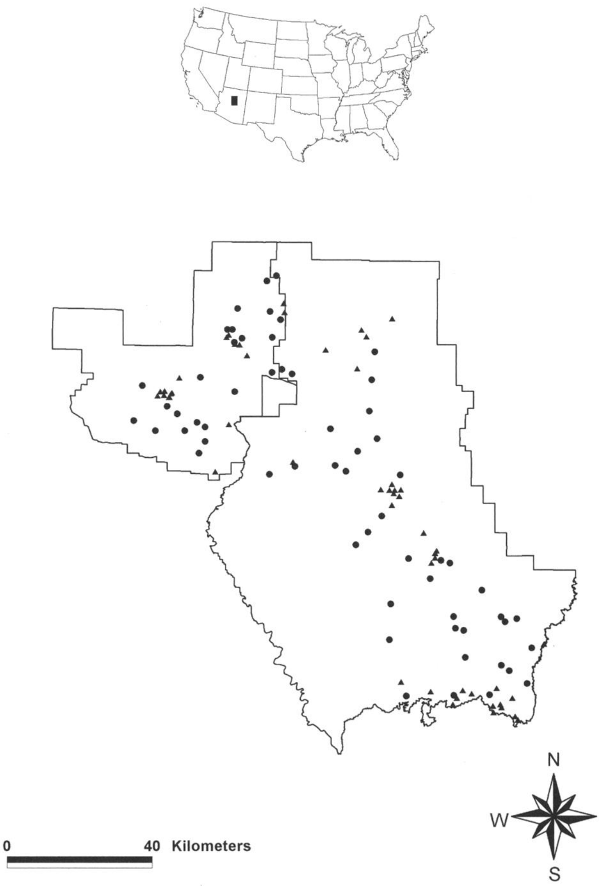

Figure 1. Location of the study area (black box, top) in northern Arizona, and locations of sampled plots within the study area (bottom). Plots were located in the Kaibab (left) and Coconino (right) National Forests. Plots in ponderosa pine forest ($n = 60$) are indicated by circles and plots in mixed-conifer forest ($n = 53$) by triangles.

The study plots included a wide range of topographic conditions and soil types, covered the entire elevational range of these forest types within this area (mixed-conifer median = 2,351 m, range = 1,886–3,050 m; ponderosa pine median = 2,144 m, range = 1,778–2,561 m), and included both commercial forest lands and administratively reserved lands such as wilderness and other roadless areas. Consequently, plots represented a wide range of forest structural conditions. Density of trees ≥20 cm in diameter at breast height (dbh) ranged 78–489 (median = 266.7) trees/ha in mixed-conifer forest and 11–689 (median = 227.8) trees/ha in ponderosa pine forest. Basal area ranged 7–52 (median = 25.2) and 1–44 (median = 19.7) m^2/ha in mixed-conifer and ponderosa pine forest, respectively (Ganey and Vojta 2011).

METHODS

We sampled snags in 113 plots (1 ha each in area, $n = 53$ and 60 plots in mixed-conifer and ponderosa pine forest, respectively) randomly established in 1997 (see Ganey 1999 for details on plot selection). We sampled all snags ≥2 m in height and ≥20 cm dbh. We did not sample smaller-diameter snags based on the assumption that they were less important to cavity-nesting birds (Balda 1975, Cunningham et al. 1980, Ganey and Vojta 2004, Chambers and Mast 2014) and roosting bats (Rabe et al. 1998, Bernardos et al. 2004, Solvesky and Chambers 2009). We sampled snags on 4 occasions (1997, 2002, 2007, and 2012). At each occasion t, we uniquely marked any new snags with numbered metal tags, and recorded fate for all previously marked snags over the interval (i) from $t-1$ to t ($n = 3$ 5-yr intervals). Fate was recorded as snag remained standing at occasion t, snag fell during interval i and was relocated as a log, or snag was not found. Thus, fate was known for most but not all snags.

We recorded 5 characteristics of snags for use as covariates in models estimating standing rates, including species, dbh (nearest cm), height (nearest m), top condition (intact vs. broken), and the ratio of snag diameter to height. We measured these characteristics at each sampling occasion, because snag height, top condition, and diameter/height ratio could change between sampling occasions. We hypothesized that standing rates would differ among species (Morrison and Raphael 1993, Landram et al. 2002, Russell et al. 2006, Angers et al. 2010, Parish et al. 2010). Because wind is an important agent of snag breakage and loss in this region (Chambers and Mast 2005, 2014; Ganey and Vojta 2005), we also hypothesized that standing rates would be positively related to snag diameter and snag diameter/height ratio, negatively related to snag height, and greater for snags with broken than with intact tops (Morrison and Raphael 1993; Chambers and Mast 2005, 2014; Ganey and Vojta 2005; Russell et al. 2006; Parish et al. 2010).

We sampled all live trees ≥20 cm dbh in a 0.09-ha subplot within each plot in 2004 and 2014. Tree density did not differ significantly within our plots between 2004 and 2014 (Wilcoxon signed-ranks test, $Z = -0.688$, $P = 0.508$). Therefore, we used the 2004 estimate of tree density as a plot-level covariate in modeling standing rates, because this represented the approximate midpoint of the period modeled (1997–2012). We hypothesized that standing rates would increase with increasing tree density because of reduced wind speeds in denser stands (Chambers and Mast 2005, but see Garber et al. 2005, Chambers and Mast 2014).

We used the National Elevation Dataset (NED; http://nationalmap.gov/viewer.html; cell size = 30 × 30 m) to generate 5 topographic-based plot covariates that might influence standing rates (Chambers and Mast 2005, 2014; Russell et al. 2006). We estimated mean elevation (m) and mean slope (deg) within each plot and calculated mean aspect (deg) using the ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA) extension from Jenness (2013), means were based on values of all cells within the plot. We transformed mean aspect to cosine of aspect, an index of relative northness ranging from −1 at due south to 1 at due north. We estimated surface ratio (an index of topographic roughness, with greater values indicating greater roughness) following Jenness (2004). We calculated topographic position index (an index of relative topographic exposure) as the mean difference between elevation for each cell in a plot and the mean elevation of all cells within a 200-m neighborhood. We hypothesized that snag standing rates would decrease with slope and topographic position index because of greater exposure to wind, and would be positively related to surface ratio, assuming that more complex topography would reduce wind speed (Chambers and Mast 2005), and to cosine aspect because the prevailing winds in this region are southerly.

Thus, covariates available for modeling standing rates included characteristics of individual snags, tree density, and topographic-based plot characteristics. We lacked data on cause of death, which may influence standing rates and had insufficient data on fire history (see below) to model fire effects (Passovoy and Fulé 2006). We also did not include snag age in models, because many snags marked in 1997 were of unknown age and new snags marked on subsequent occasions could only be aged ± 5 years. Failure to include these factors likely lowered the precision of standing rate estimates, but the estimates are directly relevant to managers faced with managing populations of snags of unknown age created by varied and unknown mortality agents.

Modeling Snag Standing Rates

We used the Burnham (1993) live–dead, mark–resight model in Program MARK (White and Burnham 1999) to estimate snag standing rates. The Burnham model typically incorporates information from both live and dead encounters to estimate survival rates of animals across t sampling occasions (Burnham 1993). We estimated standing rates of snags across 4 sampling occasions, with 3 5-year intervals (i) between sampling occasions, and live and dead encounters referred to snags that remained standing or fell during interval i, respectively. The model estimated 4 sets of parameters: S_i, $i = 1, \ldots, t-1$, the probability that a snag remained standing during interval i; p_i, $i = 1, \ldots, t-1$, the probability that a snag that remained standing during interval i was detected; r_i, $i = 1, \ldots, t-1$, the probability that a snag that fell during interval i was detected; and F, fidelity, which we set to 1 because snags could not emigrate from the plot.

Snag standing rates may be non-independent for snags in the same plot (Chambers and Mast 2005, 2014; Garber et al. 2005; Russell et al. 2006). Therefore, we treated plots as sampling units and used bootstrap analyses (Bishop et al. 2008) to resample plots in all model runs. Because of the relatively large numbers of snags, plots, and iterations (500), we were not able to model all of the data at one time, and broke the modeling process into 3 discrete steps to facilitate analysis. In step 1, we evaluated a suite of 10 models (Table S1) parameterized using only species group ($g = 6$ species groups; white fir, Douglas-fir, ponderosa pine, quaking aspen, Gambel oak, and other [all other species]) and time interval ($i = 3$ 5-yr intervals). This allowed us to select the most parsimonious base model from a set of models lacking other snag- and plot-level covariates. In step 2, we evaluated 16 models (Table S2) representing all possible combinations created by adding 4 snag covariates (dbh, height, top condition, and diameter/height ratio) to the top base model selected in step 1. In step 3, we evaluated 64 models (Table S3) representing all possible combinations created by adding 6 plot-level covariates (mean slope, mean elevation, cosine aspect, topographic position index, surface ratio, and tree density) to the top base model from step 1.

We used 500 bootstrap iterations to evaluate models in all 3 steps. We computed model weights using Akaike's Information Criterion corrected for small sample size (AIC_c) as described by Burnham and Anderson (2002), computed mean model weight as the mean of the weights from the 500 bootstrap iterations, and ranked models by mean weight. We estimated relative importance of covariates as the sum of the mean weights for all models including that covariate across the 500 bootstrap iterations; these estimates were informative because all covariates were included in the same number of models within a model set (Doherty et al. 2012). Unless otherwise indicated, we generated bootstrapped parameter estimates and associated confidence intervals from the top model resulting from each suite of models.

Seven plots experienced severe wildfire during the study (4 in mixed-conifer and 3 in ponderosa pine forest). Because severe fire melted the aluminum tags used to mark snags, we were unable to distinguish between pre-existing and newly created snags in these plots following fire. Consequently, we censored all existing snags in these plots following fire, and treated all snags observed at the first post-fire sampling occasion as new snags in analyses covering subsequent intervals. For example, if a plot burned between the 2002 and 2007 sampling occasions, existing snags in 1997 were included for the interval from 1997 to 2002 but censored thereafter, and all post-fire snags observed in 2007 were treated as new snags for the interval from 2007 to 2012.

RESULTS

We included 6,020 unique snags in analyses of standing rates. Number of standing snags present at the beginning of interval i increased over time, with 2,206, 2,555, and 4,814 snags present in 1997, 2002, and 2007, respectively. Snag populations sampled in 2002 and 2007 included 1,061 and 2,753 newly recruited snags, respectively, representing 41.5% and 57.2% of total snag numbers on those sampling occasions, respectively.

The top-ranked base model indicated that snag standing rates were influenced by species group interacting with time interval, and that detection probability differed by species group for standing snags and by an interaction between species group and time interval for fallen snags (Table 1). Two additional models also were reasonably supported (mean model weight >0.1000). Both of these models were identical to the top model for S and r, but differed for p, which was constant in the second-ranked model and was influenced by an interaction between species group and time interval in the third-ranked model.

Parameter estimates from the top model indicated that S_i was greater for Gambel oak and Douglas-fir snags than for quaking aspen, white fir, and ponderosa pine snags (Table 2). Standing rates were highest in the first sampling interval for most species, but relative ranks of the following 2 intervals differed among species. Detection rates were high for snags that remained standing (Table 3) and lower and more variable among species and intervals for fallen snags (Table 4).

There were 4 competing models (mean model weight >0.1000) among the suite of models created by adding snag covariates to the base model (Table 1). The top-ranked model included snag dbh, height, and top condition. The next best model included these variables plus snag diameter/height ratio, and the third and fourth models dropped snag height and snag diameter/height ratio, respectively, from this combination of variables. The base model without covariates included was the lowest-ranked model (Table S2), indicating that all snag covariates improved the model.

Because the top 2 models including snag covariates were approximately equally likely (Table 1), we used the model including all covariates to generate parameter estimates. Parameter estimates indicated that standing rate was positively related to both snag dbh and diameter/height ratio, negatively related to snag height, and greater for snags with broken tops than for snags with intact tops (Table 5). Confidence intervals around the parameter estimates did not include 0 for any covariates, suggesting that all contributed significantly to the model, but covariate weights indicated stronger effects for snag dbh and top condition than for snag height and snag diameter/height ratio (Table 5). Both snag dbh and top condition (and only these covariates) were included in all competing models.

Three models including both the base model and plot covariates had mean weight >0.1000 (Table 1). The top model included all 6 plot covariates and was approximately 1.5 times as likely as the next model. The second-ranked model dropped mean topographic position index from this combination of variables, and the third dropped cosine aspect (Table 1). The base model was the lowest-ranked model (Table S3), indicating that all plot covariates improved the model. Parameter estimates from the top model indicated that standing rate was positively related to surface ratio,

Table 1. Mean model weights (along with associated SD and min. and max. weights) for the top models from suites of models evaluated in 3 separate steps to estimate standing rates of snags in northern Arizona mixed-conifer and ponderosa pine forests, 1997–2012. In step 1, we evaluated 10 Burnham (1993) live–dead models to select a best base model. In step 2, we evaluated 16 models created by adding all possible combinations of 4 snag covariates to the top base model. In step 3, we evaluated 64 models created by adding all possible combinations of 6 plot covariates to the best base model. Only models with mean weights ≥0.10 are shown here (see Tables S1–S3 for all model results). We estimated mean weights from 500 bootstrap iterations using plots as sampling units.

Model structure	Mean	SD	Range
Base models[a]			
{*S*(g×t) *p*(g) *r*(g×t) *F*=1}	0.3632	0.3078	0.0001–0.9960
{*S*(g×t) *p*(.) *r*(g×t) *F*=1}	0.3191	0.3460	<0.0001–0.9877
{*S*(g×t) *p*(g×t) *r*(g×t) *F*=1}	0.2065	0.2940	<0.000–0.9999
Base model plus snag covariates[b]			
{base+dbh+height+condition}	0.3915	0.2149	0.0004–0.9817
{base+dbh+height+condition+dbh/ht}	0.3374	0.2250	0.0007–0.9983
{base+dbh+condition+dbh/ht}	0.1680	0.1693	0.0000–0.7064
{base+dbh+condition}	0.1023	0.1567	0.0000–0.7275
Base model plus plot covariates[c]			
{base+slope+elevation+aspect+topo+surface ratio+density}	0.2646	0.2494	<0.0001–0.9992
{base+slope+elevation+aspect+surface ratio+density}	0.1777	0.1914	<0.0001–0.9976
{base+slope+elevation+topo+surface ratio+density}	0.1316	0.1720	<0.0001–0.9561

[a] Notation for base models evaluated: S = the probability that a snag remained standing during a sampling interval (i, $n = 3$ 5-yr intervals), g = species or species group ($n = 6$ species or groups), t = sampling occasion ($n = 4$ occasions), p = the probability that a snag was detected given that it remained standing during interval i, r = the probability that a snag was detected given that it fell during interval i, and F= fidelity, which we set to 1 because snags could not emigrate from the plot.

[b] Snag covariates evaluated included: dbh = snag diameter at breast height (cm), height = snag height (m), condition = top condition (broken vs. intact), and dbh/ht = snag diameter/height ratio. Snag covariates were added to the top ranked base model ({*S*(g×t) *p*(g) *r*(g×t) *F*=1}.

[c] Plot covariates included: slope = mean slope (deg), elevation = mean elevation (m), aspect = cosine of slope aspect (an index of relative northness of slope aspect, ranging from −1 at due south to 1 at due north), surface ratio (Jenness 2004), topo = mean topographic position index (an index of relative topographic exposure calculated as the mean difference between elevation for each cell in a plot and the mean elevation of all cells within a 200-m neighborhood), and density = tree density (trees/ha). Plot covariates were added to the top ranked base model ({*S*(g×t) *p*(g) *r*(g×t) *F*=1}.

Table 2. Estimated rates (and associated SEs and 95% CIs) at which snags remained standing (S) during 5-year intervals between sampling occasions in northern Arizona mixed-conifer and ponderosa pine forest, by major species and 5-year time interval. We derived estimates using the top base model ({*S*(g×t) *p*(g) *r*(g×t) *F*=1})[a] and 500 bootstrapped samples of snag monitoring plots. N = number of snags standing at the beginning of interval i.

Species[b]	5-yr interval	*N*	*S*	SE	95% CI
ABCO	1997–2002	384	0.764	0.001	0.762–0.766
	2002–2007	429	0.668	0.002	0.664–0.671
	2007–2012	1,756	0.696	0.002	0.692–0.699
PIPO	1997–2002	774	0.753	0.001	0.751–0.755
	2002–2007	954	0.652	0.002	0.647–0.656
	2007–2012	1,416	0.592	0.002	0.589–0.596
POTR	1997–2002	158	0.725	0.002	0.720–0.729
	2002–2007	209	0.667	0.001	0.664–0.669
	2007–2012	399	0.793	0.002	0.789–0.797
PSME	1997–2002	228	0.830	0.001	0.827–0.833
	2002–2007	297	0.772	0.001	0.769–0.775
	2007–2012	437	0.759	0.002	0.755–0.763
QUGA	1997–2002	530	0.932	0.001	0.931–0.933
	2002–2007	591	0.826	0.002	0.823–0.829
	2007–2012	716	0.853	0.001	0.852–0.854

[a] Notation for base model: S = the probability that a snag remained standing during a sampling interval (i, $n = 3$ 5-yr intervals), g = species or species group ($n = 6$ species or groups), t = sampling occasion ($n = 4$ occasions), p = the probability that a snag was detected given that it remained standing during interval i, r = the probability that a snag was detected given that it fell during interval i, and F= fidelity, which we set to 1 because snags could not emigrate from the plot.

[b] Species acronyms: ABCO = white fir, PIPO = ponderosa pine, POTR = quaking aspen, PSME = Douglas-fir, and QUGA = Gambel oak.

elevation, tree density, and cosine aspect, and negatively related to slope and topographic position index (Table 6). Confidence intervals around parameter estimates did not include 0 except for topographic position index, and importance estimates indicated strong effects for surface ratio, elevation, and slope, with weaker effects for tree density, cosine aspect, and topographic position index (Table 6).

DISCUSSION

This study focused on estimating standing rates of snags of varying species and age created by a variety of mortality

Table 3. Estimated detection rates of snags that remained standing (p) in northern Arizona mixed-conifer and ponderosa pine forest during 3 5-year time intervals from 1997–2012, along with associated standard errors and 95% CI, by major species. We derived estimates using the top base model ({ *S* (g ×t)
p(g) *r*(g×t) *F*=1})[a] and 500 bootstrapped samples of snag monitoring plots.

Species[b]	*p*	SE	95% CI
ABCO	0.985	<0.001	0.984–0.985
PIPO	0.992	<0.001	0.992–0.993
POTR	0.992	<0.001	0.991–0.992
PSME	0.983	<0.001	0.982–0.984
QUGA	0.994	<0.001	0.994–0.995

[a] Notation for base model: S = the probability that a snag remained standing during a sampling interval (i, $n = 3$ 5-yr intervals), g = species or species group ($n = 6$ species or groups), t = sampling occasion ($n = 4$ occasions), p = the probability that a snag was detected given that it remained standing during interval i, r = the probability that a snag was detected given that it fell during interval i, and F= fidelity, which we set to 1 because snags could not emigrate from the plot.

[b] Species acronyms: ABCO = white fir, PIPO = ponderosa pine, POTR = quaking aspen, PSME = Douglas-fir, and QUGA = Gambel oak.

Table 4. Estimated detection rates for snags that fell (r) during 3 5-year time intervals in northern Arizona mixed-conifer and ponderosa pine forest, along with associated standard errors and 95% CI, by major species. We derived estimates using the top base model ($\{S(g\times t)\ p(g)\ r(g\times t)\ F=1\}$)[a] and 500 bootstrapped samples of snag monitoring plots.

Species[b]	5-yr interval	r	SE	95% CI
ABCO	1997–2002	0.868	0.004	0.861–0.875
	2002–2007	0.882	0.002	0.879–0.885
	2007–2012	0.999	<0.001	0.999–1.000
PIPO	1997–2002	0.969	<0.001	0.968–0.970
	2002–2007	0.897	0.002	0.892–0.901
	2007–2012	0.895	0.003	0.890–0.900
POTR	1997–2002	0.928	0.002	0.924–0.932
	2002–2007	0.814	0.003	0.808–0.820
	2007–2012	0.894	0.003	0.889–0.899
PSME	1997–2002	0.896	0.002	0.892–0.900
	2002–2007	0.958	0.001	0.955–0.960
	2007–2012	0.850	0.005	0.840–0.859
QUGA	1997–2002	0.782	0.003	0.776–0.789
	2002–2007	0.609	0.006	0.597–0.621
	2007–2012	0.611	0.003	0.606–0.616

[a] Notation for base model: S = the probability that a snag remained standing during a sampling interval (i, $n = 3$ 5-yr intervals), g = species or species group ($n = 6$ species or groups), t = sampling occasion ($n = 4$ occasions), p = the probability that a snag was detected given that it remained standing during interval i, r = the probability that a snag was detected given that it fell during interval i, and F = fidelity, which we set to 1 because snags could not emigrate from the plot.

[b] Species acronyms: ABCO = white fir, PIPO = ponderosa pine, POTR = quaking aspen, PSME = Douglas-fir, and QUGA = Gambel oak.

agents in a spatially variable landscape. Our focus differed from most previous studies, many of which followed single-species cohorts of snags created by a single mortality agent in 1 or a few study areas. Despite this difference, many of our results support results from previous studies. For example, observed standing rates varied among snag species (Morrison and Raphael 1993, Landram et al. 2002, Russell et al. 2006, Angers et al. 2010, Parish et al. 2010) and were influenced by characteristics of both the snags themselves and the plots in which those snags were located (Morrison and Raphael 1993; Chambers and Mast 2005, 2014; Russell et al. 2006; Parish et al. 2010; but see Lee 1998; Parish et al. 2010).

Table 5. Parameter estimates (along with associated 95% CIs) for snag covariates from 1 of 2 competing models evaluating the effects of snag covariates on standing rates of snags in northern Arizona mixed-conifer and ponderosa pine forest, 1997–2012. Because the top 2 models were approximately equally likely, we used the model containing all covariates to generate parameter estimates. We derived all estimates from 500 bootstrapped samples of snag monitoring plots and computed importance values by summing model weights across all models containing a particular covariate.

Parameter[a]	Estimate	95% CI	Importance
Dbh	0.0347	0.0342–0.0352	1.000
Top condition	−0.4937	−0.5039 to −0.4834	0.999
Height	−0.0196	−0.0209 to −0.0183	0.730
Dbh/ht	0.1348	0.0882–0.1813	0.506

[a] Snag covariates evaluated included: Dbh = snag diameter at breast height (cm), Top condition = broken (0) versus intact (1), height = snag height (m), and Dbh/ht = snag diameter/height ratio.

Table 6. Parameter estimates (along with associated 95% CIs) for plot covariates from the top model evaluating the effects of plot covariates on standing rates of snags in northern Arizona mixed-conifer and ponderosa pine forest, 1997–2012. We derived all estimates from 500 bootstrapped samples of snag monitoring plots and computed importance values by summing model weights across all models containing a particular covariate.

Parameter[a]	Estimate	95% CI	Importance
Surface ratio	18.9078	18.3043–19.5113	0.994
Mean elevation (m)	0.0009	0.0009–0.0010	0.950
Mean slope (deg)	−0.0726	−0.0758 to −0.0694	0.941
Trees/ha	0.0004	0.0004–0.0004	0.757
Cosine aspect	0.0111	0.0007–0.0215	0.656
Mean topographic index	−0.0002	−0.0008–0.0005	0.580

[a] Plot covariates not obviously labeled included: cosine aspect (an index of relative northness of slope aspect, ranging from −1 at due south to 1 at due north), surface ratio (Jenness 2004), and mean topographic position index (an index of relative exposure calculated as the mean difference between elevation for each cell in a plot and the mean elevation of all cells within a 200-m neighborhood).

We also compared standing rates for major snag species in our study with estimated standing rates from existing studies, where possible. Because most studies estimated percentage of snags standing over fixed time intervals rather than standing rates, we used mean standing rates over our 3 sampling intervals to estimate the percentage of snags standing over a 10-year period for these comparisons. Our estimates were within the range previously reported for ponderosa pine and quaking aspen, at the low end of the reported range for Douglas-fir, and below the only reported estimate for white fir (Table 7). Comparative data were not available for Gambel oak, which had the highest estimated standing rate in our study (Table 2). We recommend that these comparisons be interpreted cautiously, however, because many of the comparative data used were from geographically distant study areas and/or other forest types, and percentages of snags standing frequently were visually estimated from curves showing standing rates by time and thus were approximate.

We could not compare detection rates with previous studies because no prior studies estimated this parameter. Detection rates were nearly 1 for all standing snags of all species in this study (Table 3) but were lower and more variable among snag species and time intervals for fallen snags (Table 4). Lower detection rates for fallen snags likely were due primarily to 2 factors: 1) many snags fell with the numbered tags under the trunk where they could not be observed; and 2) numbered tags fell out of rotting wood or were removed easily by animals from fallen snags as those snags deteriorated. Estimated detection rates for fallen snags generally were high; however, and including known fates greatly improves precision of estimates of standing rates relative to estimating those rates based solely on encounters with standing snags. We also were unable to compare precision of our estimates with previous studies, most of which did not estimate variability.

Among the snag covariates we evaluated, standing rates were most strongly associated with snag diameter and top condition, with standing rates greater for larger diameter snags than for

Table 7. Percentage of snags that remained standing in various studies by snag species, mortality agent, and time. We estimated percentages for many studies from figures or incomplete data, and presented them as approximate values.

Species[a]	Mortality agent	Time (yrs)	% standing	Source
ABCO	Various	10	~68[b]	Landram et al. (2002)
		10	50[c]	This study
PIPO	Bark beetles	10	35, 45[d]	Keen (1955)
		10	~40	Schmid et al. (1985)
		5	52	Hoffman et al. (2012)
		9	~10	Chambers and Mast (2014)
	Prescribed fire	10	22, 38[e]	Harrington (1996)
	Wildfire	10	~48	Dahms (1949)
		7	59	Chambers and Mast (2005)
		10	~30	Russell et al. (2006)
	Various	8	<50	Landram et al. (2002)
		10	4[c]	This study
POTR	Various	10	>75	Lee (1998)
		9	~50	Vanderwel et al. (2006)
		10	~75	Angers et al. (2010)
		10	<30	Hogg and Michaelian (2015)
		10	53[c]	This study
PSME	Wildfire	10	>80	Russell et al. (2006)
	Various	10	60–95[f]	Parish et al. (2010)
		10	62[c]	This study

[a] Species: ABCO = white fir, PIPO = ponderosa pine, PSME = Douglas-fir, POTR = quaking aspen.
[b] Calculated based on reported annual snag fall rate.
[c] Values based on mean rate estimated across 3 5-year sampling intervals.
[d] Values shown represent study sites on loam and pumice soils, respectively.
[e] Values shown represent study sites burned in spring and summer versus autumn, respectively.
[f] Range of values indicates differences among diameter classes.

smaller diameter snags and for snags with broken tops versus snags with intact tops (Table 5). Similar patterns were noted in many previous studies (Bull 1983, Morrison and Raphael 1993, Chambers and Mast 2005, Russell et al. 2006, Parish et al. 2010). Wind is an important agent of snag breakage and/or loss in the study area (Chambers and Mast 2005, 2014; Ganey and Vojta 2005). Larger diameter snags likely are more wind resistant than thinner snags, and the multiple branches present in snags with intact tops provide greater surface area for wind to act upon, increasing the likelihood of those snags falling or breaking. Quaking aspen may sometimes provide an exception to this pattern. Hogg and Michaelian (2015) noted that standing rates of quaking aspen in their study areas declined with stand age, which presumably was correlated with diameter. This decline was primarily due to greater infection of older aspen with decay fungi (*Phellinus tremulae*).

Site characteristics also influenced standing rates in this study, with standing rates most strongly associated with surface ratio, elevation, slope, and tree density. Some (Chambers and Mast 2005, Garber et al. 2005, Russell et al. 2006) but not all (Lee 1998, Parish et al. 2010) previous studies identified site characteristics as influencing standing rates, and studies that showed a significant site effect did not always agree on how site characteristics influenced standing rates. For example, standing rates in this study were positively related to tree density, and Chambers and Mast (2005) reported that snag longevity increased with density of surrounding snags. In contrast, Garber et al. (2005) and Chambers and Mast (2014) observed lower snag longevity in denser stands. These differences among studies suggest a need for further work evaluating the effect of site characteristics on snag standing rates.

Previous studies generally documented declines in snag standing rates with increasing snag age (defined as time since death), with snag age often the strongest predictor of snag longevity (Chambers and Mast 2005, 2014; Passovoy and Fulé 2006; Russell et al. 2006; Parish et al. 2010). In contrast, standing rates in this study declined for most species of snags following the first sampling interval (Table 2), despite the fact that snag numbers were increasing in all species because of drought-mediated tree mortality and recruitment of new snags in subsequent intervals (Ganey and Vojta 2011, 2014). Thus, standing rates declined after 2002 although snag populations became increasingly dominated by newly created snags, contrary to the generally observed pattern.

Much of this decline appeared to be attributable to declines in standing rates of distinct cohorts of snags first sampled in 1997, 2002, and 2007, respectively. For example, 5-year standing rates averaged across species declined across all 3 cohorts, 10-year rates declined over the 2 cohorts sampled over a 10-year period, and the proportion of snags from the 1997 cohort that remained standing after 15 years was approximately equal to the proportion of the 2002 cohort that remained standing after 10 years (Table 8). Thus, snags first sampled in 1997, which included snags of all ages, stood longer than newly recruited snags first sampled in either 2002 or 2007. Many snags from these later cohorts likely died as a result of drought-mediated insect activity (Ganey and Vojta 2011), including bark beetles (primarily *Ips* spp.) in ponderosa pine (Negron et al. 2009, U.S. Forest Service 2009), and Douglas-fir beetle (*Dendroctonus pseudotsugae*) and fir engraver (*Scolytus ventralis*) in Douglas-fir and white fir (U.S. Forest Service 2009). Previous studies suggested that snags created by bark beetles fall more quickly than snags

Table 8. Percentages of snags (and associated 95% CIs) that remained standing over 5-year intervals for 3 cohorts of snags in northern Arizona mixed-conifer and ponderosa pine forest. Cohorts represented snags first sampled in 1997 (age in 1997 >0 yrs, $n = 2{,}324$ snags) and snags first sampled in 2002 or 2007 (age at first sampling >0 and ≤5 yrs, $n = 1{,}062$ and 2,756 snags, respectively).

	Time interval after snags were first sampled		
Snag cohort	**5 years**	**10 years**	**15 years**
1997	73.8 (72.0–75.6)	57.1 (55.1–59.1)	45.2 (43.2–47.2)
2002	71.8 (69.1–74.5)	46.4 (43.4–49.4)[a]	
2007	68.1 (66.4–69.8)[b]		

[a] Significantly fewer snags remained standing from the 2002 cohort than from the 1997 cohort at 10 years post-sampling (*Z* test for differences between proportions; Zar 2010).

[b] Significantly fewer snags from the 2007 cohort remained standing at 5 years post-sampling than for either other cohort (*Z* tests for differences between proportions; Zar 2010).

created by other mortality agents (Table 7). Thus, the increase over time in proportions of snags killed by bark beetles and other insects may explain much of the declining trend observed in standing rates. If so, and if increasingly arid climates in this area (Seager 2007) result in greater mortality from bark beetles and other forest insects, snag standing rates may be reduced relative to past eras, with the result that snags will provide more ephemeral resources than they did historically.

Regardless of the underlying causes for differences in standing rates among time intervals, those differences complicate modeling snag dynamics. Snag creation is known to be episodic, often because of disturbance events such as bark beetle infestations, wildfire, or wind events. Incorporating temporal variability in snag standing rates will add to the inherent complexity caused by variability in snag creation rates. For example, differences in time-specific standing rates from this study were large enough to result in different trajectories for existing snag populations in at least some snag species (Fig. 2).

Our results suggest that precisely modeling snag dynamics is a difficult task, requiring knowledge of temporal variability in standing rates, diameter distributions of the snags themselves, rates of height loss and top breakage in snags, data on topographic characteristics and stand structure in the area of interest, and perhaps information on causes of tree mortality. Managers typically do not have access to this level of information at present, suggesting that current modeling efforts may have to rely on coarser data and aim for lower precision. At minimum, this would require knowledge of snag creation rates and species-specific standing rates. Snag creation rates could be obtained from growth and yield models, and it may be feasible to use mean species-specific standing rates computed across time intervals in models. This clearly will reduce accuracy and precision; however, and ideally such rates should be estimated over long time frames to better incorporate temporal variability.

MANAGEMENT IMPLICATIONS

This study provides improved estimates of standing rates for multiple species of snags in southwestern mixed-conifer and ponderosa pine forests, based on a large and spatially extensive sample and a rigorous analysis. Our results suggest that these rates vary across time, among species, and with structural characteristics of the snags themselves as well as topography and stand characteristics. All of these sources of variability complicate the modeling of snag dynamics. Consequently, although this information is useful in a heuristic sense to managers concerned with snag populations, modeling snag dynamics remains difficult. Our estimates of mean species-specific standing rates could be incorporated into growth and yield models currently in use, however. This would improve modeling of snag dynamics, but models would remain imprecise because of the multiple sources of variability included in those mean estimates. Prediction could be improved by coupling such models with spatial data on topography, stand structure (e.g., stand density, species composition, and diameter distribution) and mortality factors, as well as by incorporating data on species-specific rates of height loss and top breakage.

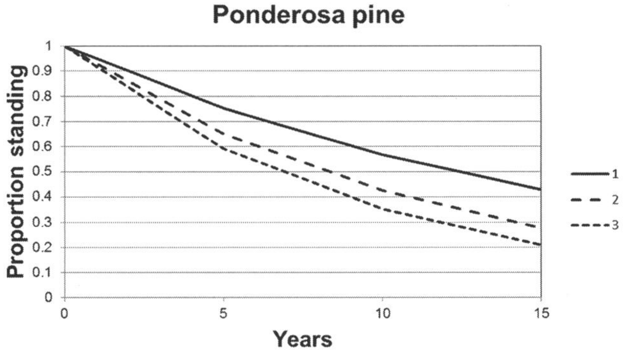

Figure 2. Example showing hypothetical proportion of existing ponderosa pine snags in northern Arizona mixed-conifer and ponderosa pine forest that would remain standing across time by snag species based on different standing rates estimated during 3 5-year sampling intervals, assuming that those rates remained constant over time. Sampling intervals represented were 1 = 1997–2002, 2 = 2002–2007, and 3 = 2007–2012.

ACKNOWLEDGMENTS

G. Martinez, M. Stoddard, B. Strohmeyer, R. White, and especially A. and J. Iniguez assisted in establishing plots, and L. Doll, D. and N. Ganey, and C. Vojta helped with plot sampling. J. Ellenwood, B. Higgins, K. Menasco, C. Nelson, and G. Sheppard (Kaibab National Forest) and C. Beyerhelm, A. Brown, H. Green, T. Randall-Parker, C. Taylor, and M. Whitney (Coconino National Forest) assisted with initial plot selection. Comments by E. Merrrill, K. Vierling, and 3 anonymous reviewers improved this paper.

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Associate Editor: Kerri Vierling.

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