

Local and Landscape-Scale Influences on the Occurrence and Density of *Dicamptodon aterrimus*, the Idaho Giant Salamander

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ABSTRACT.—Species distribution and abundance depend on a balance between local and landscape-scale processes. To successfully manage populations in regions with anthropogenic disturbances and habitat fragmentation, an understanding of important processes at each of these spatial scales is important. We used a model selection approach to identify an effective spatial scale to manage the Idaho Giant Salamander, *Dicamptodon aterrimus*. We used data from field surveys to compare support for local and landscape-scale models that explain *D. aterrimus* occurrence and density in 40 streams distributed throughout the Lochsa River basin, Idaho. Local-scale models included covariates that reflect patch quality. Landscape-scale models included variables that reflect predictions from metapopulation theory about the importance of patch size, connectivity, and fragmentation. Our results suggest that landscape-scale processes are important controls on *D. aterrimus* occurrence and that this species has broad habitat requirements within streams. Specifically, we found that probability of *D. aterrimus* occurrence was highest in roadless drainages and lowest in spatially isolated streams and in drainages with high old-growth forest density. Surprisingly, we found that *D. aterrimus* density was greatest in streams with a high proportion of embedded substrate and fine sediment. The positive association with embedded substrate may reflect adaptation to a high frequency of natural disturbances, such as landslides, in our study area. We suggest that management and conservation efforts for this species focus on protecting roadless areas and restoring stream connectivity in human-impacted areas, rather than on only improving habitat quality within streams.

Species distribution and abundance depend on a balance between local and landscape-scale processes (Ricklefs, 1987; Lawton, 1999). Local processes are generally viewed as controls on survival and reproduction associated with abiotic and biotic conditions within patches (MacArthur and Levins, 1964; Shurin and Allen, 2001). Landscape-scale processes are related to the spatial arrangement of habitat patches and the movement of individuals among those patches (Dunning et al., 1992; Hanski and Gilpin, 1997). Landscape-scale processes drive the physical dynamics of a system (Benda et al., 2004) and influence population persistence through resource availability and use (Wiens, 1989; Dunning et al., 1992), colonization of new patches and recolonization of previously occupied patches (Levins, 1970; Brown and Kodric-Brown, 1977), and can subsidize patches with declining populations (e.g., Pulliam, 1988; Lowe, 2003). To successfully manage populations in regions with anthropogenic disturbance and habitat fragmentation, an understanding of important processes at each spatial scale is critical.

Identifying an effective scale of management is especially important for the conservation of

amphibian populations, which are suffering global declines (Stuart et al., 2004). Landscape-scale processes are often given priority because amphibians are frequently assumed to form metapopulations, where dispersal among local populations promotes persistence (reviewed in Alford and Richards, 1999; Storfer, 2003; Smith and Green, 2005). Management to maintain metapopulations might favor protecting large areas with multiple patches and connectivity among these patches. However, recent reviews indicate that the assumption that landscape-scale processes are most critical to amphibian persistence is often inaccurate (Marsh and Trenham, 2001; Storfer, 2003; Smith and Green, 2005), and numerous studies have demonstrated that amphibian distribution and abundance are best predicted by local factors (Bradford et al., 2003; Knapp et al., 2003) or a mix of local and landscape-scale factors (Sjogren-Gulve, 1994; Lowe and Bolger, 2002). In cases where local conditions determine persistence, management might focus on local environmental factors that influence patch quality, such as substrate composition, so that local sites can support self-sustaining populations (Petranka and Holbrook, 2006). These contrasting views on an effective spatial scale for managing amphibian populations underscore the need for studies assessing controls on amphibian distribution and abundance at multiple spatial scales.

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Management at an incorrect spatial scale can result in ineffective conservation (e.g., Novinger and Rahel, 2003).

There is a general lack of information on the spatial structure and conservation status of stream amphibian populations, even though these species can make up over 95% of stream vertebrate biomass (Hawkins et al., 1983; Peterman et al., 2008) and are thought to play a key role in ecosystem dynamics (Davic and Welsh, 2004). Prior studies on how spatial structure (i.e., the number and location of patches in a landscape) influences local population dynamics have focused primarily on pond-breeding amphibians (Sjogren-Gulve, 1994; Trenham et al., 2001), whereas most studies on stream amphibians have focused on habitat associations at multiple spatial scales (e.g., Welsh and Ollivier, 1998; Lowe and Bolger, 2002; Stoddard and Hayes, 2005) and biotic interactions at fine spatial scales (Hairston, 1987; Sih et al., 1992). The influence of spatial structure on local population dynamics has rarely been considered for stream amphibians (but see Lowe, 2003; Lowe et al., 2006), even though they occupy a naturally fragmented and complex mosaic of stream habitats that have become fragmented by human-related disturbances.

The size, quality, and configuration of patches are landscape-scale variables known to affect local population persistence and occurrence across taxa (Dunning et al., 1992; Fahrig and Merriam, 1994; Dunham and Rieman, 1999). In amphibians, population persistence is correlated with patch size and connectivity and negatively correlated with habitat fragmentation and habitat alteration (reviewed in Cushman, 2006). Large patches often have greater resistance and resilience to disturbance because populations are larger (Marsh and Pearman, 1997), there is a broader diversity of habitat conditions and resources within patches (Schlosser, 1995), and the scale of a given disturbance relative to the size of the patch is smaller (Stoddard and Hayes, 2005). Patch connectivity decreases extinction risk by increasing demographic and genetic input from immigrants, by increasing the chance of recolonization after extinction and by increasing opportunities for resource supplementation and complementation among patches (reviewed in Dunning et al., 1992; Hastings and Harrison, 1994). Finally, habitat fragmentation and alteration of the intervening habitats can effectively increase patch isolation by reducing rates of movement among patches (reviewed in Saunders et al., 1991). Greater understanding of how patch size, patch connectivity, and fragmentation and alteration of intervening habitat affect

stream amphibians will help in developing effective conservation strategies.

Here, we used model selection to identify an effective spatial scale to manage a stream salamander species, *Dicamptodon aterrimus* (Idaho Giant Salamander), which is listed as a species of concern in the northern Rocky Mountains. Little is known about *D. aterrimus*, but available information suggests that its distribution is patchy across and within stream drainages (Carstens et al., 2005). In the region where *D. aterrimus* occurs, many stream drainages have undergone timber harvest and road building, anthropogenic disturbances that can reduce habitat quality within streams and reduce population connectivity among streams (Carr and Fahrig, 2001; Fagan, 2002). Additionally, these drainages experience natural disturbances such as fire, floods, and landslides, which can create local extinctions of stream organisms in suitable habitat patches (e.g., Welsh and Ollivier, 1998; Dunham and Rieman, 1999; Pilliod et al., 2003). We used data from field surveys to compare support for local and landscape-scale models that describe *D. aterrimus* occurrence in 40 streams in one northern Idaho river basin. To increase knowledge of *D. aterrimus* natural history, we also compared support for local-scale models explaining variation in *D. aterrimus* density within streams. Local-scale models include covariates that reflect patch quality, whereas landscape-scale models include covariates that reflect predictions from metapopulation and landscape ecology theory about the importance of patch size, connectivity, and fragmentation. We had three objectives: (1) to identify an effective spatial scale to manage *D. aterrimus*; (2) to identify *D. aterrimus* habitat associations at each spatial scale; and (3) to explore important correlates of *D. aterrimus* density at the local scale.

MATERIALS AND METHODS

Study Species and Site.—*Dicamptodon aterrimus* is a large salamander (up to 220 mm snout-vent length) found in or near streams and rivers in the Rocky Mountains of northern and central Idaho and extreme western Montana (Stebbins, 2003). This species exhibits facultative paedomorphosis, a polymorphism that results in the coexistence of gilled and fully aquatic paedomorphic adults and terrestrial metamorphic adults in the same populations. No studies have addressed the natural history and habitat associations of *D. aterrimus*, but its similarity to the Pacific Giant Salamander (*Dicamptodon tenebrosus*) would suggest that *D. aterrimus* has narrow physiological tolerances and requires specific local habitat conditions. Past studies

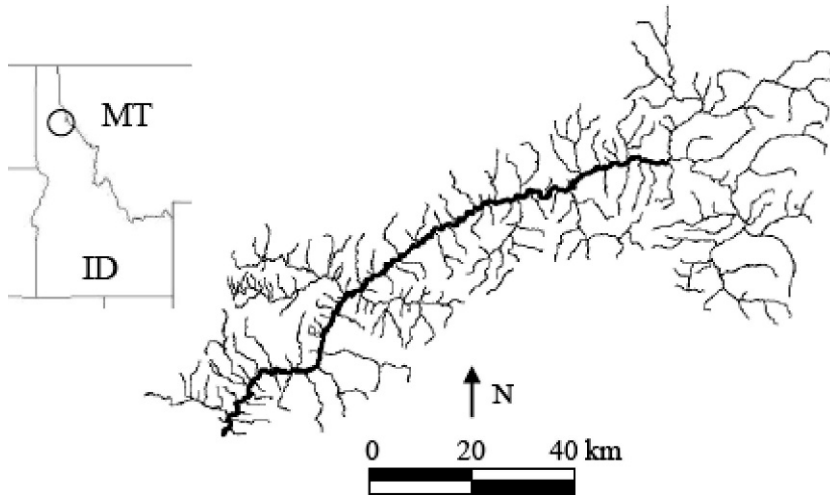


FIG. 1. Map of Lochsa River basin, northwestern Idaho showing stream catchments that flow into the mainstem of the Lochsa River (bold).

indicate that aquatic individuals of *D. tenebrosus* occur in cold-shaded headwater streams with unembedded cobble substrate (Bury et al., 1991; Roni, 2002) and that terrestrial adults inhabit moist coniferous forests (Nussbaum et al., 1983).

We conducted this study in 40 headwater streams within the Lochsa River basin of the Clearwater River, Idaho County, Idaho (Fig. 1). The Lochsa is an eighth-order river (drainage area $\approx 3,000 \text{ km}^2$) with an elevation range of 425–2,630 m. Annual precipitation is approximately 100 cm, and summers are hot and dry. Basin geology is predominantly granitic Idaho batholith. The majority of the land in the basin is part of the Clearwater National Forest or owned by the Plum Creek Timber Company; portions of the headwaters are also in the Selway-Bitterroot Wilderness Area. Six percent of the Clearwater National forest and timber company lands have been logged, but the wilderness area has not been logged. Together, the Clearwater National Forest and Plum Creek Timber Company lands have an average road density of 0.80 road km per km^2 (Jones, 1999).

Lower-elevation streams in the Lochsa River basin are dominated by Pacific maritime forests, which include western red cedar (*Thuja plicata*) and Douglas-fir (*Pseudotsuga menziesii*). Higher-elevation streams are set in subalpine forests containing lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Pinus engelmannii*). The streams and rivers have multiple fish species, including bull trout (*Salvelinus confluentus*), steelhead and rainbow trout (*Oncorhynchus mykiss*), westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), and sculpin (*Cottus* sp.). Amphibian species include *D. aterrimus* and Rocky Mountain Tailed Frogs (*Ascaphus montanus*).

Fires and landslides are common disturbances in this region. Fire regimes are mixed: infrequent, patchy stand-replacement fires dominate in upper-elevation forests and frequent, lower-severity, surface fires dominate at lower elevations (Brown et al., 1994). The combination of fire-affected soils, weathering granitic rocks, steep slopes, and rain-on-snow events (defined as rain that falls on existing snow cover; MacDonald and Hoffman, 1995) has produced landslides throughout the basin. As a result, total sediment volume in streams can exceed water quality standards for salmonids, even in the roadless Selway-Bitterroot Wilderness Area (McClelland et al., 1997; Jones, 1999).

Spatial Scale Definitions.—A goal of this research was to identify local and landscape-scale variables that predict the occurrence and density of *D. aterrimus* within patches of potentially suitable habitat. We assumed that individual headwater stream drainages satisfied the Hanksi and Gilpin (1997) definition of a patch: a continuous area of space with all necessary resources for the persistence of a local population. We have found *D. aterrimus* in larger streams, but preliminary surveys and discussions with freshwater managers in the region suggested that occurrence and local densities are higher in headwater streams (J. Sauder, Idaho Fish and Game, pers. comm.; B. A. Maxell, Montana Natural Heritage Program, pers. comm.). Previous research on *D. tenebrosus* supports this assumption: both occurrence and density of *D. tenebrosus* are higher in first- and second-order streams than in larger streams and rivers (e.g., Grialou et al., 2000; Johnston and Frid, 2002; Roni, 2002), and telemetry data suggest that most individuals move less than

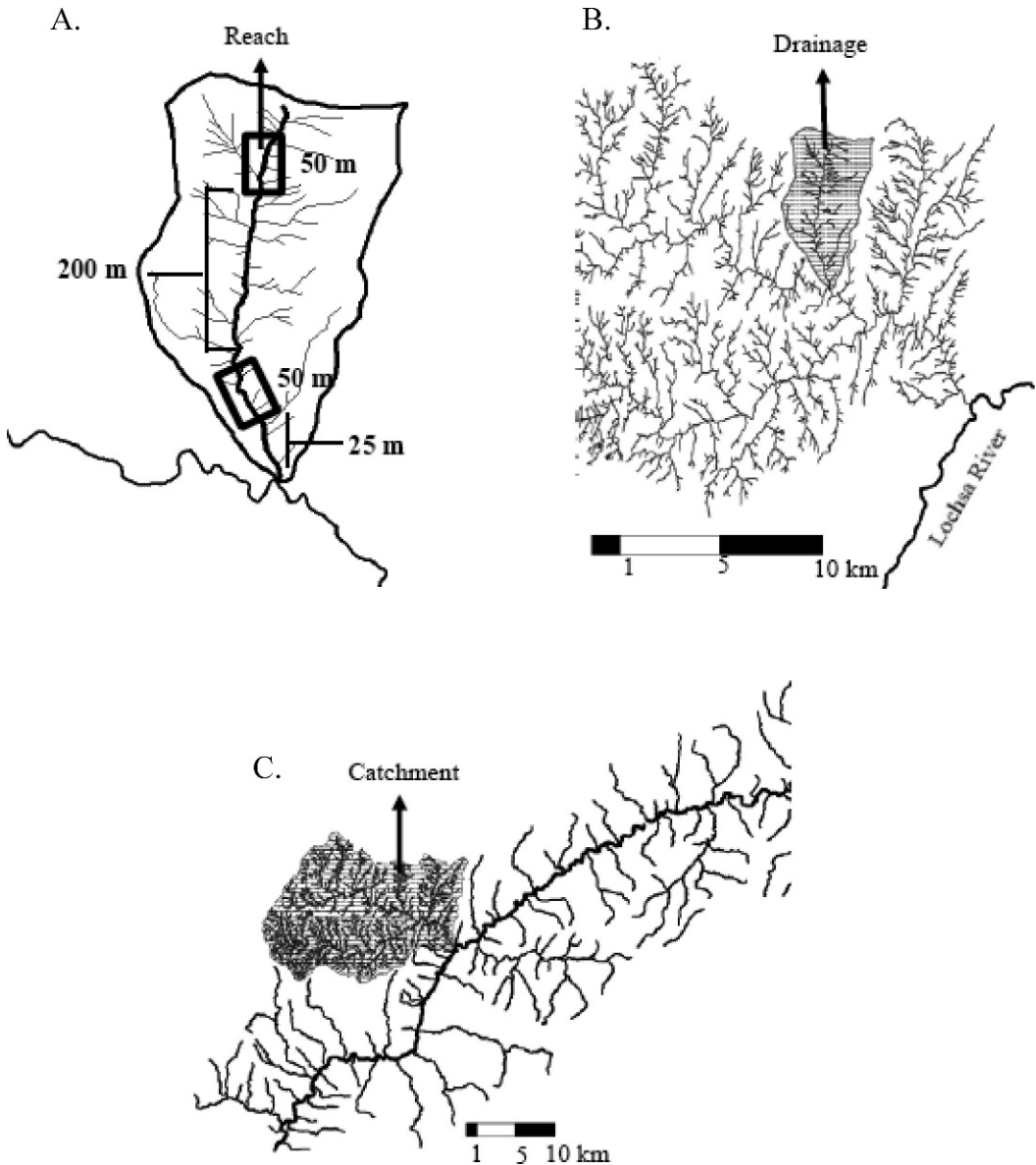


FIG. 2. Schematic of multiscale sampling design used in the Lochsa River basin, Idaho. Shaded areas show a stream reach (A), a stream drainage (B), and a stream catchment (C). Landscape-scale variables were measured within drainages. Local-scale variables were measured within stream reaches.

30 m along streams over a season (Johnston and Frid, 2002). The headwater streams we sampled were fed by drainages of 1–30 km² (Fig. 2B), and multiple drainages were aggregated within catchments of 25–200 km² (Fig. 2C).

Survey Methods.—Within each catchment, we randomly selected 2–3 headwater drainages and sampled the main stream in each drainage. Within each stream, we surveyed two 50-m reaches separated by 200 m for *D. aterrimus* occurrence and density (Fig. 2A). The lower

reach began 25 m upstream of the confluence with a similar or higher-order stream (Fig. 2A). We used a backpack electrofisher (Smith and Root, LR 24, pulsed DC with 400–520 volts) to search for salamanders within the stream. Comparisons with light-touch surveys in five of our sampled streams suggest that electroshocking is an effective tool for assessing *D. aterrimus* occurrence and density. We found more than 10 *D. aterrimus* per stream when using an electroshocker and found 0–2 *D.*

aterrimus in these same plots when using light-touch surveys. We did not survey for *D. aterrimus* terrestrial adults in the riparian area because they are extremely cryptic and believed to be rare (J. Sauder, Idaho Fish and Game, pers. comm.); therefore, our inferences pertain to the occurrence and density of aquatic *D. aterrimus*.

To determine detection probability, all reaches were surveyed three times within one season (MacKenzie and Royle, 2005). Two of these surveys were conducted within a 6-h period, and the third survey was conducted 20–30 days later. We recorded the number of salamanders captured during each survey and noted the presence of stream fishes. All surveys were done at base flow conditions in July and August 2007. To test the independence of surveys conducted within a 6-h period, we clipped tails of all IGS captured in the first survey and noted individuals recaptured in the second survey of the 6-h period. We used the exact binomial test of goodness of fit to evaluate independence between captured and recaptured *D. aterrimus* in the first and second surveys.

We used *D. aterrimus* occurrence (presence/absence) and density within a stream as response variables. *Dicamptodon aterrimus* were declared present in a headwater stream if they were detected in at least one 50-m reach in at least one of the three surveys. Compared to other studies that assessed salamander detection probability (e.g., Bailey et al., 2004), we had very high detection probability: 39 of 40 study reaches had *D. aterrimus* always present or always absent in all three surveys. Consequently, we assumed a detection probability of 1.0 for all sites. We calculated density for each headwater stream as the mean number of salamanders per m² captured in the lower and upper stream reaches over the three surveys.

Habitat Assessment, Local Scale.—We measured only local abiotic and biotic variables that have been shown to be important for stream salamanders, particularly *Dicamptodon* species. Abiotic variables included mesohabitat type (e.g., pool, riffle, or cascade; Welsh and Lind, 2002), substrate size and composition (Parker, 1991; Welsh and Ollivier, 1998), stream width (Stoddard and Hayes, 2005), canopy cover (Welsh and Lind, 2002), and aspect (Stoddard and Hayes, 2005). Biotic variables included fish presence (Sih et al., 1992). We recognize that other local variables can influence stream salamander occurrence and density; however, predictive models with a large number of variables are difficult for managers to embrace (Stoddard and Hayes, 2005) and have reduced statistical power in studies like ours, when sample size is logistically constrained (Burnham and Anderson, 2002).

We assessed local variables within each stream reach. We recorded mesohabitat as percent occurrence of pools, riffles, and cascades over each 50-m reach (Hawkins et al., 1993). We measured substrate composition and stream width at four random, 1-m wide transects that extended between bank-full channel edges within each reach. At six random points along each transect, we recorded the proportion of substrate in four categories (Lane, 1947): boulder-bedrock (>256.0 mm), cobble (64.0–256.0 mm), gravel-pebble (2.0–64 mm), and fines (<2.0 mm). We also recorded the proportion of substrate that was embedded, defined as having visible vertical surfaces buried in either silt or sand (Welsh et al., 1997; Lowe and Bolger, 2002). Stream reach aspect (0–360°) was measured at the most downstream transect of each reach. Abiotic variables were averaged across the two study reaches within each headwater stream. Occurrence of salmonid fishes was recorded as presence or absence within each headwater stream. To test the assumption that *D. aterrimus* capture probability was independent of local habitat conditions, we marked all salamanders captured in the first of our two surveys within a 6-h period, and then tested the correlation between proportion recaptured in the second survey and local variables.

To reduce the likelihood of missing important variables other than those we hypothesized were important, we also collected data on the elevation, stream gradient, stream temperature, and acidity (pH) of all sampled stream reaches. Elevation was recorded at the most downstream transect of each reach with a global positioning system (eTrex, Garmin, Kansas City, KS). Stream gradient was estimated as the difference in elevation between the upstream and downstream ends of each plot divided by the distance between these points. Stream temperature at the farthest upstream transect of each reach was recorded hourly from June 20 through September 1 (Thermochron iButton, Dallas Semiconductor, Dallas, TX). We included the overall mean summer temperature (T) and maximum summer temperature (T_{\max}) in analyses. We recorded pH at the downstream end of each reach with a portable pH meter (Oakton, Inc., Vernon Hills, IL). Elevation, gradient, T , T_{\max} , and pH measurements were averaged for the two study reaches within each headwater stream.

Habitat Assessment, Landscape Scale.—We derived indices of patch size, patch connectivity, habitat fragmentation, and habitat alteration within each drainage using the most recent GIS coverages in the Clearwater National Forest GIS library (<http://www.fs.fed.us/r1/>

clearwater/gis/library.htm). We defined patch size using two covariates: total stream distance in the drainage and link magnitude (number of headwater streams in the drainage; Rich et al., 2003). We defined patch connectivity as the distance to the nearest stream in a neighboring headwater drainage, but logistical constraints did not allow us to determine the occupancy status of these nearest neighbor streams. In our model, patch connectivity can potentially represent: (1) a metapopulation effect of colonization/recolonization (Hanski and Gilpin, 1997); (2) source-sink dynamics (Pulliam, 1988); (3) a "Moran effect" that describes correlated environments; and (4) habitat complementation or neighborhood effects that describes resource use and availability (Dunning et al., 1992). The occupancy status of the nearest neighbor stream is not critical to our test of landscape versus local-scale predictors of *D. aterrimus* occurrence because patch occupancy and patch suitability are expected to change over time in a dynamic landscape that has a high frequency of natural disturbance, such as the Lochsa River basin. Unoccupied patches with suitable habitat are generally predicted to be critical to species persistence in metapopulation models (Hanski and Gilpin, 1997).

Because *D. aterrimus* can move within the stream channel or overland, we measured distance to the nearest stream along the channel network (i.e., minimum distance along the stream corridor from the mouth of the sampled headwater drainage to the mouth of the nearest headwater drainage) and by the Euclidean distance to this nearest stream (i.e., straight-line topographic distance from any stream segment within a sampled headwater drainage to any stream segment within a neighboring headwater drainage; Dunham and Rieman, 1999; Gresswell and Torgersen, 2006). We characterized habitat fragmentation and alteration by road density and forest structure. Roads can lead to direct mortality of stream amphibians (Trombulak and Frissell, 2000), act as barriers to dispersal (deMaynadier and Hunter, 2000), and increase sedimentation within streams (Welsh and Ollivier, 1998). We quantified road density as length of roads standardized by headwater drainage area (km of road per km²) using the 2001 Inventoried Roadless Area data layer for the Clearwater National Forest. We described forest structure by the density of old-growth trees based on the northern Idaho old growth standards (Green et al., 1992), which takes into account tree age and size. Previous studies have found that occurrence of stream amphibians is related to conditions in surrounding forests, including density, age, and size of forests (Welsh and Lind, 2002; Stoddard and Hayes,

2005). We used the density of old-growth trees (trees per km²) derived from the 2004 Forest Inventory Vegetation Data.

Statistical Analysis, Approach.—We used model selection to identify the most plausible statistical models for predicting *D. aterrimus* probability of occurrence and density when present. Prior to this analysis, we identified highly correlated pairs of variables (those with $r \geq 0.7$; Welsh and Lind, 2002) and used principal components analysis (PCA) to reduce collinearity among these variables. We then used combinations of these variables to predict (1) *D. aterrimus* occurrence as a function of local- or landscape-scale variables and (2) *D. aterrimus* density as a function of local-scale variables. With the exception of a global model, we did not include models that mixed local- and landscape-scale variables because our primary objective was to determine which of the two spatial scales better describes patterns of *D. aterrimus* occurrence. Finally, we used Akaike's Information Criterion (AIC)-based methods to select the best models of *D. aterrimus* occurrence and density from sets of candidate models (Burnham and Anderson, 2002). We used log, square-root, and arcsine-square-root transformations on predictor variables where necessary.

Statistical Analysis, Local-Scale Models.—Four categories of variables defined local-scale conditions: mesohabitat type, substrate composition, aspect, and fish presence. Proportions of riffles and cascades were positively correlated with the proportion of gravel-pebble, cobble, and boulder-bedrock substrate. We used PCA to produce one axis that accounted for 58% of the variation in these measures (coefficients of the first eigenvector: riffles = -0.53, cascades = 0.52, gravel-pebble = 0.20, cobble = -0.47, boulder-bedrock = 0.43). Therefore, high values reflect streams dominated by cascades, gravel-pebble, and boulder-bedrock substrate. Proportions of embedded and fine substrate were positively correlated; thus, we used PCA to produce one axis that accounted for 75% of this variation (coefficients of the first eigenvector: embedded substrate = 0.71, proportion of fines substrate = 0.71). These procedures yielded six local variables (Table 1): (1) proportion of stream with cascades and gravel-pebble/boulder-bedrock substrate; (2) proportion of pools per stream; (3) proportion of fine-embedded substrate per stream; (4) stream width; (5) aspect; and (6) fish presence. These local-scale variables were not correlated with any of the landscape-scale variables.

We only considered local-scale models that had four or fewer variables because complex models with many variables are of limited practical value for management, and including

TABLE 1. Abbreviations and definitions of local and landscape-scale variables used in competing models to predict *Dicamptodon aterrimus* occupancy and density in headwater streams within the Lochsa River basin, Idaho.

Variable	Abbreviation	Definition
<i>Local</i>		
Pools	P	Average proportion of pools per stream
Embedded substrate	ES	First axis from a PCA of average proportions of fine substrate and embedded substrate
Stream type	ST	First axis from a PCA on average proportion of gravel-pebble, cobble, boulder-bedrock substrate and average proportion of cascades and riffles per stream
Aspect	A	Downstream orientation of the stream, 0–360°
Stream width	SW	Average width (m) of bank-full channel edges at high-flow conditions
Fish presence	FP	Occupancy (presence/absence) of salmonid fish
<i>Landscape</i>		
Patch connectivity	PC	First axis from a PCA on distance (km) along the stream corridor to the nearest drainage and Euclidean distances (km).
Patch size	PS	First axis from a PCA on stream length (km) and link magnitude
Road density	RD	Length of roads (km) per drainage km ²
Old growth density	OG	Mean number of old growth trees per 0.004 km ²

additional variables inflates the number of potential models beyond the number that can be reliably analyzed given our sample size (Burnham and Anderson, 2002; Stoddard and Hayes, 2005). By restricting models to those with no more than four variables, we were left with 56 possible local models.

Statistical Analysis, Landscape-Scale Models.—Four categories of variables defined landscape-scale conditions: stream size (total stream length and link magnitude); stream isolation (minimum distance along the stream channel and Euclidean distance to the stream); habitat fragmentation; and habitat alteration (road density and old-growth tree density; Table 1). Total stream length and link magnitude were correlated; thus, they were subjected to PCA to produce a single axis that accounted for 86% of the variation (coefficients of the first eigenvector: total stream length = 0.71, link magnitude = 0.71). Therefore, high values reflect longer streams with many links. Minimum stream channel distance and Euclidean distance were correlated, so they were subjected to PCA to produce a single axis that accounted for 98% of the variation (coefficients of the first eigenvector: minimum stream channel distance = 0.71, Euclidean distance = 0.71). Therefore, high values reflect increasing isolation (low connectivity). Road density and old-growth density were not correlated. We considered linear models with all possible combinations of these variables, which yielded 16 possible landscape models, including the landscape core model that included all landscape variables.

Statistical Analysis, Model Selection.—To predict *D. aterrimus* occurrence, we compared the relative likelihood of the global model (all local and landscape-scale variables), the 56 local models, the 16 landscape models, one landscape-core model (all four landscape variables), one local-core model (all six local variables), and one local-abiotic model that included all five abiotic variables. Logistic regression was used to determine the relative likelihood of each candidate model given the data. We evaluated the strength of support for alternative models using AIC_c , a bias-corrected version of AIC for small sample size (Burnham and Anderson, 2002). To ensure that AIC_c was the correct criterion to use, we tested for overdispersion of the variance (\hat{c}) by using the observed chi-squared goodness-of-fit statistic (χ^2) from the global model divided by its degrees of freedom. Values of $\hat{c} > 1$ indicate overdispersion, but all of our values were approximately 1; thus, we used AIC_c (Mackenzie et al., 2005).

To predict *D. aterrimus* density, we compared the relative likelihood of the global model (all six local variables), the 56 local models, and one local-abiotic model that included all five abiotic variables. We used multiple linear regression to determine the relative likelihood of each candidate model given the data. We evaluated the strength of support for alternative models using AIC_c and tested for overdispersion of the variance.

We determined strength of support for the model using ΔAIC_c values, AIC_c weights (ω), and evidence ratios (Burnham and Anderson, 2002). Models with $\Delta AIC_c \leq 4$ for small sample

TABLE 2. Model selection results (AIC values corrected for small sample size) for the (A) occupancy and of *Dicamptodon aterrimus* in headwater streams in the Lochsa River basin, Idaho. K refers to the number of parameters in each model, including the intercept. Boldface type indicates the best model and all those with an Akaike weight (w) > 0.1. The evidence ratio (w_i/w_1) indicates the multiplicative probability by which the best model (w_1) is more likely than competing models (w_i), given the set of candidate models and the data. Covariate abbreviations are listed in Table 1.

Model name	Log-likelihood	K	ΔAIC_c	w	Evidence ratio
Occupancy					
Landscape: PC, RD, OG	-19.65	4	0.00	0.23	1.00
Landscape: RD	-23.44	2	2.04	0.08	2.88
Landscape: PC, RD	-22.07	3	2.04	0.08	2.88
Landscape: PC, PS, RD, OG	-19.57	5	2.48	0.07	3.29
Landscape: RD, OG	-22.52	3	2.83	0.06	3.83
Local: A	-24.23	2	3.33	0.04	5.75
Landscape: PC	-24.55	2	3.84	0.03	7.67
Global: all local and landscape	-17.86	11	18.88	0.00	-
Landscape core: PC, PS, RD, OG	-19.57	5	2.48	0.07	3.29
Local core: P, ES, ST, A, SW, FP	-24.09	7	16.35	0.00	-

size ($n/K < 40$; where n = sample size and K = number of parameters) have empirical support as being plausible (Burnham and Anderson, 2002). We only present models with $\Delta AIC_c \leq 4$ because $n/K < 40$ for all models. To assess the importance of individual parameters within the presented models, we calculated importance weights by summing ω values of all models in which the parameter occurs (Burnham and Anderson, 2002). Parameters with importance weights > 0.20 are considered to be significant (Stoddard and Hayes, 2005). Finally, coefficients (β) of local and landscape habitat covariates for *D. aterrimus* occurrence and relative density were obtained by averaging across all models weighted by ω (i.e., model averaging; Burnham and Anderson, 2002). Odds ratios were calculated from *D. aterrimus* occurrence coefficient estimates as $\exp(\beta)$. An odds ratio of 1.0 indicates no difference between the proportion of sample points with or without salamanders, whereas odds ratios close to zero or substantially greater than 1.0 indicate a large difference. Odds ratios less than 1.0 indicate a negative effect, whereas ratios greater than 1.0 indicate a positive effect (Keating and Cherry, 2004).

Additional Variables.—To ensure that stream occurrence patterns were not influenced by physiochemical variables, we used *t*-tests to compare the average elevation, gradient, T , T_{max} , and acidity between streams with and without *D. aterrimus*. All statistical analyses were performed in JMP 7.0 (SAS Institute, Cary, NC, 2007).

RESULTS

We found *D. aterrimus* presence in 18 of 40 sampled headwater streams, with densities ranging from 0.01–0.24 individuals per m^2 . Detection probability of *D. aterrimus* was ex-

tremely high. Capture history of 17 of the 18 streams with *D. aterrimus* present was 1-1-1, whereas one stream had a capture history of 0-1-1. Capture history of the 22 streams with *D. aterrimus* absence was always 0-0-0. Surveys that occurred twice within a 6-h period were independent of one another. The probability of detecting *D. aterrimus* in the second survey was not influenced by the first survey (exact binomial test of independence: $P < 0.0001$). We captured 201 individuals in the first survey and 147 individuals in the second survey, 40 of which were recaptures from the first survey. The probability of recapture was not correlated with any local-scale variables ($r^2 < 0.10$, $P > 0.05$).

Support for landscape-scale influences on *D. aterrimus* occurrence was greater than support for local-scale influences (Table 2). The most plausible model for *D. aterrimus* occurrence included roads, patch isolation, and old-growth tree density; its evidence ratio was six times greater than the most supported local model. Probability of *D. aterrimus* occurrence was highest in headwater stream drainages with low road and old-growth tree density and low patch isolation (Fig. 3). Road density and patch isolation had the highest importance weights and had odds ratios < 1.0, which indicate that increases in these variables had a negative effect on probability of *D. aterrimus* occurrence (Table 3). The odds ratio for old-growth tree density was extremely low because of the large standard error. The only local-scale model with $\Delta AIC_c < 4$ included aspect. *Dicamptodon aterrimus* occurrence was associated with a western (200–300°) patch aspect. There was little evidence for other local-scale influences on *D. aterrimus* occurrence. Results were the same

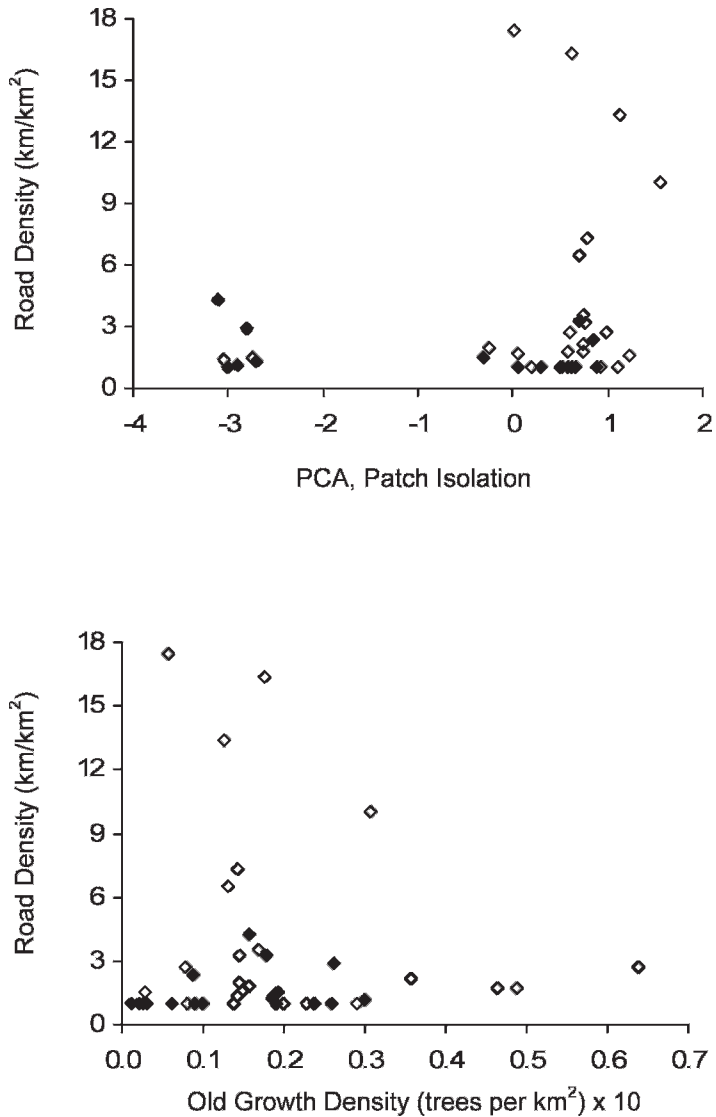


FIG. 3. Relationships between *Dicamptodon aterrimus* occurrence (solid diamonds = present, open diamonds = absence) and road density, patch isolation (top), and old growth tree density (bottom). Principal components analysis (PCA) was used to reduce multicollinearity among variables describing patch isolation. High values reflect increasing isolation. An $X = 1$ transformation was necessary to display road density values of zero.

when we used program PRESENCE (<http://www.mbr-pwrc.usgs.gov/software/doc/presence/presence.zhtml>), which incorporates variation in detection probability, to assess occurrence models.

The most plausible model of *D. aterrimus* density included only embedded substrate (Fig. 4), and all models with a $\Delta AIC_c < 4$ included this variable (Table 4). Parameter importance weights indicated that embedded substrate was the best predictor of *D. aterrimus*

density (Table 5). Surprisingly, *D. aterrimus* density was greatest in patches with a high proportion of embedded substrate. Less plausible models suggest that *D. aterrimus* relative density was greatest in western aspects (200–300°) and fishless patches.

Physiochemical characteristics did not explain *D. aterrimus* occurrence patterns. There was no difference between streams with and without *D. aterrimus* in elevation ($t_{38} = 1.07$, $P = 0.29$), gradient ($t_{38} = -0.47$, $P = 0.28$), average

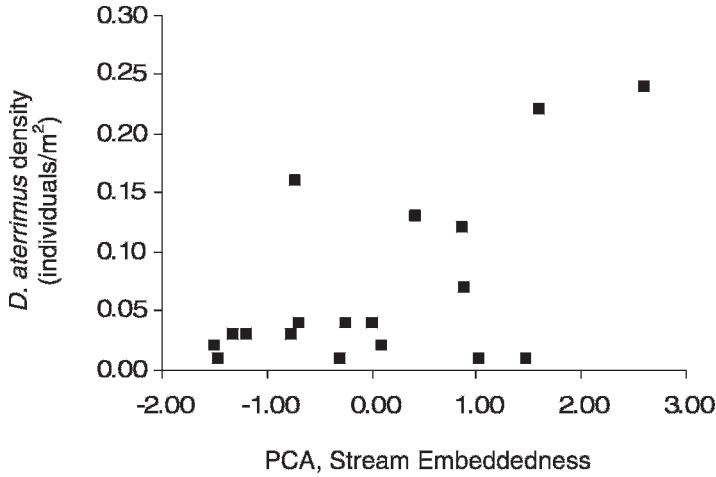


FIG. 4. Relationship between *Dicamptodon aterrimus* density (individual/m²) and a principle component axis representing the proportion of embedded and fine substrates. High values reflect a high proportion of embedded and fine substrate.

summer temperature ($t_{38} = -0.11, P = 0.92$), maximum summer temperature ($t_{38} = -0.12, P = 0.91$), and pH ($t_{38} = 0.77, P = 0.94$). Across all streams, elevation ranged from 530–1,600 m, gradient ranged from 0.25–9.50%, average summer temperature ranged from 8.3–15.1°C, maximum summer temperature ranged from 14.0–20.0°C, and pH ranged from 5.5–8.8.

DISCUSSION

To identify an effective scale of management for *D. aterrimus* in the Lochsa River basin, we compared model support for local and landscape-scale predictors of *D. aterrimus* occurrence in 40 headwater streams. Our results suggest that management and conservation efforts for

TABLE 3. Importance weights, coefficients (range), 95% confidence intervals and odds ratios of local and landscape habitat covariates predicting *Dicamptodon aterrimus* occupancy obtained by averaging across all models weighted by the Akaike weights (Burnham and Anderson, 2002). The intercept is not shown. Boldface indicates estimates for which the 95% confidence intervals did not overlap zero.

Scale	Importance weight	Coefficient estimate	95% C.I.	Odds ratio
(A) Occupancy				
<i>Local</i>				
P	0.07	-0.03 (-0.04 to -0.03)	0.06	0.93
ES	0.08	-0.08 (-0.20 to 0.00)	0.05	0.92
ST	0.07	-0.04 (-0.07 to 0.24)	0.12	1.04
A	0.16	0.03 (0.02 to 0.11)	0.07	1.03
SW	0.07	-0.09 (-0.80 to -0.02)	0.54	0.91
FP	0.07	-0.01 (-0.02 to 0.00)	0.18	1.01
<i>Landscape</i>				
PI	0.46	-0.55 (-0.41 to -0.07)	0.26	0.58
PS	0.17	-0.04 (-0.09 to -0.02)	0.04	0.96
RD	0.60	-0.40 (-0.52 to -0.34)	0.14	0.67
OG	0.42	-70.54 (-38.47 to -81.12)	26.30	2.32E-31

this species would be more effective at the landscape scale than at the local scale. The five most supported models of *D. aterrimus* occurrence were composed of only landscape-scale predictors, and the importance weights of all landscape-scale predictors were greater than local-scale predictors. Specifically, we found that *D. aterrimus* occurrence was highest in unfragmented headwater drainages with few roads, lowest in spatially isolated streams, and insensitive to patch size and local-scale variables that influence stream habitat quality. Our research suggests that patch spatial structure in the surrounding landscape influences *D. aterrimus* occurrence and that developing effective forest management rules that minimize road establishment and habitat fragmentation are essential for protecting populations of this stream amphibian.

In a similar analysis of pond amphibian occurrence and density, Van Buskirk (2005) also found greater model support for landscape-scale covariates than for local-scale covariates. He suggested that his results could be interpreted in two ways: (1) rejection of the focus on local processes because results require explanation at the level of the metapopulation; and (2) rejection of the focus on amphibian metapopulation dynamics because landscape-scale processes reflect the availability and condition of local habitat. Although we did not rigorously test these alternative hypotheses, we believe that our results provide greater support for rejection of the focus on local processes. First, the probability of *D. aterrimus* occurrence was best predicted by landscape-scale models that reflect predictions from metapopulation theory about the importance of patch fragmentation and connectivity. Second, low support for local-scale models and low importance weights for local-scale covariates suggest that *D. aterrimus* is tolerant of a wide range of local conditions in a stream. Finally, the lack of correlation between landscape and local-scale covariates suggests that landscape-scale processes were not closely linked to our metrics of local habitat condition. For example, we found no correlation between road density at the landscape scale and fine-embedded substrate at the local scale, even though fine-embedded substrate was the best predictor of *D. aterrimus* density. However, it is possible that landscape-scale covariates were correlated with local habitat variables that we did not measure (e.g., stream invertebrate production may be related to old-growth tree density, Hawkins et al., 1982).

Our results provide greater support for the rejection of the focus on local processes, but we cannot readily assume that *D. aterrimus* has a metapopulation structure. The significance

of road density may affect the movement of individuals between patches to make use of nonsubstitutable and substitutable resources (Dunning et al., 2002), rather than affecting dispersal, colonization, recolonization, and rescue dynamics. Similarly, patch connectivity may be correlated with environmental and geographic attributes such that a site near an occupied site may tend to have similar characteristics to those of an occupied site (Bradford et al., 2003). Discrimination between metapopulation dynamics and landscape physiognomy and composition is necessary to understand mechanistically the role of patch spatial structure on *D. aterrimus* occurrence.

The importance of road density and spatial connectivity in predicting *D. aterrimus* occurrence could be related to the ability of *D. aterrimus* individuals to rescue and recolonize declining or locally extinct populations. Roads may impede salamander movement between streams by altering the intervening terrestrial habitat, or they may impede movement along streams with the presence of road crossings and culverts. Previous studies have shown that roads limit overland movement because of salamander physiological restrictions and predator-avoidance behavior (Marsh et al., 2005; Semlitsch et al., 2007). Road crossings of streams and the associated culverts may also limit movements of organisms within the stream channel because of excessive water velocity and insufficient water depth (Warren and Pardew, 1998). Within federal lands in the northern Rocky Mountains, there are 1.3 culverts per road kilometer (FEMAT, 1993). Relative to fish, stream salamanders are poor swimmers, suggesting that culverts may significantly limit *D. aterrimus* movement along streams significantly (Sagar, 2004). Also, culverts may create predation hotspots that affect salamanders directly through increased mortality from large fish that accumulate in culvert outlets or indirectly through predator-avoidance behavior. However, these mechanisms remain speculative because we do not know the spatial extent, frequency, and pathways of movement in *D. aterrimus*. Future research is needed that addresses specifically the influence of culverts and roads on stream salamander movement.

The high importance weights of road density and stream connectivity in our occurrence models may relate to a reduced ability of *D. aterrimus* to recolonize suitable streams after natural disturbances in human-altered stream drainages. Natural disturbances, such as floods and debris flows, have been linked to impaired habitat quality and lower densities of *D. tenebrosus* and stream fishes (e.g., *Cottus* sp.) in

Oregon streams (Harvey, 1987; Swanson et al., 1998). Furthermore, land use activities in the surrounding drainage, such as road construction and timber harvest, are believed to exacerbate the impact of natural disturbance on the recolonization of biotic communities (Gregory et al., 1991; Swanson et al., 1998). The Lochsa River basin has a high frequency of natural disturbance that includes fire, rain on snow floods, and landslides (Jones, 1999). These disturbances are often confined to local stream reaches and are spatially heterogeneous within and across stream networks. For example, 49% of the Lochsa River basin has burned since 1910, and there is an average of 57 fire starts per year (Brown et al., 1994), but most fire starts burn less than 1 km². The combination of fire-damaged soils and rain-on-snow floods results in frequent landslide mass wasting events and debris flows that affect stream channels. In 1996–97, there were 907 landslides in this region; however, streams adjacent to roads and timber harvest may be more vulnerable to landslides, as 60% of the 1996–97 landslides were related to cut and fill slopes along roads and 12% were associated with timber harvest (Jones, 1999). All streams in our study area seem to be vulnerable to natural disturbance, but streams in drainages with roads may have an elevated extinction risk.

The negative relationship we observed between *D. aterrimus* occurrence and old-growth tree density may reflect a habitat condition that we did not measure, such as standing stock of primary production and invertebrate biomass. Previous studies on stream salamanders in the Pacific Northwest have shown increased occurrence and abundance of *Dicamptodon* species in streams running through clearcut and second-growth timber stands relative to streams in old-growth stands (Hawkins et al., 1983; Richardson and Neill, 1998; Steele et al., 2003). These increases are thought to be linked to increases in primary production and invertebrate biomass caused by greater light penetration and warmer temperatures of streams with removed riparian canopy cover (e.g., Hawkins et al., 1982). We are reluctant to make inferences about the influence of timber harvest on *D. aterrimus* and stream community dynamics because the covariate of old-growth density had a lower importance weight than road density and stream isolation. In addition, we believe that our metric of old-growth forest (northern Idaho old growth standards) failed to discern effects of timber harvest from effects of fire on stand structure. In our study area, fires have consumed old-growth trees in areas with and without roads; thus, most stands are mixed aged, similar to harvested areas. The occurrence of fire may explain

why road density is not correlated with forest stand structure.

We found that the *D. aterrimus* density was greatest in streams with a high proportion of fine-embedded substrate. For most stream amphibians, fine-embedded substrate is negatively correlated with occurrence and abundance because interstitial spaces between substrate provide egg-laying sites (Bruce, 1978), important refuge from natural disturbances (e.g., high-flow events) and predation (Sih et al., 1992), and are linked to increases in stream invertebrate richness and abundance (Flecker and Allan, 1984). A simple hypothesis to explain the observed relationship between *D. aterrimus* density and fine-embedded substrate is that sampling efficiency of *D. aterrimus* is greater when substrates are more embedded. We can reject this hypothesis because probability of recapture was not correlated with embedded substrate or any other local-scale variables. Rather, the positive association with fine-embedded substrate may reflect adaptation to natural disturbances such as fires and landslides that add sediment to streams (Lytle and Poff, 2004). Streams in the Selway-Bitterroot Wilderness Area, where only natural disturbances occur, have greater stream sediment volumes than streams in the adjacent national forest land, where roads and timber harvest also occur (Jones, 1999). Having evolved with high stream sediment loads in the Lochsa River basin, *D. aterrimus* may be able to burrow through the fine sediment to seek refugia, or they may use microhabitat sites that our surveys did not record, such as undercut banks. It is interesting to note that this species may not need refugia from fish predation: models of *D. aterrimus* occurrence and density had weak support for the covariate of fish presence (Tables 2–5).

Conclusion.—We found that landscape-scale models were the best predictors of *D. aterrimus* occurrence in the Lochsa River basin. Specifically, we found that probability of *D. aterrimus* occurrence was greatest in roadless drainages and lowest in isolated stream drainages. In addition, we found that the relative density of *D. aterrimus* was greatest in streams with a high proportion of embedded substrate and fine sediment. These results suggest that *D. aterrimus* patches are spatially structured across stream networks and that *D. aterrimus* is tolerant of a wide range of local conditions within streams. Further research is needed on *D. aterrimus* natural history for a mechanistic understanding of local habitat associations. We suggest that management efforts focus on protecting roadless areas and restoring stream and overland connec-

TABLE 4. Model selection results (AIC values corrected for small sample size) for the relative density of *Dicamptodon aterrimus* in headwater streams in the Lochsa River basin, Idaho, USA. K refers to the number of parameters in each model, including the intercept. Boldface type indicates the best model and all those with an Akaike weight (w) > 0.1. The evidence ratio (w_j/w_i) indicates the multiplicative probability by which the best model (w_j) is more likely than competing models (w_i), given the set of candidate models and the data. Covariate abbreviations are listed in Table 1.

Model name	Log-likelihood	K	ΔAIC_c	w	Evidence ratio
Density					
ES	-51.31	2	0.00	0.21	1
ES, FP	-51.97	3	1.67	0.09	2.33
ES, SW	-51.75	3	2.10	0.07	3.00
ES, A	-51.66	3	2.28	0.07	3.00
ES, ST	-51.66	3	2.29	0.07	3.00
ES, P	-51.53	3	2.54	0.06	3.50
ES, P, FP	-52.62	4	3.86	0.03	7.00
Global: P, ES, ST, A, SW, FP	-53.15	7	17.90	0.00	—

tivity in human-impacted areas, rather than on only improving habitat quality within a stream.

Our analysis of models relating *D. aterrimus* occurrence and density to local and landscape factors is a useful starting point for understanding the spatial ecology and habitat associations of this stream salamander species. Our results support findings of other studies of amphibians and stream fishes in the Pacific Northwest and Northern Rocky Mountains that show the importance of roadless areas and stream connectivity to population persistence (e.g., Dunham and Rieman, 1999; Rieman and Dunham, 2000; Welsh and Ollivier, 1998). We also found that *D. aterrimus* had broad habitat requirements and was positively associated with embedded substrate. These results conflict with data on other stream amphibian species about local habitat associations and question the broad application of amphibian occurrence

and abundance as ecosystem indicators of human land-use. We caution that our management recommendations are based on limited information about *D. aterrimus* occurrence and density patterns. Our understanding of the conservation biology of this and other stream amphibians would be strengthened with future research using direct (i.e., mark-capture-recapture and radio-telemetry) and indirect (i.e., genetics) methods to determine the spatial structure of populations, the frequency of dispersal between populations, and dispersal pathways.

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TABLE 5. Importance weights, coefficients (range), and 95% confidence intervals of local habitat covariates predicting *Dicamptodon aterrimus* density, obtained by averaging across all models weighted by the Akaike weights (Burnham and Anderson, 2002). The intercept is not shown. Boldface indicates estimates for which the 95% confidence intervals did not overlap zero.

Scale	Importance weight	Coefficient estimate	95% C.I.
P	0.22	0.09 (0.02 to 0.80)	0.16
ES	0.79	0.03 (0.02 to 0.04)	0.00
ST	0.20	0.01 (0.00 to 0.02)	0.01
A	0.26	-0.14 (-0.24 to 0.07)	0.13
SW	0.23	-0.08 (-0.19 to 0.01)	0.08
FP	0.28	-0.04 (-0.11 to -0.02)	0.03

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LITERATURE CITED

- ALFORD, R. A., AND S. J. RICHARDS. 1999. Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30:133–165.
- BAILEY, L., T. R. SIMONS, AND K. H. POLLOCK. 2004. Estimating site occurrence and species detection probability parameters for terrestrial salamanders. *Ecological Applications* 14:692–702.
- BENDA, L., N. L. POFF, D. MILLER, T. DUNNE, G. REEVES, M. POLLOCK, AND G. PESS. 2004. Network dynamics hypothesis how river networks structure riverine habitats. *BioScience* 54:413–427.
- BRADFORD, D. F., A. C. NEALE, M. S. NASH, D. W. SADA, AND J. R. JAEGER. 2003. Habitat patch occurrence by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. *Ecology* 84:1012–1023.
- BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- BROWN, J. K., S. F. ARNO, S. W. BARRETT, AND J. P. MENAKIS. 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. *International Journal of Wildland Fire* 4:157–168.
- BRUCE, R. C. 1978. Life-history patterns of the salamander *Gyrinophilus porphyriticus* in the Cowee Mountains, North Carolina. *Herpetologica* 34:325–332.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. Springer-Verlag, New York.
- BURY, R. B., F. S. CORN, K. B. AUBRY, F. F. GILBERT, AND L. L. C. JONES. 1991. Aquatic amphibian communities in Oregon and Washington. *In* L. F. Rugiero, K. B. Aubry, A. B. Carey, and M. H. Huff (tech. coords.), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests*, pp. 353–362. USDA Forest Service General Technical Report PNW-285.
- CARR, L. W., AND L. FAHRIG. 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15:1071–1078.
- CARSTENS, B. C., J. D. DEGENHARDT, A. L. STEVENSON, AND J. SULLIVAN. 2005. Accounting for coalescent stochasticity in testing phylogeographical hypotheses: modeling Pleistocene population structure in the Idaho Giant Salamander *Dicamptodon aterrimus*. *Molecular Ecology* 14:255–265.
- CUSHMAN, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128:231–240.
- DAVIC, R. D., AND H. H. WELSH JR. 2004. On the ecological role of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35:405–434.
- DEMAYNADIER, P. G., AND M. L. HUNTER JR. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340–352.
- DUNHAM, J. B., AND B. E. RIEMAN. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642–655.
- DUNNING, J. B., B. J. DANIELSON, AND H. R. PULLIAM. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- FAGAN, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249.
- FAHRIG, L., AND G. MERRIAM. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- FEMAT. 1993. *Forest Ecosystem Management: An Ecological, Economic, and Social Assessment*, Portland, OR. Report of Forest Ecosystem Management Assessment Team (FEMAT), Government Printing Office, Washington, DC.
- FLECKER, A. S., AND J. D. ALLAN. 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distributions. *Oecologia* 64:306–313.
- GREEN, P., J. JOY, D. SIRUCEK, W. HANN, A. ZACK, AND B. NAUMANN. 1992. *Old-Growth Forest Types of the Northern Region*. Northern Region, R-1 SES 4/92. Missoula, MT.
- GREGORY, S. V., F. J. SWANSON, W. A. MCKEE, AND K. W. CUMMINS. 1991. An ecosystem perspective of riparian zones. *Bioscience* 41:540–551.
- GRESSWELL, R. E., AND C. E. TORGENSEN. 2006. A spatially explicit approach for evaluating relationships among coastal cutthroat trout, habitat, and disturbance in small Oregon streams. *American Fisheries Society Symposium* 48:457–471.
- GRIALOU, J. A., S. D. WEST, AND R. N. WILKINS. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. *Journal of Wildlife Management* 64:105–113.
- HAIRSTON, N. G. 1987. *Community Ecology and Salamander Guilds*. Cambridge University Press, Cambridge.
- HANSKI, I., AND M. E. GILPIN. 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, CA.
- HARVEY, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* 116:851–855.
- HASTINGS, A., AND S. HARRISON. 1994. Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25:167–188.
- HAWKINS, C. P., M. L. MURPHY, AND N. H. ANDERSON. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840–1856.
- HAWKINS, C. P., M. L. MURPHY, N. H. ANDERSON, AND M. A. WILZBACH. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams in the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1173–1182.

- HAWKINS, C. P., J. L. KERSHNER, P. A. BISSON, M. D. BRYANT, L. M. DECKER, S. V. GREGORY, D. A. MCCULLOUGH, C. K. OVERTON, G. H. REEVES, R. J. STEEDMAN, AND M. K. YOUNG. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18:3–12.
- JOHNSTON, B., AND L. FRID. 2002. Clearcut logging restricts the movements of terrestrial Pacific Giant Salamanders (*Dicamptodon tenebrosus* Good). *Canadian Journal of Zoology* 80:2170–2177.
- JONES, D. 1999. Hydrology and Water Quality Report for the LRB Analysis, 12 July 1999, Clearwater National Forest, Orofino, ID.
- KEATING, K. A., AND S. CHERRY. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68:774–789.
- KNAPP, R. A., K. R. MATTHEWS, H. K. PREISLER, AND R. JELLISON. 2003. Developing probabilistic models to predict amphibian site occurrence in a patchy landscape. *Ecological Applications* 13:1069–1082.
- LANE, E. W. 1947. Report of the Subcommittee on Sediment Terminology. Transactions, American Geophysical Union 28:936–938.
- LAWTON, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–192.
- LEVINS, R. 1970. Extinction. In M. Gerstenhaber (ed.). *Some Mathematical Problems in Biology*, pp. 75–107. American Mathematical Society, Providence, RI.
- LOWE, W. H. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. *Ecology* 84:2145–2154.
- LOWE, W. H., AND D. T. BOLGER. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. *Conservation Biology* 16:183–193.
- LOWE, W. H., G. E. LIKENS, M. A. MCPEEK, AND D. C. BUSO. 2006. Linking direct and indirect data on dispersal: isolation by slope in a headwater stream salamander. *Ecology* 87:334–339.
- LYTLE, D. H., AND N. L. POFF. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94–100.
- MACARTHUR, R., AND R. LEVINS. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the United States of America* 51:1207–1210.
- MACDONALD, L. H., AND J. A. HOFFMAN. 1995. Causes of peak flows in northwestern Montana and northeastern Idaho. *Journal of the American Water Resources Association* 31:79–95.
- MACKENZIE, D. I., AND J. A. ROYLE. 2005. Designing efficient occupancy studies: general advice and tips on allocation of survey effort. *Journal of Applied Ecology* 42:1105–1114.
- MACKENZIE, D. I., J. D. NICHOLS, N. SUTTON, K. KAWANISHI, AND L. L. BAILEY. 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86:1101–1113.
- MARSH, D. M., AND P. B. PEARMAN. 1997. Effects of habitat fragmentation on the abundance of two species of Leptodactylid frogs in an Andean montane forest. *Conservation Biology* 11:1323–1328.
- MARSH, D. M., AND P. C. TRENHAM. 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15:40–49.
- MARSH, D. M., G. S. MILAM, N. R. GORHAM, AND N. G. BECKMAN. 2005. Forest roads as partial barriers to terrestrial salamander movement. *Conservation Biology* 19:2004–2008.
- MCCLELLAND, D. E., R. B. FOLTZ, W. D. WILSON, T. W. CUNDY, R. HEINEMANN, J. A. SAURBIER, AND R. L. SCHUSTER. 1997. Assessment of the 1995 and 1996 floods and landslides on the Clearwater National Forest, Part I: Landslide Assessment. A Report to the Regional Forester, Northern Region, U.S. Forest Service, December 1997.
- NOVINGER, D. C., AND F. J. RAHEL. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology* 17:772–781.
- NUSSBAUM, R. A., E. D. BRODIE JR., AND R. M. STORM. 1983. *Amphibians and Reptiles of the Pacific Northwest*. University of Idaho Press, Moscow.
- PARKER, M. S. 1991. Relationship between cover availability and larval Pacific Giant Salamander density. *Journal of Herpetology* 25:355–357.
- PETERMAN, W. E., J. A. CRAWFORD, AND R. D. SEMLITSCH. 2008. Productivity and significance of headwater streams: population structure and biomass of the Black-Bellied Salamander (*Desmognathus quadramaculatus*). *Freshwater Biology* 53:347–357.
- PETRANKA, J. W., AND C. T. HOLBROOK. 2006. Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? *Restoration Ecology* 14:404–411.
- PILLIOD, D. S., R. B. BURY, E. J. HYDE, C. A. PEARL, AND P. S. CORN. 2003. Fire and amphibians in North America. *Forest Ecology and Management* 178:163–181.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- RICH, C. F., JR., T. E. MCMAHON, B. E. RIEMAN, AND W. L. THOMPSON. 2003. Local habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. *Transactions of the American Fisheries Society* 132:1053–1064.
- RICHARDSON, J. S., AND W. E. NEILL. 1998. Headwater amphibians and forestry in British Columbia: Pacific Giant Salamanders and Tailed Frogs. *Northwest Science* 72:122–123.
- RICKLEFS, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167.
- RIEMAN, B. E., AND J. B. DUNHAM. 2000. Metapopulations and salmonid fishes: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* 9:51–64.
- RONI, P. 2002. Habitat use by fishes and Pacific Giant Salamanders in small western Oregon and Washington streams. *Transactions of the American Fisheries Society* 131:743–761.
- SAGAR, J. P. 2004. Movement and Demography of Larval Coastal Giant Salamanders (*Dicamptodon tenebrosus*) in Streams with Culverts in the Oregon Coast Range. Unpubl. master's thesis, Oregon State University, Corvallis.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.

- SCHLOSSER, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* 76:908–925.
- SEMLITSCH, R. D., T. J. RYAN, K. HAMED, M. CHATFIELD, B. DREHMAN, N. PEKAREK, M. SPATH, AND A. WATLAND. 2007. Salamander abundance along road edges and within abandoned logging roads in Appalachian forests. *Conservation Biology* 21:159–167.
- SHURIN, J. B., AND E. G. ALLEN. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *American Naturalist* 158:624–637.
- SIH, A., L. B. KATS, AND R. D. MOORE. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology* 73:1418–1430.
- SJOGREN-GULVE, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* 75:1357–1367.
- SMITH, M. A., AND D. M. GREEN. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28:110–128.
- STEBBINS, R. C. 2003. *Western Reptiles and Amphibians*. 3rd ed. Houghton Mifflin Company, Boston, MA.
- STEELE, C. A., E. D. BRODIE JR., AND J. G. MACCRACKEN. 2003. Relationships between abundance of cascade torrent salamanders and forest age. *Journal of Wildlife Management* 67:447–453.
- STODDARD, M. A., AND J. P. HAYES. 2005. The influence of forest management on headwater stream amphibians at multiple spatial scales. *Ecological Applications* 15:811–823.
- STORFER, A. 2003. Amphibian declines: future directions. *Diversity and Distributions* 9:151–163.
- STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 3:1783–1786.
- SWANSON, F. J., S. L. JOHNSON, S. V. GREGORY, AND S. A. ACKER. 1998. Flood disturbance in a forested mountain landscape. *Bioscience* 48:681–689.
- TRENHAM, P. C., W. D. KOENIG, AND H. B. SHAFFER. 2001. Spatially autocorrelated demography and inter-pond dispersal in the salamander, *Ambystoma californiense*. *Ecology* 82:3519–3530.
- TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- VAN BUSKIRK, J. 2005. Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86:1936–1947.
- WARREN, M. L., AND M. G. PARDEW. 1998. Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* 127:637–644.
- WELSH, H. H., L. M. OLLIVIER, AND D. G. HANKIN. 1997. A habitat-based design for sampling and monitoring stream amphibians with an illustration from Redwood National Park. *Northwestern Naturalist* 78:1–16.
- WELSH, H. H., JR., AND A. J. LIND. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou Region of California and Oregon. *Journal of Wildlife Management* 66:581–602.
- WELSH, H. H., JR., AND L. M. OLLIVIER. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's Redwoods. *Ecological Applications* 8:1118–1132.
- WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.

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