

Engaging Birds in Vegetation Restoration after Elwha Dam Removal

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ABSTRACT

Elwha River restoration is humanity's largest dam removal project to date. Reservoir revegetation will be most effective if it is rapid and spatially extensive to stabilize residual sediment, impede invasive plants, and restore other riparian functions. I evaluated how birds could enhance Elwha restoration by dispersing native seeds to reservoir sediment deposits. I evaluated three factors affecting avian seed dispersal: (1) number of native woody plants with bird-dispersed seeds; (2) identity and abundance of seed-dispersing birds; and (3) distribution of avian seed deposition. (1) I sorted Elwha early seral woody plants into species dispersed by birds vs. other mechanisms. (2) I recorded avian flights from seed sources, and I estimated disperser abundances from Elwha avian inventory data. (3) I assessed patterns of avian seed dispersal by evaluating eight causal hypotheses, using fresh scat as a seed surrogate. I recorded scat density and habitat characteristics along random transects in Lake Mills reservoir delta and Geyser Valley floodplain. I evaluated models for each hypothesis using Akaike's Information Criterion. Birds disperse seeds of most (59%) native woody plants likely to establish in the reservoirs. American robins (*Turdus migratorius*) accounted for most flights between seed sources and sediment deposits, with mean abundance >1 bird/ha. Most avian scats occurred on logs, and scat density increased with log volume. These results suggest birds can disperse native seeds throughout Elwha restoration sites. Revegetation programs associated with dam removal can leverage birds as restoration agents by retaining or placing large woody debris to recruit fruit-bearing plants.

Keywords: American robin, avian seed dispersal, large woody debris, Olympic National Park, scat distribution

Growing interest in dam removal as a means to achieve restoration objectives (Hart et al. 2002) has revealed a need for information about post-removal restoration methods and results. The ongoing removal of two large dams on the Elwha River, Washington, USA, represents an important opportunity to address this knowledge gap (Duda et al. 2008). Dam removals on the Elwha commenced in September 2011, and have exposed terraces of bare sediment that will remain in the reservoir beds. Additionally, the large volumes of sediment that accumulated in the two reservoirs will create new deposits as they are transported down river (Shafroth et al. 2002, Bromley 2008, Chenoweth et al. 2011). Riparian plant community establishment

in sediment deposits is expected to perform important restoration functions, including stabilizing sediment (Bednarek 2001) and slowing or preventing spread of introduced plants (Chenoweth et al. 2011).

Three goals drive the Elwha revegetation and restoration program (Chenoweth et al. 2011):

1. Minimize invasive exotic species cover and spread.
2. Restore ecosystem processes, particularly stabilize terrestrial landforms.
3. Establish native forests within the range of variation in composition, structure, and diversity observed in unmanaged valleys in the lower Elwha watershed.

Achieving these goals requires rapid implementation across the dewatered reservoir beds. Delays or incomplete coverage would provide opportunities for invasive plants to establish or

expose unstable sediment deposits to erosion. Gaps in revegetation treatments are inevitable, however, due to budget and access constraints. The reservoir revegetation plan identifies unfunded needs that exceed the project budget by a factor of two (Chenoweth et al. 2011). Access to some reservoir areas will be limited by steep and unstable slopes. Seeds of grasses and forbs will be distributed in large numbers using aircraft, but planting most woody species will require ground access and expensive labor (Chenoweth et al. 2011).

Recruiting animals as seed dispersal agents could resolve this dilemma if animal vectors fulfill the following conditions: (1) animals disperse seeds of the appropriate plants; (2) seed dispersers are sufficiently abundant; (3) animals deposit seeds in locations suitable for plant establishment throughout the restoration zone. This study focused on seed dispersal by

birds due to their importance reported in other systems (Robinson and Handel 1993, Debussche and Isenmann 1994, Duncan 2006, Zahawi and Augspurger 2006, Rost et al. 2009) and because birds include the most abundant and mobile frugivores in the area.

Seed dispersal by animals, or zoochory, is a complex process emerging from multiple steps driven by many interacting factors (Wang and Smith 2002, Schupp et al. 2010, Herrera et al. 2011, Uriarte et al. 2011). For example, seed dispersers may compete for food and other resources, affecting disperser abundances and distributions. Seed source distributions affect frugivore foraging behavior and movement patterns, which determine seed deposition sites. Seed disperser diets and movement behavior vary in space and time, complicating spatial distributions of dispersed seeds. Landscape structure affects each of the above factors. Finally, all four of these factors vary in space and time, making seed dispersal patterns difficult to understand from first principles.

I studied bird-mediated seed dispersal using a phenomenological approach with three objectives: (1) identify potential Elwha seed dispersers by determining which birds fly from seed sources to reservoir substrates and by measuring their abundances; (2) determine the spatial distribution of bird-dispersed seeds in reservoir and floodplain substrates by evaluating several *a priori* hypotheses for seed deposition locations; (3) identify opportunities to leverage bird activity in support of the vegetation restoration program.

Methods

Study System

This study focused on seed dispersal in sediment deposits in the larger Elwha reservoir, where forest restoration is likely to be most challenging (Chenoweth et al. 2011). The Elwha River is located west of Port Angeles,

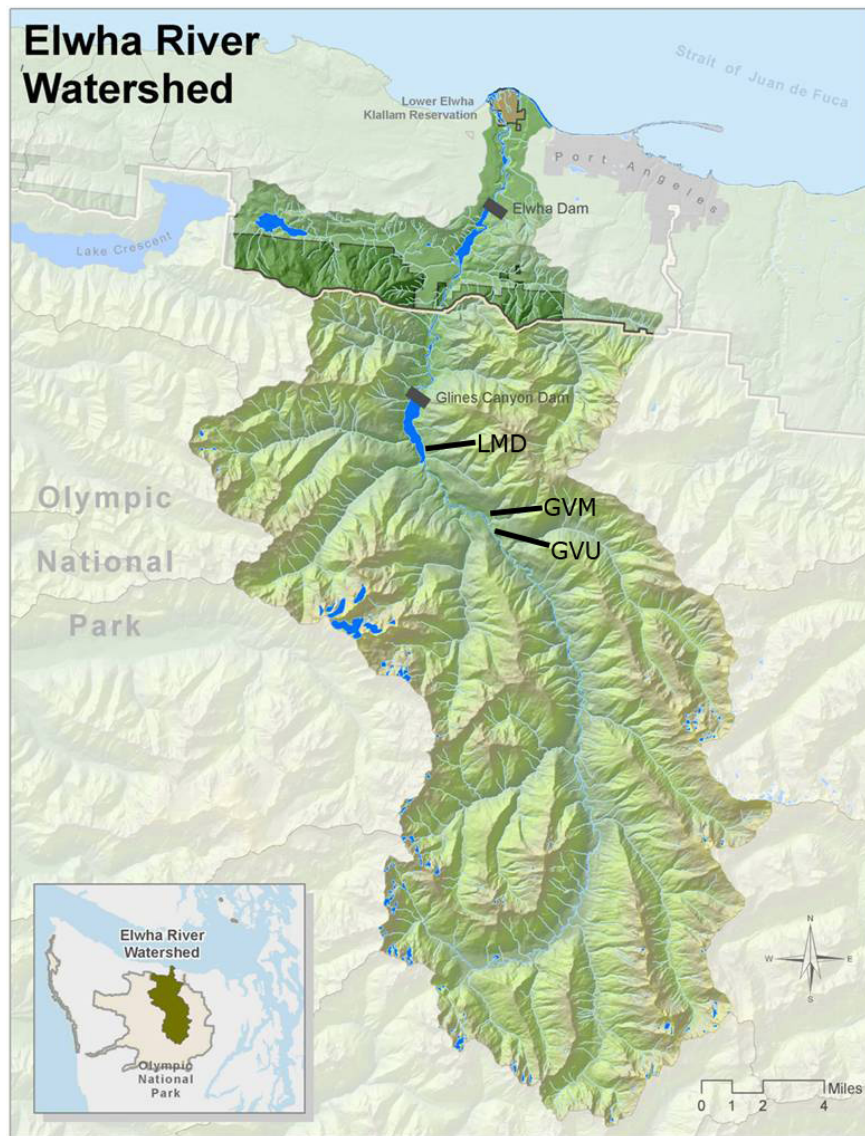


Figure 1. Map of the Elwha River basin, dams, and study sites in northwestern Washington, USA. Dam removals began in September 2011. Removal of Elwha Dam was completed in March 2012, and removal of Glines Canyon Dam is expected to conclude in summer 2013. The three study areas are located upstream of both dam sites. Lake Mills Delta (LMD) is at the southern (upstream) end of Lake Mills reservoir. Geyser Valley middle (GVM) and upper (GVU) sites are near the southeastern (upstream) end of Geyser Valley, the nearest and largest valley reach upstream of the reservoir. Base map provided by Olympic National Park.

WA, USA (Figure 1). The river flows north over 70 kilometers from headwaters in the Olympic Mountains to the Strait of Juan de Fuca. The Elwha watershed comprises 19% of Olympic National Park. Watershed vegetation is dominated by Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with a mosaic of other habitats in the riparian corridor, including areas dominated by Western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), bigleaf maple

(*Acer macrophyllum*), black cottonwood (*Populus balsamifera*), willow (*Salix* spp.), and mixed conifer and hardwood stands (National Park Service 1996).

The two dams were located in the lower third of the river, 7.9 km and 17.7 km above the mouth (Figure 1). The dams flooded roughly 315 ha of riparian and terrestrial habitat early in the 20th century: Elwha Dam impounded Lake Aldwell (138 ha) in 1913 and Glines Canyon Dam

impounded Lake Mills (177 ha) in 1927. Nearly 18 million cubic meters of sediment accumulated in the reservoirs (Bountry 2012). Approximately half the sediment is expected to flush downriver and the remainder is expected to remain in the reservoir beds (Bromley 2008, Chenoweth et al. 2011).

Plant establishment in the reservoir beds is likely to be slow due to several unfavorable conditions (Michel et al. 2011). Sediment nutrient concentrations and moisture availability will be low, although phosphorous may not limit plant establishment (Cavaliere and Homann 2012). Soil water derived from precipitation will evaporate rapidly in open areas exposed to sun and wind. Snags, residual living plants, and soil microbes will be rare or absent. Large woody debris is abundant, but concentrated at the forest edge, where drifting logs accumulated on the reservoirs. Much area will be distant from established forest, other seed sources and organic debris. Reservoir sediments lack a seed bank, because few seeds survive prolonged inundation. Plant establishment will be most difficult low in the reservoirs, where fine sediments will be deepest and most extensive (Chenoweth et al. 2011).

Sampling Areas

I selected three study areas in the Elwha riparian zone representing a temporal gradient in early successional riparian habitat (Figure 1). The earliest sere was in the Lake Mills delta (LMD). Two sites in the Geyser Valley (GV) floodplain represented early (GVU) and intermediate (GVM) stages in plant colonization of riparian sediments (Figure 1). LMD consists of exposed sediment deposits where the free-flowing Elwha discharged into the larger reservoir. Sediment deposition expanded LMD for decades, creating substrates colonized by vegetation dominated by willows (*Salix spp.*) and red alder (*Alnus rubra*). Delta vegetation followed a gradient in stand age and height, from well-developed alder

forests on older deposits upriver, to newly exposed islands of bare sediment extending into the reservoir. In late summer 2010, most vegetation and large woody debris (LWD) were removed from LMD to facilitate sediment transport during reservoir drawdown and dam removal. Trees were clearcut and sediment deposits were bulldozed, leaving a level expanse of bare sediment. A large pile of logs was placed in the active river channel and a new channel was dredged through the middle of LMD. The resulting terrestrial substrate was relatively flat, free of vegetation, and cleared of most LWD. High flows during winter 2010–2011 storms dismantled most of the constructed LWD pile, and deposited some of those logs on the expanse of bare sediment. These conditions are in flux during dam removal as plants colonize bare sediment and high flows induce channel migration, transport sediment, and redistribute LWD. Current and prior LMD conditions can be viewed on the Elwha River Restoration Project webcam: www.videomonitoring.com/construction/olympic/js.htm.

Geyser Valley is the largest unconstrained reach upriver of the dams. It lies 2.2 kilometers southeast of Lake Mills, between two narrow gorges. Data collection focused on the upriver (southeastern) end of the valley, where recent flooding and river channel migration left sediment deposits with relatively sparse vegetation. LWD accumulations are extensive there, but woody vegetation is limited to alder saplings and willow. Geyser Valley is considered a model for reservoir restoration, and this portion of the valley represents conditions early in the plant establishment process. The “upper” Geyser Valley (GVU) site was inundated in December 2007 by high flows discharging from the Grand Canyon of the Elwha and a large tributary stream. It contains several large logs and sparse alder saplings. Riparian habitat development is most advanced in the “middle” Geyser Valley (GVM) site, where alders and willows have

grown for two decades (Acker et al. 2008).

I collected data for this work during rain-free portions of May and June 2009–2011, prior to initiation of dam removal and reservoir drawdown. I recorded avian flight behavior and seed deposition data on the same days at each sampling area. Coarse sediments and cobbles dominated the ground surface in all three sites. Seed dispersal into fine sediments also is important, but they remained submerged during the sampling period.

Avian Flight Patterns

I recorded avian flight behavior during late mornings to early afternoons. I observed avian flights in each study area from locations with unobstructed views. I recorded flights of all birds flying from established forest to open or sparsely vegetated substrates within a 50 meter wide view corridor. Observation time totaled 402 minutes. For each bird observed, I recorded species, flight distance, flight origin, and the object or substrate where flight terminated.

Avian Seed Deposition

I used avian scat deposition as a surrogate for avian seed dispersal. Avian scat provides an imperfect surrogate; scat density is not equivalent to seed density, because some scats may contain multiple seeds, and others none. I assessed avian seed dispersal by measuring patterns in freshly deposited bird scat. Scats were detected easily because their white uric acid contrasted with most substrates. Because rates of scat degradation may differ among substrates, I restricted sampling to freshly deposited scat in two ways. First, I sampled within 1–3 days of the last rainfall. Second, I excluded old uric acid stains and recorded only fresh scat containing raised fecal matter.

I sampled avian scat deposition using transects oriented perpendicular to the river, extending from established forest to the active river channel. I selected transect locations

at random distances along the length of each study area. Transects were 1 meter wide, and subdivided into 1 m² measurement units. I sampled a total of 717 square meter units in 7 transects in the three study areas: 170 meters (2 transects) in GVU, 328 meters (3 transects) in GVM, and 219 meters (2 transects) in LMD. In each square meter, I recorded number of fresh scats, substrate type and variables corresponding to scat deposition hypotheses: distance to nearest forest, distance to the river, woody plant density, woody plant height, LWD volume, and LWD height. Although scat may have been deposited by birds flying from any direction, I restricted “distance to forest” measurements to the nearest forest because all observed flights originated from nearby forests.

Model Development—*a priori* Models/Hypotheses

I developed eight *a priori* hypotheses for avian scat deposition, based on seed dispersal literature from other regions, with modifications for local conditions (Table 1). The hypotheses consist of combinations of three habitat variables known to affect avian scat deposition: distance to established forest, density of young trees, and LWD volume (references in Table 1). I also considered two additional variables, tree height (Debussche and Isenmann 1994) and LWD height (Zanini and Ganade 2005, Rost et al. 2009, 2010), but excluded them from further analysis because they correlated strongly with tree density and LWD volume, respectively. I considered linear, concave, and convex effects of each variable on scat deposition using linear, logarithmic, and exponential transformations. To limit the number of models in the candidate set (Burnham and Anderson 2002), I selected the transformation that maximized R^2 in the univariate model for each variable, and applied that transformation in all models containing that variable (Table 2).

Table 1. Hypotheses for avian scat deposition patterns in Elwha sediment deposits and floodplain substrates. References cited for univariate hypotheses provide supporting evidence from other study systems. The model for each hypothesis follows its verbal statement: y_j is scat density in the j^{th} square meter x'_{ij} plot; x_{ij} is the value of the i^{th} habitat variable in the j^{th} square meter plot, and x'_{ij} is the value of x_{ij} after transformation given in Table 2. x_1 is distance to forest; x_2 is tree density; and x_3 is LWD volume, α is scat density at zero value for all variables in the model, β_i is the coefficient for variable x_i , and ϵ_j is a random deviate for the j^{th} square meter plot.

Hypothesis	
1	Scat deposition is random (Null hypothesis) $y_j = \epsilon_j$
2	Scat deposition declines with distance from forest References: Robinson & Handel 1993, 2000; Debussche & Isenmann 1994; Uriarte et al. 2010 $y_j = \alpha + \beta_1 x'_{1j} + \epsilon_j$
3	Scat deposition increases with tree density References: Robinson & Handel 1993; Zahawi & Augspurger 2006; Corbin & Holl 2012 $y_j = \alpha + \beta_2 x'_{2j} + \epsilon_j$
4	Scat deposition increases with LWD volume References: Rost et al. 2009, 2010 $y_j = \alpha + \beta_3 x'_{3j} + \epsilon_j$
5	Scat deposition declines with distance from forest, increases with tree density $y_j = \alpha + \beta_1 x'_{1j} + \beta_2 x'_{2j} + \epsilon_j$
6	Scat deposition declines with distance from forest, increases with LWD volume $y_j = \alpha + \beta_1 x'_{1j} + \beta_3 x'_{3j} + \epsilon_j$
7	Scat deposition increases with tree density, increases with LWD volume $y_j = \alpha + \beta_2 x'_{2j} + \beta_3 x'_{3j} + \epsilon_j$
8	Scat deposition declines with distance from forest, increases with tree density, and increases with LWD volume $y_j = \alpha + \beta_1 x'_{1j} + \beta_2 x'_{2j} + \beta_3 x'_{3j} + \epsilon_j$

Table 2. Transformations applied to habitat variables used to explain avian scat distribution in each study area. Transformations were selected by maximizing R^2 in univariate models for hypotheses 2–4 (Table 1). Transformations used the following functional forms, in which x and x' represent original and transformed values respectively.

Linear: $x'_i = x_i$; **Logarithmic:** $x'_i = \log(x_i + 1)$; **Exponential:** $x'_i = \exp(x_i)$.

Variable	Study Area		
	LMD	GVU	GVM
Distance to forest	exponential	linear	linear
Tree density	linear	linear	logarithmic
LWD volume	logarithmic	linear	exponential

Table 3. Native woody plants common in early seral stages of the Elwha riparian zone. Species dispersed by birds are in bold font. Adapted from Table 11 in Chenoweth et al. 2011.

Botanical Name	Vernacular Name	Life Form
<i>Acer macrophyllum</i>	Big-leaf maple	Tree
<i>Alnus rubra</i>	Red alder	Tree
<i>Crataegus douglasii</i>	Black hawthorn	Tree
<i>Malus fusca</i>	Western crabapple	Tree
<i>Populus basamifera</i>	Black cottonwood	Tree
<i>Prunus emarginata</i>	Bitter cherry	Tree
<i>Pseudotsuga menziesii</i>	Douglas fir	Tree
<i>Abies grandis</i>	Grand fir	Tree
<i>Cornus nuttallii</i>	Pacific dogwood	Tree
<i>Alnus viridis</i>	Sitka alder	Shrub
<i>Amelanchier alnifolia</i>	Western serviceberry	Shrub
<i>Ceanothus sanguineus</i>	Redstem ceanothus	Shrub
<i>Cornus sericea</i>	Red-stemmed dogwood	Shrub
<i>Holodiscus discolor</i>	Ocean spray	Shrub
<i>Lonicera involucrata</i>	Black twinberry	Shrub
<i>Mahonia aquifolium</i>	Tall Oregon grape	Shrub
<i>Oemleria cerasiformis</i>	Indian plum	Shrub
<i>Oplopanax horridus</i>	Devil's club	Shrub
<i>Philadelphus lewisii</i>	Mock orange	Shrub
<i>Physocarpus capitatus</i>	Ninebark	Shrub
<i>Ribes bracteosum</i>	Stink currant	Shrub
<i>Ribes divaricatum</i>	Spreading gooseberry	Shrub
<i>Ribes lacustre</i>	Prickly currant	Shrub
<i>Ribes lobbii</i>	Gummy gooseberry	Shrub
<i>Ribes sanguineum</i>	Red-flowering currant	Shrub
<i>Rosa nutkana</i>	Nootka rose	Shrub
<i>Rubus leucodermis</i>	Black-cap raspberry	Shrub
<i>Rubus parviflorus</i>	Thimbleberry	Shrub
<i>Rubus spectabilis</i>	Salmonberry	Shrub
<i>Rubus ursinus</i>	Trailing blackberry	Shrub
<i>Salix lucida</i>	Pacific willow	Shrub
<i>Salix scouleriana</i>	Scouler willow	Shrub
<i>Salix sitchensis</i>	Sitka willow	Shrub
<i>Sambucus cerulea</i>	Blue elderberry	Shrub
<i>Sambucus racemosa</i>	Red elderberry	Shrub
<i>Spirea douglasii</i>	Douglas' spirea	Shrub
<i>Symphoricarpos albus</i>	Common snowberry	Shrub
<i>Acer circinatum</i>	Vine maple	Shrub
<i>Acer glabrum</i>	Rocky Mountain maple	Shrub

Table 4. Avian scat density and distribution relative to habitat characteristics in Elwha sediment deposits and floodplain sites. Values for scat density and distance to forest are means (standard deviations). Fraction with trees is the fraction of scats observed within sample quadrats (1m²) containing tree saplings.

Location	Scat Density (#/m ²)	Distance to forest (m)	Fraction with trees	Fraction on LWD
LMD	0.85 (3.22)	83.0 (37.9)	0.09	0.99
GVU	0.28 (0.79)	51.5 (15.4)	0.19	0.56
GVM	0.35 (2.11)	70.6 (33.6)	0.86	0.50

Model Selection

I fit models for each hypothesis to transect data using R (version 2.0.1 for Linux; R Foundation for Statistical Computing 2012). I fit models for all hypotheses using least squares linear regression. I conducted model selection for each study area individually, based on evidence that scat deposition patterns differed in the three sites. I evaluated relative empirical support for each model using information-theoretic methods (Burnham and Anderson 2002). I calculated values of Akaike's Information Criterion (AIC), rescaled scores (DAIC), and Akaike weights (w) for the models.

Results

Plants with Bird-dispersed Seeds

Of the 39 woody species common to early seral stages (Chenoweth et al. 2011), 23 (59%) produce fruits dispersed by birds (Table 3). In contrast, birds disperse only 5 of 31 (16%) invasive introduced species of concern in the Elwha (Chenoweth et al. 2011): English ivy (*Hedera helix*), English holly (*Ilex aquifolium*), laurel cherry (*Prunus laurocerasus*), Himalayan blackberry (*Rubus discolor*), evergreen blackberry (*Rubus laciniatus*). In addition, these five invasives are found at low density, are distant from reservoir sites (Joshua Chenoweth, University of Washington, pers. comm.), or do not germinate in Elwha sediments (Michel et al. 2011).

Avian Flight Patterns

I observed three species flying from established forests to or over sediment deposits in Lake Mills the Geyser Valley. One species, American robin (*Turdus migratorius*), accounted for 81% of those flights. I observed four additional species flying in the opposite direction, from sediment deposits to established forest, for a total of seven species flying in either direction. American robins accounted for 75% of all flights between forest and sediment deposits.

Avian Scat Distribution

Avian scat deposition occurred throughout transects sampled in all study areas, up to 140 meters from established forest. At LMD, the 140 m transect length spanned nearly half the 290 m distance between forests on opposite banks of the reservoir. Avian scat density was greater in LMD than in Gvu and GVM (Table 4). Scat distributions were highly clumped, as large standard deviations in density suggest, with high densities on logs and no scat in most other locations.

Scat distribution differed among sites, corresponding to habitat differences and the gradient in time since disturbance. Most scats occurred on LWD (Table 4), particularly at LMD where 99% of scats were on LWD and nearly all logs had fresh scat. Scat was most often associated with young trees at GVM (Table 4), where tree colonization of floodplain sediment was more advanced.

Scat Distribution and Model Selection

Scat model selection differed among study sites, consistent with differences in habitat structure and time since disturbance (Tables 5–7). AIC scores for models that differentiated among sites were lower (better) by an order of magnitude than AIC scores for models fit to the global data set. Model selection results provided overwhelming support for the importance of LWD in avian scat deposition at both LMD and Gvu sites (Tables 5–6; Figure 2). The data provide strong empirical support (e.g., $\Delta AIC_i \leq 2$) exclusively for models containing LWD at LMD and Gvu. All other models for both sites received negligibly low support (Tables 5–6). Although bivariate models had lowest AIC scores, those models improved fit only marginally over the univariate LWD model, as measured by R^2 values. In addition, estimated coefficient values for LWD terms (b_3) differed by at most 5%, regardless of other variables in the models (Table 8).

Table 5. Scat distribution model selection results for LMD, using Akaike's information criterion (AIC). $n = 219$. K : number of model parameters, including residual variance; ΔAIC : rescaled AIC score, $\Delta AIC_i = AIC_i - \min(AIC)$; w : Akaike weight.

Model	K	AIC	ΔAIC	w	R^2
Null (random distribution)	2	1136.59	637.21	$<10^{-140}$	0
exp(Distance to forest)	3	1137.25	637.87	$<10^{-140}$	0.006
Tree density	3	1121.58	622.20	$<10^{-135}$	0.075
log(LWD volume)	3	512.83	13.46	0.00087	0.943
exp(Distance to forest), Tree density	4	1122.03	622.65	$<10^{-135}$	0.081
log(LWD volume), exp(Distance to forest)	4	499.37	0	0.73	0.946
log(LWD volume), Tree density	4	514.81	15.44	0.00032	0.943
log(LWD volume), exp(Distance to forest), Tree density	5	501.37	2.00	0.27	0.946

Table 6. Scat distribution model selection results for Gvu, using AIC. $n = 170$. K : number of model parameters, including residual variance; ΔAIC : rescaled AIC score, $\Delta AIC_i = AIC_i - \min(AIC)$; w : Akaike weight.

Model	K	AIC	ΔAIC	w	R^2
Null (random distribution)	2	406.85	109.91	$<10^{-24}$	0
Distance to forest	3	405.37	108.52	10^{-24}	0.020
Tree density	3	388.76	91.81	$<10^{-20}$	0.111
LWD volume	3	297.29	0.34	0.33	0.481
Distance to forest, Tree density	4	389.01	92.07	$<10^{-20}$	0.121
LWD volume, Distance to forest	4	299.06	2.11	0.13	0.482
LWD volume, Tree density	4	296.94	0	0.39	0.488
LWD volume, Distance to forest, Tree density	5	298.82	1.88	0.15	0.489

Table 7. Scat distribution model selection results for GVM, using AIC. $n = 328$. K : number of model parameters, including residual variance; ΔAIC : rescaled AIC score, $\Delta AIC_i = AIC_i - \min(AIC)$; w : Akaike weight.

Model	K	AIC	ΔAIC	w	R^2
Null (random distribution)	2	1423.39	616.47	$<10^{-134}$	0
Distance to forest	3	1423.30	616.37	$<10^{-134}$	0.006
log(Tree density)	3	905.01	98.09	$<10^{-21}$	0.795
exp(LWD volume)	3	1180.87	373.95	$<10^{-81}$	0.525
Distance to forest, log(Tree density)	4	906.06	99.14	$<10^{-21}$	0.796
exp(LWD volume), Dist. forest	4	1180.66	373.74	$<10^{-81}$	0.529
exp(LWD volume), log(Tree density)	4	806.92	0	0.57	0.849
exp(LWD vol.), Dist. forest, log(Tree density)	5	807.46	0.53	0.43	0.850

For GVM, model selection revealed strong support for both tree density and LWD volume, and little support for distance to forest (Table 7). GVM scat distribution was affected most strongly by tree density and secondarily by LWD volume, as comparisons of AIC scores and R^2 values between univariate and multivariate models show. Table 8 provides further evidence for both tree density and LWD

volume at GVM: coefficient values for either variable (b_1 , b_3) change substantially by including the other variable.

Discussion

Birds may play an important role in Elwha forest restoration because they fulfill all three conditions for effective seed dispersers: frugivorous diet,

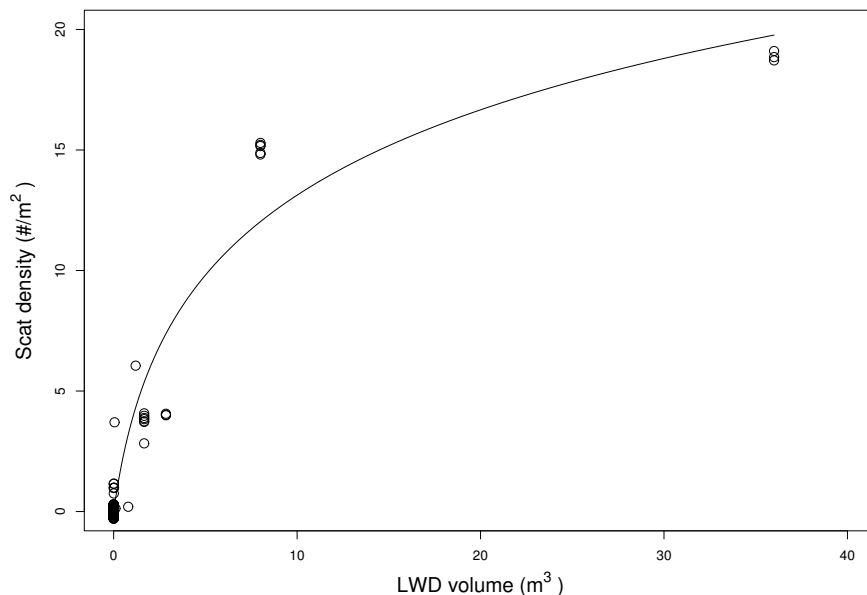


Figure 2. Scat distribution data (o) and the model (—) with greatest empirical support for LMD, $y_i = \alpha + \beta \log(x_i) + \varepsilon_i$. Point locations ($n = 219$) include a small amount of random jitter to distinguish overlapping points. Model parameter estimates are in Table 8.

sufficient abundance, and activity throughout restoration sites. First, birds disperse seeds of most (59%) native woody plants common to early seres in the Elwha. Second, American robin, the primary avian seed disperser, occurs at moderate to high density throughout seed source habitats surrounding the Lake Mills reservoir. Third, birds deposited scat across LMD, suggesting they could disperse seeds throughout the reservoir beds.

Only a few of 42 bird species detected in an avian inventory of the Elwha riparian zone (Gelarden 2008) are potentially important seed dispersers, according to dietary, abundance, and activity criteria. Of those species, only American robin met all 3 criteria strongly. First, fruit is a large portion of the American robin diet (Martin et al. 1951, White and Stiles 1990), suggesting robins could disperse seeds of many plants in Table 3. Second, American robin abundance at the forest-reservoir edge is moderate to high. Robin density averaged 0.94 birds/ha (SE = 0.20 birds/ha) at 40 Lake Mills reservoir sampling sites in the Elwha avian inventory (Gelarden 2008). Total American robin density likely was double this value, because the survey method overlooks most females

and non-territorial males (Ralph et al. 1995). Similar American robin densities along the reservoir edge are forecast by a habitat model fit to American robin inventory data (Figure 3; Gelarden 2008, Gelarden and McLaughlin 2013, *this issue*). Third, American robin behavior is conducive to seed dispersal to reservoir sediments. Robins nest in forests and often forage in open areas. Consequently, robins fly frequently between seed source habitats and sediment deposits, as reported here. These dietary, abundance, and behavioral characteristics suggest a strong potential for American robin to disperse seeds in Elwha restoration sites. Reports from other continents also found the majority of seeds were dispersed by 1–2 bird species (Zahawi and Augspurger 2006), particularly thrushes (Rost et al. 2009, Salvade et al. 2011, Uriarte et al. 2011).

Scat distribution data suggest that avian seed dispersal in Elwha reservoir beds will be strongly associated with logs. Nearly all scat found at LMD was on LWD, and LWD volume accounted for 94% of the variation in scat density. Scat density at LMD was affected by other habitat variables little if at all (univariate model $R^2 < 0.1$). Some models containing

other variables performed well, but only when they also included LWD volume.

These results can be explained by LMD habitat structure and American robin behavior. Few trees currently exist in the reservoir bed because most of it was flooded for 84 years and the remainder was clearcut prior to dam removal. Hence, most perch sites in the reservoir that might attract forest birds were on LWD. The importance of LWD perches to Elwha seed dispersal is comparable to other perch structures in many systems (Robinson and Handel 1993, Debussche and Isenmann 1994, Zanini and Ganade 2005, Rost et al. 2009, 2010, Corbin and Holl 2012). Although I often observed American robins foraging on bare sediments, almost all birds flying from forest to open sediment landed on elevated perches first. Most scats in LMD were on LWD probably because frugivorous birds often excrete feces as they land on or fly from perches (Kohri et al. 2011). Distance from forest had little effect on scat distribution likely because LWD perch sites were limiting; LWD locations rather than distance determined bird flights and scat deposition.

The catalytic role of LWD in avian seed dispersal may decline as forest restoration proceeds. The contrasting importance of LWD in LMD and GVU vs. GVM sites may reflect a successional gradient in habitat structure, particularly increasing abundance of perch sites. As trees establish in sediment deposits, they may attract more seed dispersing birds, leading to a shifting balance in the importance of LWD vs. trees in seed deposition. More study of this process is needed. Regardless, the critical role of LWD in reservoir restoration is clear; LWD attracts birds early in revegetation when seed dispersal is most important.

These results have several implications for Elwha forest restoration and other dam removal projects. First, birds can act as restoration agents because they disperse local seeds into Elwha restoration sites, similar to

Table 8. Parameter estimates and standard errors (SE) for scat distribution models for LMD, GVU, and GVM study areas. Values for a and b_i are regression estimates for parameters α and β_i in the linear model, $y_j = \alpha + \beta_1 x'_{1j} + \beta_2 x'_{2j} + \beta_3 x'_{3j} + \varepsilon_j$, where y_j is scat density in the j^{th} square meter plot; x'_{ij} is the transformed value of the i^{th} habitat variable in the j^{th} square meter plot; x_1 is distance to forest; x_2 is tree density; and x_3 is LWD volume. Table 2 lists variable transformations. $p(b_i)$ is the p -value for the hypothesis $\beta_i = 0$.

Model	Site	a (SE)	b_1 (SE)	$p(b_1)$	b_2 (SE)	$p(b_2)$	b_3 (SE)	$p(b_3)$	R^2
Distance to forest	LMD	0.83(0.22)	$10^{-60}(10^{-60})$	0.25					0.006
	GVU	-0.05(0.19)	0.007(0.004)	0.06					0.020
	GVM	0.06(0.23)	0.005(0.004)	0.15					0.006
Tree density	LMD	0.77(0.21)			2.31(0.55)	$<10^{-4}$			0.075
	GVU	0.24(0.06)			1.56(0.34)	$<10^{-6}$			0.111
	GVM	0.18(0.05)			16.0(0.45)	$<10^{-15}$			0.795
LWD volume	LMD	-0.004(0.05)					5.48(0.09)	$<10^{-15}$	0.943
	GVU	0.15(0.05)					2.15(0.17)	$<10^{-15}$	0.481
	GVM	-3.80(0.23)					3.99(0.21)	$<10^{-15}$	0.525
Distance to forest, Tree density	LMD	0.74(0.21)	$10^{-60}(10^{-60})$	0.22	2.31(0.55)	$<10^{-4}$			0.081
	GVU	0.02(0.18)	0.005(0.004)	0.19	1.50(0.34)	$<10^{-4}$			0.121
	GVM	0.09(0.11)	0.002(0.002)	0.33	15.96(0.45)	$<10^{-15}$			0.796
Distance to forest, LWD volume	LMD	0.009(0.05)	$-10^{-60}(10^{-61})$	10^{-4}			5.53(0.09)	$<10^{-15}$	0.946
	GVU	0.091(0.14)	0.001(0.003)	0.63			2.14(0.18)	$<10^{-15}$	0.482
	GVM	-4.00(0.27)	0.004(0.003)	0.14			3.98(0.21)	$<10^{-15}$	0.529
Tree density, LWD volume	LMD	-0.004(0.05)			0.02(0.14)	0.88	5.47(0.10)	$<10^{-15}$	0.943
	GVU	0.15(0.05)			0.42(0.28)	0.13	2.05(0.18)	$<10^{-15}$	0.488
	GVM	-1.46(0.16)			12.82(0.49)	$<10^{-15}$	1.61(1.5)	$<10^{-15}$	0.849
Distance to forest, Tree density, LWD volume	LMD	0.009(0.05)	$-10^{-60}(10^{-61})$	10^{-4}	-0.008(0.1)	0.95	5.53(0.09)	$<10^{-15}$	0.946
	GVU	0.102(0.13)	0.001(0.003)	0.73	0.42(0.28)	0.14	2.04(0.19)	$<10^{-15}$	0.489
	GVM	-1.55(0.18)	0.002(0.001)	0.23	12.79(0.49)	$<10^{-15}$	1.61(0.15)	$<10^{-15}$	0.850

other regions (Robinson and Handel 1993, 2000; Holl et al. 2000; Zahawi and Augspurger 2006). Second, birds tend to deposit seeds in locations suitable for plant establishment. Scat left on LWD often falls or washes down to germination sites with favorable microclimates and protection from ungulate herbivores (Chenoweth et al. 2011), resulting in higher plant survival rates. Third, restoration programs can leverage limited project resources by supporting avian seed dispersal. I found abundant avian scat below elevated perch structures and almost no scat elsewhere. For Elwha restoration, this implies retaining LWD throughout the reservoir beds or redistributing it from accumulations at reservoir perimeters. Large woody debris attracts birds to sediment deposits lacking other perch sites. LWD is particularly important early in the restoration process before woody plants become established and when seed dispersal is needed most

to impede establishment of invasive plants. If LWD is removed or collected in a small number of locations, bird-dispersed seeds will be concentrated at the few remaining LWD structures, limiting the spatial extent of sediment stabilization and weed suppression. Zoochory does not occur as “seed rain,” but rather as directed dispersal at LWD. Logs and the birds they attract should be treated as important components in reservoir vegetation restoration.

Uncertainties and Limitations

Several caveats pertain to results presented here. First, I did not identify the sources of bird scats or determine whether birds leaving scats flew from seed sources. Species restricted to open habitats would not disperse seeds of forest plants, but most birds observed on LMD sediment deposits nested in forest habitats. Second, data collection did not coincide with fruiting seasons of most plants. If avian flight patterns

vary markedly between seasons, due to courtship behavior, territorial defense, or foraging for young, seed dispersal patterns may differ from scat deposition reported here. Substantial seasonal differences are unlikely because American robins tend to fly between forested and open areas throughout the year. Third, I did not determine seed content in avian scat. A more complete assessment of avian seed dispersal will require identifying seeds contained in bird scats using methods beyond the scope of this study (Robinson and Handel 2000, Michel et al. 2011). Fourth, sampling in LMD was limited to exposed sediments. Scat deposition in the lower reservoir may differ from results reported here if those sediments, which were submerged for decades, lack food resources to attract American robins and other forest birds. Finally, seed dispersal does not ensure plant establishment. Plant survival in reservoir sediments is uncertain (Shafroth et

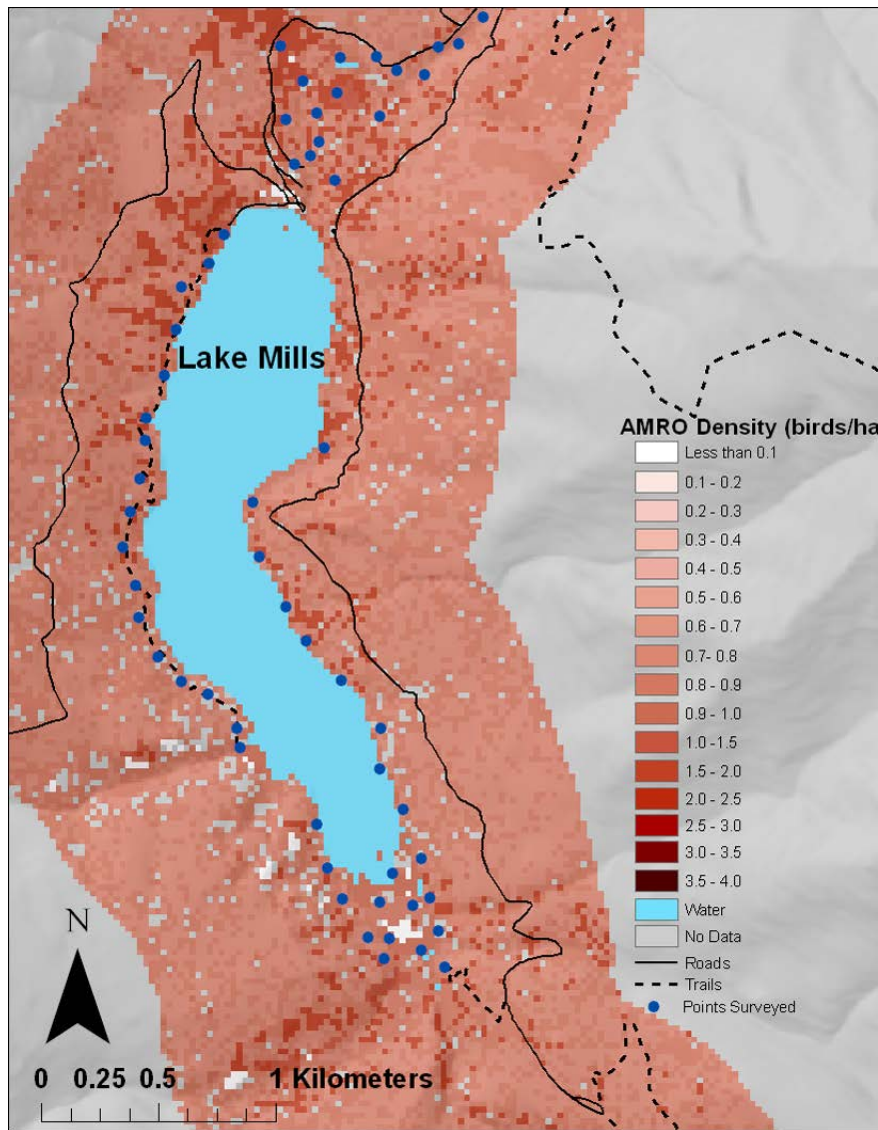


Figure 3. American robin (*Turdus migratorius*) habitat-specific species density map for the Lake Mills reservoir reach, Elwha River. Density estimates were derived from numbers of birds detected during variable circular plot sampling. The map was generated by merging habitat-specific American robin density estimates with a habitat data layer for Olympic National Park (Gelarden 2008). The upper limit of the Lake Mills delta is located at the trail terminus at the bottom center of the map.

al. 2002) and likely to be low due to few nutrients, growing season drought (Chenoweth et al. 2011, Michel et al. 2011), and herbivory (Beschta and Ripple 2008).

Research Needs

Additional research is needed to address these uncertainties and to determine seed dispersal patterns in dynamic reservoir conditions. Seed composition and viability in avian scat should be measured to determine which seeds are being dispersed effectively. Replicating this work at

more sites over time would help clarify whether or how seed dispersal varies across successional gradients. More research is needed on processes leading to plant establishment after seed dispersal (Wang and Smith 2002, Schupp et al. 2010). In particular, herbivores strongly suppress plant growth in other parts of Olympic National Park (Beschta and Ripple 2008), and may affect forest restoration in the Elwha. Young cottonwoods and other plants favored by ungulate browsers are rare in the Elwha riparian zone. In October 2012, the revegetation program

employed a helicopter to redistribute LWD to the Lake Mills reservoir bed to create plant establishment sites protected from herbivores and harsh growing conditions. Effectiveness of this approach needs study, including success of active plantings and bird-dispersed plants.

Recommendations

1. Restoration programs should consider birds as potential restoration agents at all steps from planning to implementation. Optimally, active restoration would support seed dispersers to leverage project resources. At minimum, project activities should not impede or displace seed dispersers.
2. Leave LWD and other perch sites in place. These structures attract avian seed dispersers and function as “nucleation” sites (Robinson and Handel 2000, Corbin and Holl 2012).
3. Consider distributing LWD across restoration sites, particularly where increased plant establishment is desired. Distributing LWD will increase the number of sites receiving directed seed dispersal. This strategy may be especially opportune in many dam removal projects, because LWD accumulates at the edges of reservoirs where its restoration value is limited (Chenoweth et al. 2011).
4. In restoration programs with resources or foresight to include monitoring and experimental treatments (e.g., Woodward et al. 2008, Chenoweth et al. 2011), zoochory should be included as a factor in study design.

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