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Note

Movement and Survival of an Amphibian in Relation to Sediment and Culvert Design

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ABSTRACT Habitat disturbance from stream culverts can affect aquatic organisms by increasing sedimentation or forming barriers to movement. Land managers are replacing many culverts to reduce these negative effects, primarily for stream fishes. However, these management actions are likely to have broad implications for many organisms, including amphibians in small streams. To assess the effects of culverts on movement and survival of the Idaho giant salamander (*Dicamptodon aterrimus*), we used capture-mark-recapture surveys and measured sediment in streams with 2 culvert types (i.e., unimproved culverts, improved culverts) and in streams without culverts (i.e., reference streams). We predicted culverts would increase stream sediment levels, limit movement, and reduce survival of Idaho giant salamanders. We also determined the effect of sediment levels on survival of salamanders because although sediment is often associated with distribution and abundance of stream amphibians, links with vital rates remain unclear. To estimate survival, we used a spatial Cormack–Jolly–Seber (CJS) model that explicitly incorporated information on movement, eliminating bias in apparent survival estimated from traditional (i.e., non-spatial) CJS models caused by permanent emigration beyond the study area. To demonstrate the importance of using spatial data in studies of wildlife populations, we compared estimates from the spatial CJS to estimates of apparent survival from a traditional CJS model. Although high levels of sediment reduced survival of salamanders, culvert type was unrelated to sediment levels or true survival of salamanders. Across all streams, we documented only 15 movement events between study reaches. All movement events were downstream, and they occurred disproportionately in 1 stream, which precluded measuring the effect of culvert design on movement. Although movement was low overall, the variance among streams was high enough to bias estimates of apparent survival compared to true survival. Our results suggest that where sedimentation occurs from roads and culverts, survival of the Idaho giant salamander could be reduced. Though culverts clearly do not completely block downstream movements of Idaho giant salamanders, the degree to which culvert improvements affect movements under roads in comparison to unimproved culverts remains unclear, especially for rare, but potentially important, upstream movements. © 2016 The Wildlife Society.

KEY WORDS barriers, culverts, *Dicamptodon*, movement, sediment, spatial Cormack–Jolly–Seber, stream amphibians.

Habitat loss and disturbance remain the leading causes of wildlife population declines, whether alone or in combination with other stressors (Foley et al. 2005, Lindenmayer and Fischer 2013). Small streams are especially susceptible to habitat disturbances, and because of their linear nature, effects of disturbances often extend far from their origin (Resh et al. 1988, Jones et al. 2000). Culverts, pipes that carry streams beneath roadways, are a common habitat disturbance in small streams in human-altered landscapes (Park et al. 2008, Anderson et al. 2014). Culverts can affect aquatic organisms by increasing sedimentation or forming barriers to movement (Eaglin and Hubert 1993, Warren and Pardew 1998, Foster and Keller 2011). Sedimentation occurs when culverts fail or when high water flows scour road beds (Forman and Alexander 1998, Madej 2001). By forming impassable reaches due to perched outlets and amplified water velocities, culverts can also impede dispersal or movement of animals (Warren and Pardew 1998, Gibson et al. 2005, Foster and Keller 2011).

To reduce the negative effects of road-stream crossings on habitat and to facilitate animal movement, land managers in the United States are replacing many traditional culverts with improved culverts (Clarkin et al. 2005, Poplar-Jeffers et al. 2009). Improved culverts generally include natural stream bottom throughout their length to reduce flow rates and

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allow upstream and downstream movement (Schaefer et al. 2003, Benton et al. 2008), alignment of culvert gradients with the stream to remove vertical barriers to upstream movement (Warren and Pardew 1998), and construction of culverts wider than the wetted width of streams to reduce scour and sedimentation (MacPherson et al. 2012). Traditional, or unimproved, culverts generally lack natural substrate throughout the length of the culvert, are often narrower than the wetted width of streams during base flow, and generally have perched outlets that are above the grade of the streams (Anderson et al. 2014). Culvert replacements are typically prioritized in fish-bearing streams but likely have broad implications for stream communities.

The Idaho giant salamander (*Dicamptodon aterrimus*; Cope 1889) is 1 of 4 members of the family Dicamptodontidae endemic to the northwest United States and southwest Canada (Stebbins 2003). This salamander inhabits small, cold streams in northeastern Idaho and extreme western Montana. It is a species of concern in both states because of its small geographic range and fragmented distribution. The Idaho giant salamander is facultatively paedomorphic, meaning individuals may become reproductively mature in the larval form or metamorphose into terrestrial adults (Nussbaum 1976). Hence, it is capable of dispersing within streams or on land, although molecular evidence indicates that populations are connected primarily by dispersal along stream corridors (Mullen et al. 2010).

The Idaho giant salamander may be particularly susceptible to the effects of culverts on local habitat conditions or movement. One of the few studies of this species reported that occurrence was negatively correlated with road density, which is often associated with increased rates of sedimentation (Eaglin and Hubert 1993, Wellman et al. 2000, Sepulveda and Lowe 2009). Filling of interstitial spaces among substrates by sediment reduces habitat quality and can affect stream organisms directly, or indirectly via trophic effects (Wood and Armitage 1997, Henley et al. 2000; but see Keitzer and Goforth 2012). However, despite the often strong, negative associations between abundance of stream amphibians and sediment, the mechanisms that influence this relationship have not been well established (Corn and Bury 1989, Welsh and Ollivier 1998, Gillespie 2002).

In addition to increasing sediment, culverts may limit movements of Idaho giant salamanders and other stream organisms (Warren and Pardew 1998, Foster and Keller 2011, Anderson et al. 2014). Because populations of Idaho giant salamanders are connected along the stream corridor (Mullen et al. 2010), barriers that block movements along streams could reduce population connectivity, especially to headwater reaches above culverts. Barriers to migrants can produce population isolation, potentially causing population declines through genetic or demographic mechanisms (Madsen et al. 1996, Lowe 2003, Wofford et al. 2005).

We hypothesized that habitat disturbance from culverts would increase sediment levels in streams and reduce movement and survival of the Idaho giant salamander. We predicted that unimproved culverts, and to a lesser extent improved culverts, would reduce survival and movement of salamanders compared with reference streams lacking culverts. We then compared our survival estimates from spatial Cormack–Jolly–Seber (CJS) models (Schaub and Royle 2014) to apparent survival from non-spatial CJS models. Finally, we provide the first robust estimates of true annual survival for a stream amphibian.

STUDY AREA

We sampled streams in the Lochsa, St. Joe, and St. Regis river basins in Idaho and Montana (Fig. 1). We considered the 3 basins to be within 2 geographic regions: the northern and southern regions. The northern region included streams in the Saint Joe ($n = 3$) and Saint Regis basins ($n = 1$) because these basins share a watershed boundary but not a local watershed. The Lochsa is spatially separated from the Saint Joe and Saint Regis basins, so we considered streams within this basin ($n = 5$) to be within the southern region. Elevations of the study streams ranged from approximately 750 m to 1,300 m. The climate of the region is characterized by wet cold winters and hot dry summers. Both regions are dominated by mixed-conifer forests on mountainous terrain, have a long history of logging activity and road building, and

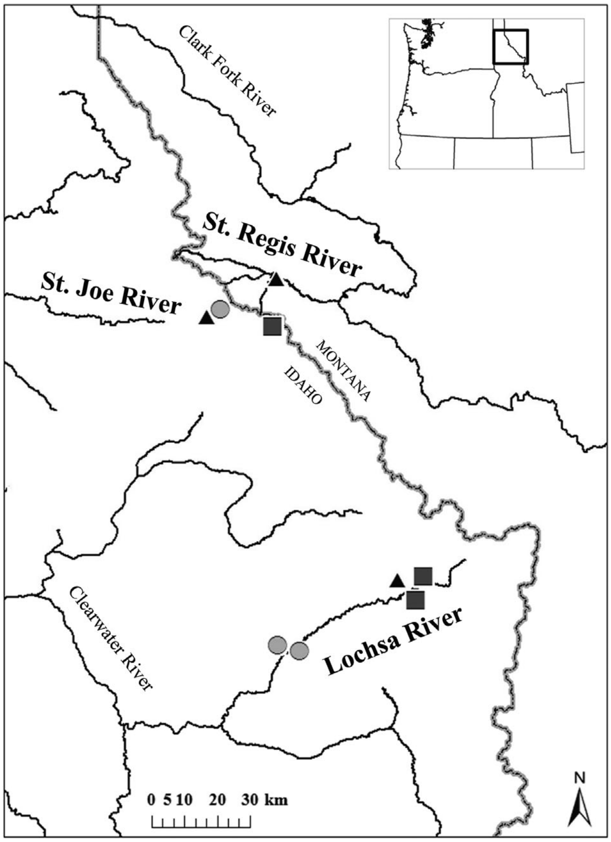

Figure 1. Locations of 9 streams in Idaho and Montana, USA, where we conducted capture-mark-recapture surveys for Idaho giant salamanders during 2012–2013. The streams are separated into 3 categories: 3 streams bisected by unimproved culverts (triangles), 3 streams bisected by improved culverts (squares), and 3 streams not bisected by either type of culvert (circles).

are a mix of private and United States Forest Service (USFS) ownership. All of our study streams were on USFS land.

METHODS

Field Methods

To assess the effects of culverts on the movement and survival of the Idaho giant salamander, we conducted capture-mark-recapture (CMR) surveys in 9 streams representing 2 culvert types and reference streams. Three streams were bisected by unimproved culverts, 3 streams were bisected by improved culverts, and 3 streams not bisected by either type of culvert served as a reference group. In each stream bisected by a culvert, we surveyed 80-m reaches directly above and below the culvert (Fig. 2). In the reference streams, we established the downstream and upstream survey reaches separated by a 20-m dummy reach; 20 m was the mean length of the culverts. The lower ends of each downstream reach in reference streams were set ≥30 m above the closest downstream confluence. We use the term intervening reach to refer to the stream section between the upstream and downstream study reaches for all culvert types (Fig. 2).

Idaho giant salamanders are patchily distributed and often occur in low numbers, which can limit inference from CMR studies (Pollock et al. 1990). Therefore, to ensure we could generate reasonably precise estimates of survival and movement, we sought study streams with relatively high abundances of the species. To find these study locations, we surveyed 150 streams within the range of the Idaho giant salamander in 2011, noting relative abundance of salamanders and attributes of culverts. From these 150 streams, we selected 3 streams with relatively high abundances of salamanders from each of the 2 culvert types and 3 from streams with no culverts for intensive CMR surveys during 2012–2013 (Honeycutt 2014). Because our streams were not selected randomly, inference from this study is limited to the 9 streams we sampled.

We quantified several measures of local-scale habitat that we hypothesized could affect Idaho giant salamanders, or could confound culvert type comparisons. We measured percent fine sediment because it has often been negatively associated with abundance of stream salamanders (Waters 1995, Lowe et al. 2004). We measured wetted width, percent of pool habitat, and stream gradient because they might affect sediment accumulation. Other than stream gradient, we measured habitat variables in 1-m-long transects that spanned the width of the stream. We randomly selected 1 transect location within each 10 m of channel length in each study stream, resulting in 16 habitat transects/stream. We estimated percent fine sediment by visually estimating the percent of area within the transect that was covered with particles <2 mm in diameter (Lane 1947). We measured wetted width at base flows at the end of August. We visually estimated the percent of pool habitat in each transect. We measured stream gradient along 10-m stream sections at each 1-m habitat transect.

We conducted CMR surveys during 3 survey periods in 2012 (20 Jun–09 Sep) and 2013 (30 Jun–04 Sep) in all streams except Float Creek, where in 2012 we conducted surveys during only 2 periods. Intervals between survey periods within years ranged from 14 to 27 days. During the first survey period at each stream, we surveyed 50 m upstream and downstream of intervening reaches. To recapture individuals that may have emigrated from these initial 50-m reaches, we extended the terminuses of downstream and upstream reaches by 10 m in each of the second, third, and fourth survey periods. We maintained reach lengths at 80 m for the fifth and sixth survey periods because of logistical constraints associated with larger survey areas. We marked all new salamanders encountered in these extended sections. We surveyed streams with a 3-observer crew and a backpack electrofishing unit (Smith-Root LR-24, Vancouver, WA, USA), which is an effective method for detecting aquatic Idaho giant salamanders (Cossel et al. 2012).

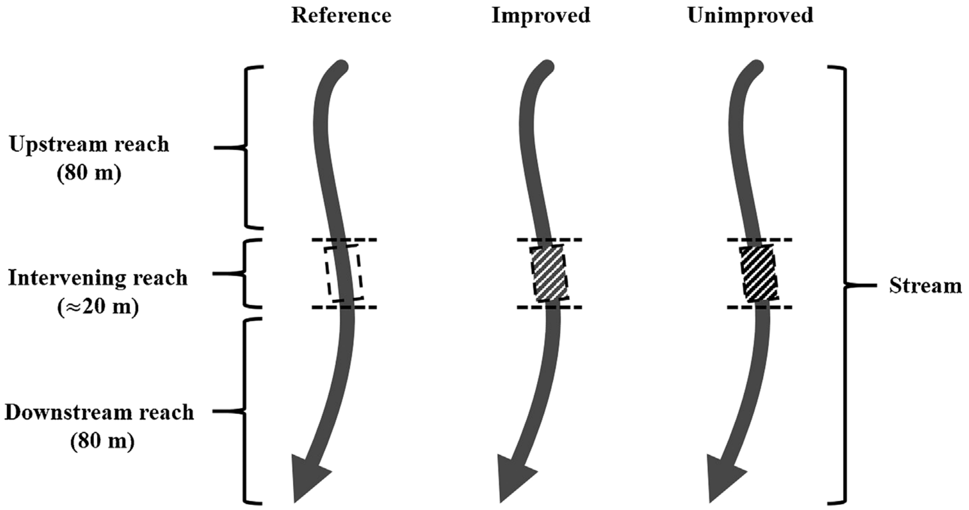

Figure 2. Layout of study reaches in streams with 2 culvert types and reference streams without culverts, Idaho and Montana, USA. We use the term intervening reach to refer to the stream section between the upstream and downstream study reaches for all culvert types. We define a reach as a continuous segment of stream that is wholly above or wholly below the intervening reach.

Upon capture, we placed salamanders in individual plastic bags with water and recorded each individual's location along the study reach (±1 m). During processing, individuals remained in their bags and were kept cool by placing the bags in 20-L buckets with stream water. We anesthetized new captures with an approximately 150 mg/L solution of tricaine methanesulfonate or 0.025 mL/L solution of benzocaine. We assigned unique marks to individuals with visible implantable elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA, USA) and measured snout-vent length (SVL). Finally, 2 observers examined the VIE marks of recaptures using ultra-violet light. Once anesthetized individuals regained full mobility, all individuals were released at their point of capture. We captured larvae, paedomorphs, and terrestrial Idaho giant salamanders during our surveys, but only included larvae and paedomorphs in our analyses because our sampling method (electrofishing) was strongly biased against terrestrial animals. Animal handling for this project was carried out under the following permits: The University of Montana Institutional Animal Care and Use Committee protocol 023-12; Idaho Fish and Game Permit 110613; and Montana Fish, Wildlife, and Parks Permits 24-2012 and 16-2013.

Statistical Analysis

Sediment.—We treated sediment as a proportion using beta-distributed generalized linear mixed-effects models in the R package glmmADMB (Eskelson et al. 2011, Fournier et al. 2012, R Core Team 2014). Because calculations under the beta distribution do not accept values of 0 or 1, we adjusted these values by adding or subtracting 0.01, respectively. We used maximum likelihood estimates and Akaike's Information Criterion corrected for small sample sizes (AIC_c) to select the most parsimonious structures from candidate model sets (Burnham and Anderson 2002). Each of the following models contained a random intercept for stream.

We accounted for differences in geomorphology and habitat among streams that potentially influenced sediment prior to assessing the specific influence of culverts on sediment. Specifically, streams with improved culverts were lower in watersheds than those with unimproved culverts and, hence, were also wider, less steep, and had less pool habitat than streams with unimproved culverts (Table S1, available online in Supporting Information). These differences reflect prioritization of culvert improvements to stream reaches lower in watersheds to optimize restoration of habitat and passage for fishes, particularly salmonids. In our models, we accounted for these differences by building a set of nuisance structures using the following variables: region, log-transformed wetted width, log-transformed stream gradient, and log-transformed percent pool. Our model set included structures with these variables as single terms and as additive combinations. We incorporated the highest ranking nuisance structure into each model in a second model set to test the specific effects of culverts on sediment levels. This second model set included terms for reach position (upstream vs. downstream reach) and culvert type (unimproved vs. improved vs. reference). Specifically, this second set included the following models: the null model containing only the nuisance structure, a model containing a reach position × culvert type interaction along with the nuisance structure, and a model containing culvert type with the nuisance structure. From this second model set, we selected the most parsimonious model to explain the effects of culverts on sediment.

Survival and movement.—Initial analysis of our CMR data indicated streams containing salamanders with relatively high mean movement rates had relatively low apparent survival, suggesting that differences in apparent survival associated with culvert type could have resulted from different emigration rates among streams. To investigate this hypothesis, we compared estimates of apparent and true survival using state-space models implemented in JAGS with the R package R2jags (Plummer 2003, Kéry and Schaub 2012, Su and Yajim 2015). We used the CJS framework to model apparent annual survival (Lebreton et al. 1992), which we refer to as the traditional CJS model, and a recently developed spatial CJS model to estimate true annual survival (Schaub and Royle 2014). We used these models to test the effects of culvert type (unimproved vs. improved vs. reference) and sediment on the survival of salamanders. From the spatial CJS, we also generated a mean survival estimate across all 9 study streams. Though our survey design was originally built on a robust design framework with multiple secondary surveys within each primary survey session (Pollock 1982), we collapsed all secondary sessions within each primary session to fit within the framework of simpler CJS models. The programming script we used to execute these models is provided (available online in Supporting Information).

The spatial CJS differs from the traditional CJS model by incorporating information on individual movements and locations in relation to the dimensions of study streams, which allows for estimation of movement distributions concurrently with capture probability and survival (Schaub and Royle 2014). In turn, the addition of location information to the CJS model allows for determination of probabilities of permanent emigration. The Schaub and Royle (2014) spatial CJS model consists of 2 state processes and an observation process. The 2 state processes represent unknown but true qualities of 1) whether an individual is alive or dead during a survey and 2) the location of an individual in respect to the boundaries of the study area during a survey. The observation process describes if an individual was detected during a survey and where the individual was detected within the study area. Including these 3 processes in the spatial CJS model allows for estimation of permanent emigration out of the study area and survival, whereas in the traditional CJS these parameters are confounded.

We made several assumptions in the spatial and traditional CJS models. We assumed birth, death, emigration, and immigration could occur between, but not within, survey periods. We assumed survival and recapture probability of an individual came from a random Bernoulli process, no spatial variation in survival within streams, and that we identified the individuals and their locations without error (Lebreton et al. 1992, Schaub and Royle 2014). When an individual was captured >1 time during a survey period, we used the average location of the individual. We also assumed no individual, age class, or temporal heterogeneity in survival probabilities and that salamanders could have been captured anywhere within the banks of the study reaches (Schaub and Royle 2014). We accounted for variation in time intervals between capture periods among streams by weighting the average of the interval lengths between time periods from all streams by the cumulative number of individuals released from each stream prior to the interval. Importantly, the spatial CJS model makes no assumption about movement direction.

We assumed paedomorphs and larvae would not leave the water; therefore, we used a 1-dimensional version of the spatial CJS model. This assumption may not hold in all cases because some larvae can transform and leave the stream; however, rates of transformation for this species are presumed to be low and molecular data suggest dispersal by all stages occurs primarily along streams (Mullen et al. 2010). Because we suspected movement distributions of individuals varied among streams, we allowed a separate distribution for each stream. We assumed variation in movement within any stream could be described by a t-distribution with degrees of freedom estimated from a uniform distribution ranging from 2 to 1,000, which allowed for flexibility of the t-distribution shape (Schaub and Royle 2014). To account for increasing lengths of study reaches between survey periods, we extended the spatial CJS model of Schaub and Royle (2014) by accounting for the lengths of study reaches at each survey period.

Prior to assessing the effects of culvert type (unimproved vs. improved vs. reference) and sediment on survival, we assessed the structure of recapture probability within Program MARK by ranking competing structures using AIC$_c$ (Lebreton et al. 1992, White and Burnham 1999, Burnham and Anderson 2002). We included the following terms in model selection: salamander SVL, electrofishing effort, survey period, stream, sediment, and an interaction of SVL × sediment. We found recapture probability was best described by an additive structure including time as a random variable, salamander SVL, and sediment (Sagar et al. 2007, Honeycutt 2014). Specifically, our model structure of recapture probability described a system where smaller salamanders and individuals in reaches with higher sediment were more likely to be recaptured, and where recapture probability varied as a random process among sampling sessions but not among streams.

We used uninformative priors for all model parameters in the traditional and spatial CJS models. We ran 5 Markov chains for each model, each with 20,000 iterations including a burn-in period of 5,000 iterations, and thinned chains by excluding every other iteration. We confirmed sufficient iterations in Markov chains with the Gelman–Rubin test, and assumed chain convergence was reached when scale reduction factors for all parameters were <1.1 (Gelman and Rubin 1992).

Despite replication within each culvert type, rare in intensive CMR studies, we did not have large enough sample sizes to include stream as a random variable for estimating mean apparent or true survival for each culvert type. Consequently, we estimated mean survival for each culvert type by pooling data across streams for each culvert type. This form of data-pooling is typical for CMR studies across multiple study sites or groups, resulting in variances that are negatively biased (Schwarz 2002). However, to estimate mean true survival across the entire region, we did include stream as a random variable and did not pool data across streams. Including stream as a random variable allowed us to model a single posterior distribution of mean survival from the 9 streams, and, therefore, our region-wide estimate is free from data-pooling and bias in the variance.

Our models were nested in the following structure: $s(\text{random stream effect} + \text{sediment}) \times p(\text{random time} + \text{SVL} + \text{sediment}) \times m(\text{stream})$, where s is true survival, p is recapture probability, and m is movement variance. When m is removed from the model, s is replaced with ϕ, which is apparent survival. To test the effect of culvert type, we replaced the random stream effect with a fixed effect of culvert type. Our best estimates of true and apparent survival are derived from models lacking an effect of sediment on survival. However, we also report survival estimates from models with sediment included, which assume equal sediment among culvert types, to demonstrate how accounting for the effects of sediment level influences the perceived effect of culvert type. We used mean levels of sediment for each reach.

RESULTS

Mean sediment was greatest in reference streams, followed by streams with unimproved culverts and streams with improved culverts. However, after accounting for the nuisance effects of region and pool cover, we found no evidence culvert type affected sediment levels ($\Delta\text{AIC}_c = 6.3$ between nuisance and culvert type models). As expected, stream width, gradient, and percent pool cover varied among culvert types, which reflected bias in installation of improved culverts in larger, salmonid-bearing streams (Table S1).

We captured and marked 790 larval and paedomorphic Idaho giant salamanders across the 9 study streams. After accounting for movement with the spatial CJS, estimates of survival for streams with no culverts and improved culverts changed little from the estimates of apparent survival; however, the survival estimate for streams with unimproved culvert was 12% higher than apparent survival for that culvert type (Table 1, Fig. 3A and C). Mean apparent survival from the traditional CJS model was highest in streams with improved culverts, followed by streams with unimproved culverts and streams with no culverts (Table 1, Fig. 3A). Across individual streams, mean true survival ranged from 0.393 (95% CI: 0.216–0.554) to 0.508 (95% CI: 0.339–0.799; Table 2). Mean true annual survival across the study area was 0.455 (95% CI: 0.322–0.642), before accounting for the effects of sediment.

Table 1. Mean estimates and 95% credible intervals for apparent and true survival from capture-mark-recapture surveys for Idaho giant salamanders during 2012–2013 in 9 streams of Idaho and Montana, USA. Three streams were bisected by unimproved culverts, 3 streams were bisected by improved culverts, and 3 streams not bisected by either type of culvert were used as a reference group (no culvert). The estimates are shown before accounting for the effect of sediment. We estimated apparent survival from a traditional Cormack–Jolly–Seber (CJS) model and true survival from a spatial CJS model.

	Apparent survival		True survival	
Stream type	$\bar{x}$	**95% CI**	$\bar{x}$	**95% CI**
All streams	0.448	0.314–0.636	0.455	0.322–0.642
Unimproved	0.428	0.296–0.586	0.480	0.330–0.658
Improved	0.506	0.312–0.736	0.503	0.302–0.766
Reference	0.407	0.272–0.565	0.394	0.266–0.543

Increasing amounts of sediment reduced true survival (Global model, coeff. = −0.389, 95% CI: −1.152 to 0.074). The effect of sediment level on true survival was most evident in reference streams, the streams with the highest sediment level. After accounting for the influence of sediment in this group of streams, estimated true survival was similar across the 2 culvert types and reference streams, suggesting culverts themselves had no effect on the true survival of Idaho giant salamanders (Fig. 3D).

One of the primary goals of this project was to test for variation in the frequency of movements through culverts, but these events were rare. Across all 9 study streams, we detected only 15 individuals that moved between reaches within streams. In all cases the individuals moved from upstream to downstream reaches. Eleven of these movements occurred in Bird 1, a stream with an unimproved culvert; another occurred in a different stream with an unimproved culvert. The other 3 movement events occurred in 2 different streams with improved culverts and 1 reference stream. These movements occurred both within and between sampling years, and were not associated with a single pulse such as a rain event. Post-hoc analyses of our data indicated that movement was not correlated with naïve density or stream gradient. We incidentally detected 2 salamanders inside of improved culverts during our field studies. Estimated mean movement distances among streams, including those movements between reaches, varied from 3.1 m to 22.8 m, with the highest in Bird 1 (Table 2).

DISCUSSION

Our results showed increased sedimentation negatively affected survival of Idaho giant salamanders. We found no evidence, however, that culverts affected sediment levels or movement and survival of the salamanders. Our results also illustrate how incorporating information on movements of individuals can affect survival estimates.

Though our results do not show sediment was affected by culverts, salamander survival declined with increasing

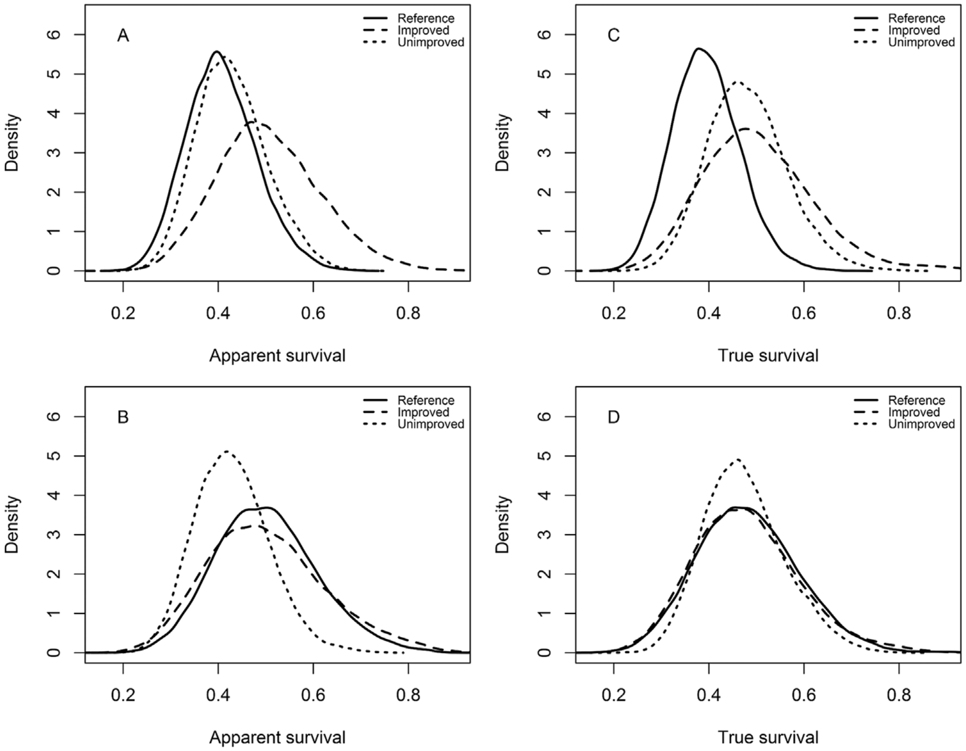

Figure 3. The posterior density distributions of apparent (A and B) and true survival (C and D) from capture-mark-recapture surveys for Idaho giant salamanders in 9 streams during 2012–2013 in Idaho and Montana, USA. Distributions in panels B and D represent predicted apparent and true survival after accounting for differences in sediment among the streams. The streams are separated into 3 categories: 3 streams bisected by unimproved culverts, 3 streams bisected by improved culverts, and 3 streams not bisected by either type of culvert (reference). We estimated apparent survival from a traditional Cormack–Jolly–Seber (CJS) model and true survival from a spatial CJS model.

Table 2. Mean estimates and standard deviations of movement distance (m), apparent survival, and true survival based on capture-mark-recapture surveys for Idaho giant salamanders during 2012–2013 in 9 streams of Idaho and Montana, USA. We estimated apparent survival from a traditional Cormack–Jolly–Seber (CJS) model and movement and true survival from a spatial CJS model. Estimates are from models not including sediment. The estimates include both movements within and between reaches.

		Movement		Apparent survival		True survival	
Stream	Culvert type	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Bird-1	Unimproved	22.8	35.3	0.379	0.074	0.427	0.080
Mayo	Unimproved	3.5	5.9	0.517	0.121	0.508	0.114
Waw[a]	Unimproved	10.3	14.4	0.449	0.117	0.459	0.111
Float	Improved	9.0	20.2	0.458	0.116	0.458	0.107
Badger	Improved	5.2	9.6	0.426	0.096	0.430	0.092
Wendover	Improved	4.1	5.1	0.509	0.134	0.503	0.127
Lone Knob	Reference	5.6	8.9	0.440	0.082	0.438	0.078
Pagoda	Reference	8.6	12.5	0.375	0.086	0.393	0.085
Bird-2	Reference	3.1	4.5	0.477	0.123	0.474	0.114

[a] Waw'aalamnime Creek.

sediment levels. The effect of sediment was evidenced by the largest adjustment in predicted survival for salamanders in streams without culverts, the class of streams with the highest mean sediment (Fig. 3C and D). This result is consistent with previous studies reporting that the distribution and abundance of amphibians and other streams species are negatively associated with sediment (Corn and Bury 1989, Welsh and Ollivier 1998), but the proximal mechanisms behind these relationships were unknown. One possible explanation of this result is that increased sedimentation fills hiding spaces and increases predation (Lowe et al. 2004, Kemp et al. 2011). Further, cover availability has been positively associated with Pacific giant salamander (*D. tenebrosus*) density (Parker 1991), which suggests *Dicamptodon* spp. seek cover that can be reduced by sedimentation. Recapture probability in our study increased with sediment level, which suggests salamanders were less able to hide and thus more exposed to predators such as fishes and other Idaho giant salamanders.

Our results did not show an effect of culvert type on sediment levels in streams. Surprisingly, reference streams and those with unimproved culverts tended to have greater mean sediment levels than streams with improved culverts. We suspect these differences resulted because streams lacking culverts and with unimproved culverts were relatively small, with woody debris and pools that retained sediment. In contrast, streams with improved culverts were larger and dominated by riffle morphology, where sediment is more likely to be flushed during spring snowmelt (Waters 1995). These patterns in sediment may also have been caused by differences in local geology or landscape features (Lewis and Stanford 1992, Bugosh 1999). Also, by constraining stream selection to those with high abundances of salamanders, we may have inadvertently chose streams with relatively high habitat quality or low sediment levels, and, therefore, the associations between culverts and sedimentation that we measured may not be representative across the landscape. Finally, the effects of sedimentation from culverts are often temporary or isolated, with increased sedimentation occurring mainly during and immediately after installation or after culvert failures, respectively (Madej 2001).

We predicted movement of Idaho giant salamanders between reaches would be lesser through unimproved culverts compared with improved culverts or reference streams. We were unable to explicitly test this prediction because we detected little movement between reaches in any culvert type. Our data clearly indicate that culverts do not block all downstream movement of Idaho giant salamanders, but to what degree culverts block movements in either direction remains unknown and likely varies among stream salamanders and other stream vertebrates. Sagar (2004) studied movement by >2,000 marked Pacific giant salamanders in 14 Oregon streams. Even though only 60% of movements were downstream, they observed a disproportionate number of downstream transitions through culverts compared to upstream (14 vs. 2). Further, their data show salamanders were less likely to enter culverts than reference reaches. These points suggest Pacific giant salamander movement could be affected by culverts. Studies of the effects of culverts on movement of fishes indicate effects vary by species and are highly dependent upon the specific physical structure of culverts (Warren and Pardew 1998, Mahlum et al. 2014).

Observations of *Dicamptodon* spp. in our study and others indicate their movement distributions are downstream biased; however, upstream movements do occur in these species and are common in other stream salamanders. Our data confirmed Idaho giant salamander movements are downstream biased, but we still detected 2 individuals that moved upstream >20 m ($\bar{x}$ length of intervening reaches in our study) within sampling reaches. Similarly, in 4 streams in the same study area, Idaho giant salamander movements were downstream biased, but a small portion of individuals moved upstream (Sepulveda and Lowe 2011). Although seemingly rare, we suspect upstream movements by *Dicamptodon* spp. are important for maintaining headwater populations genetically and demographically. The potential for culverts to block upstream movement may be especially important in areas where a large fraction of the breeding population of giant salamanders and other salamanders is aquatic (i.e., paedomorphic) rather than terrestrial. In contrast to the downstream biased movements of

Dicamptodon spp., some stream salamanders in the Appalachians seem more likely to move upstream than downstream (Lowe 2003, Cecala et al. 2009). This variation in movement patterns suggests the effects of culverts on movement and population connectivity could vary among species.

Estimates of survival and movement are rare for headwater amphibians, but they are crucial for the conservation and management of these species. In similar studies as ours, estimated annual apparent survival of the Pacific giant salamander in Oregon ranged from 0.13 (SE = 0.03) for first year larvae to 0.28 (SE = 0.08) for second and third year larvae (Sagar et al. 2007). Estimated apparent survival (extrapolated from estimated monthly survival) of the spring salamander (*Gyrinophilus porphyriticus*) in a New Hampshire stream was approximately 0.69 (Lowe 2003), whereas estimated apparent survival (extrapolated from estimated monthly survival) of the northern dusky salamander (*Desmognathus fuscus*) was 0.25–0.69, depending on drought conditions (Price et al. 2012). In our study, estimated mean movement distances among streams varied from 3.1 m to 22.8 m. Because our estimates of movement distributions account for permanent emigration, survival, and recapture probability, they are free from bias associated with emigration compared to models that do not account for this parameter.

Despite the small number of movement events, variation in movement distances among streams was great enough to bias estimates of apparent survival. Differences between apparent and true survival were greatest for salamanders in streams with unimproved culverts ($\leq$0.052, or a 12% difference without sediment in the model; Table 1). This effect resulted primarily from the concentration of emigration from the sampled reaches in 1 stream with an unimproved culvert. By explicitly incorporating movement data, the spatial CJS model provided survival estimates that were less biased by these movements (Zimmerman et al. 2007, Schaub and Royle 2014). The bias in our estimates of apparent survival in streams was smaller than that reported by Schaub and Royle (2014). But their data were from red-backed shrikes (*Lanius collurio*), a more mobile species that likely left the sampled area more frequently than the salamanders we studied. Also, because we extended study reaches between sampling occasions, we likely recaptured individuals that would have otherwise emigrated from the study area, possibly reducing the difference in our estimates of true and apparent survival.

Including spatial information in studies of wildlife survival may be beneficial in systems where emigration from the study area is likely, rates of emigration from the study area are not known, or emigration is not controlled by study design. If study areas are large relative to movement patterns of the individuals being studied, then emigration will be negligible and apparent and true survival will be similar, as was the case for 8 of our 9 study streams. However, in study areas undersized relative to movement rates, or where capture locations are near the boundary of the study area, apparent survival may underestimate survival more severely (Zimmerman et al. 2007, Schaub and Royle 2014). For stream amphibians that primarily disperse over land, a sampling design that includes terrestrial areas and uses the 2-dimensional version of the spatial CJS model could lessen bias in survival estimates caused by emigration. More generally, survival models containing spatial information and executed in the Bayesian framework allow wildlife scientists flexibility in study design and data analysis (Royle et al. 2013).

MANAGEMENT IMPLICATIONS

A major limitation to making accurate management recommendations is the lack of basic life-history information for many species. For example, our expectation that culverts would affect survival and movement of Idaho giant salamanders was predicated on the assumptions that culverts reduce habitat quality for salamanders and block in-stream movement. These predictions were based, in part, on the assumption that a large fraction of adult Idaho giant salamanders are paedomorphic rather than terrestrial (e.g., Sepulveda and Lowe 2009). However, if terrestrial adults are more common than assumed, then culverts may be less of a threat to long-term population stability. More broadly, variation in life-history and movement patterns among species of stream amphibians makes it difficult to generalize about the effects of culverts. Based on our results and those from other studies of culvert effects on stream salamanders (Sagar et al. 2007, Ward et al. 2008), we suspect the current focus of culvert improvement in large streams that are low in watersheds may only produce coincidental benefits for stream amphibians and other stream taxa that primarily occur high in watersheds (Meyer et al. 2007). But in areas where culvert replacements focus on headwaters, culvert replacement may have broader benefits to the stream community.

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