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Habitat Fragmentation and Extinction Risk of Lahontan Cutthroat Trout

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Abstract.—We used survey data collected by the Nevada Division of Wildlife to analyze presence or absence of Lahontan cutthroat trout *Oncorhynchus clarki henshawi* in relation to habitat fragmentation (isolation), habitat size and shape, presence or absence of nonnative salmonids, elevation, latitude, longitude, and precipitation regime for 119 stream basins in the eastern Lahontan basin. Multiple logistic regression analysis revealed stream basin isolation to be the only significant correlate of Lahontan cutthroat trout occurrence. Eighty-nine percent of stream basins connected to another basin containing Lahontan cutthroat trout also supported Lahontan cutthroat trout, while only 32% of isolated stream basins supported Lahontan cutthroat trout. This analysis highlights the potentially negative effect of habitat fragmentation on population persistence for this threatened species.

Fisheries management in coldwater streams has often focused on small-scale habitat restoration to enhance production (see Reeves et al. 1991). The ever-increasing list of imperiled fishes in such systems (Williams et al. 1989; Nehlsen et al. 1991), however, has shifted much of the management emphasis from population production to population persistence (Minckley and Deacon 1991; Rieman et al. 1993). The need to identify factors affecting population viability of imperiled species is a major challenge to fishery managers, who must address urgent conservation problems with limited financial resources and time. Detailed demographic and time series data required for population viability analyses are expensive and difficult to collect. Current methods of analysis are also controversial (Boyce 1992; Caughley 1994; Mills et al. 1996).

In contrast, patterns of species occurrence (presence or absence) are much less expensive and easier to determine. Although such data are less detailed, they have nonetheless proven valuable in ecology and conservation biology (MacArthur and Wilson 1967; Taylor 1991; Rieman and McIntyre 1995; Hanski et al. 1996). Here, we present results of a large-scale analysis of Lahontan cutthroat trout *Oncorhynchus clarki henshawi* occurrence in stream habitats of the eastern Lahontan basin, in northern Nevada (Figure 1).

Lahontan cutthroat trout is a federally listed threatened subspecies (Office of the Federal Register 40[1975]:29864; Coffin and Cowan 1995). Recent studies have indicated that a large-scale perspective may be necessary to understand the factors associated with local extinctions of stream-living Lahontan cutthroat trout populations (Dunham 1996). Comparative ecological studies of populations in fragmented and interconnected stream basins suggested that fragmentation of stream habitats has led to a loss of recolonization potential, reduced life history and habitat diversity, and decreased individual movement (Dunham 1996).

In general, fragmentation of stream habitats may increase the risk of extinction by reducing habitat area, complexity, and connectivity (Rieman and McIntyre 1993, 1995, 1996; Reeves et al. 1995; Schlosser and Angermeier 1995). Because habitat fragmentation simultaneously decreases the average area and connectivity of occupied habitats, the effects of reduced habitat area and isolation may

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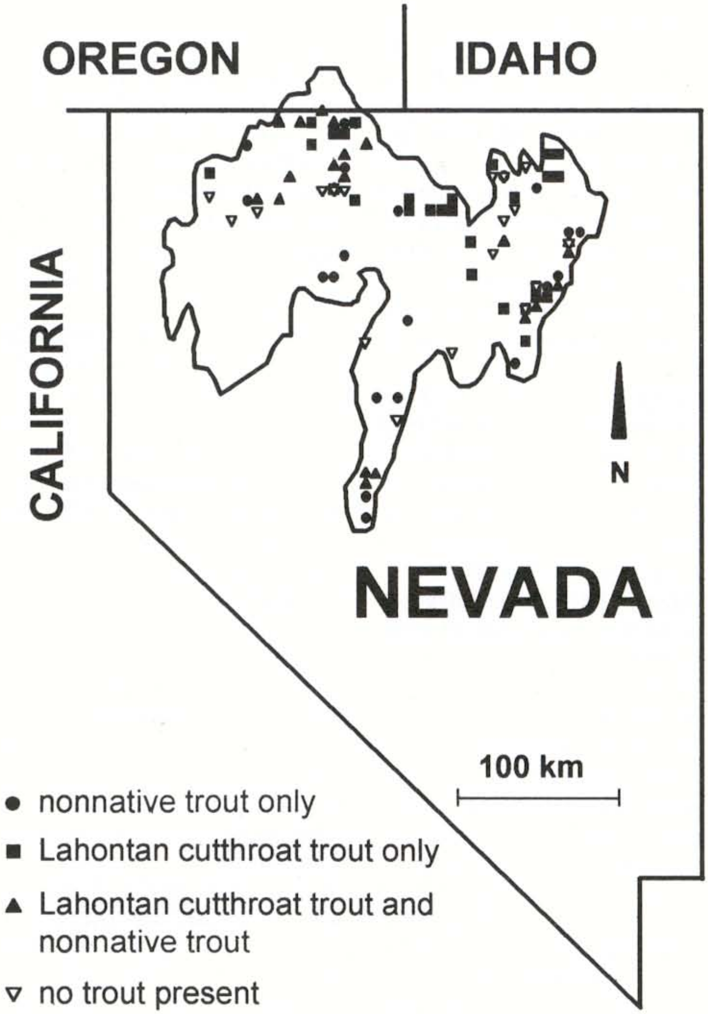

FIGURE 1.—Geographic distribution of the 119 stream basins sampled within the eastern Lahontan basin of Nevada and southeastern Oregon (solid outline). Symbols represent occurrences of nonnative trout and Lahontan cutthroat trout.

act together to increase the risk of extinction (MacArthur and Wilson 1967; Fahrig and Merriam 1994; Harrison and Taylor 1996). These observations suggest that habitat fragmentation may increase the risk of extinction of stream-living Lahontan cutthroat trout populations.

We investigated the potential impacts of habitat fragmentation on extinction risk in an analysis of Lahontan cutthroat trout in 119 stream basins in the eastern Lahontan basin. Presence or absence of Lahontan cutthroat trout was related to habitat fragmentation, habitat size and shape, presence or absence of nonnative salmonid fishes, elevation, latitude, longitude, and precipitation regime. Results of this analysis were used to identify potentially important factors associated with local extinctions and assess extinction risk among populations.

Methods

Lahontan cutthroat trout are endemic to the Lahontan basin, located in the northwest region of the Great Basin of northern Nevada, northeastern California, and southeastern Oregon (Behnke 1992). Cutthroat trout colonized the Lahontan Basin as early as the mid-Pleistocene (Behnke 1992). Historically, cutthroat trout had access to myriad stream habitats and large lakes in the basin. The most recent high stand of pluvial Lake Lahontan occurred about 14,000 years ago, when the lake covered approximately 22,100 km^2 (La Rivers 1962; Benson et al. 1990). Lake Lahontan desiccated to present levels by about 8,000 years ago, isolating cutthroat populations in the eastern (Quinn and Humboldt river) basins from those in the western basins draining the eastern Sierra Nevada mountains (Loudenslager and Gall 1980; Behnke 1992). Behnke (1992) considers the eastern form of Lahontan cutthroat trout to be a unique subspecies, but a formal description has yet to be published.

The geographic range of Lahontan cutthroat trout includes a broad diversity of habitats from cold, oligotrophic, alpine and subalpine lakes and streams, to streams and lakes in the warmer interior deserts of the Lahontan basin (La Rivers 1962). Our study included Lahontan cutthroat trout stream habitats from the Quinn and Humboldt river systems in Nevada (Figure 1). In the last 150 years, Lahontan cutthroat trout have been virtually eliminated from the western Lahontan basin and currently persist in only about 10% of their original habitat in the eastern basin (Coffin and Cowan 1995). Loss of cutthroat trout populations has been attributed to habitat loss and degradation, interactions with nonnative salmonids, and overexploitation (Coffin and Cowan 1995).

Data collection and analysis.—In summary, our approach was to (1) examine a large database of stream basins surveyed by the Nevada Division of Wildlife (NDOW) within the historic range of Lahontan cutthroat trout, (2) establish fish presence or absence in each from NDOW records, (3) summarize data on physical and biotic characteristics of stream basins, and (4) analyze cutthroat trout occurrence in relation to these characteristics.

Cutthroat trout occurrences were validated from the NDOW surveys, historical records (Snyder 1917; Coffin 1981, 1983; Gerstung 1988; Coffin and Cowan 1995), and consultations with NDOW biologists. With the exception of a single stream basin surveyed by us, only stream basins surveyed by NDOW were included in the analysis (NDOW, unpublished data). Stream basins surveyed by NDOW were selected if they were thought to have potential to support Lahontan cutthroat trout or nonnative trout fisheries (Coffin 1983). These were often higher-elevation habitats, rather than a random sample of all stream basins formerly occupied by Lahontan cutthroat trout (Coffin and Cowan 1995). Accordingly, we restricted our inferences from the analysis to these stream basins or those closely associated with them (e.g., other stream basins in the NDOW database).

Stream basin surveys consisted of single- or multiple-pass electrofishing at several sites in each stream basin. The number and spacing of sites surveyed varied, depending on the number and total length of perennial streams. Most stream basins had been sampled at least twice within the past 20 years. All sampling was conducted as streams approached base flows in summer and fall (June–October).

Fish sampling was intensive in all stream basins, but effort was clearly unequal, which introduced a potential bias in determination of occurrence. Two lines of evidence suggest potential problems with "false absences" are of little concern. First, in our field reconnaissance of over 50 currently unoccupied streams (J.B.D. and G.L.V., personal observations), we never found Lahontan cutthroat trout in previously undocumented localities. Second, the Lahontan cutthroat data were reviewed by experienced agency biologists (P. Coffin, J. French, G. Johnson, R. Phenix, and M. Sevon, personal communications) to minimize error in determination of occurrence.

In a few cases, determination of cutthroat occurrence was complicated by hybridization of cutthroat with rainbow trout *Oncorhynchus mykiss* or other subspecies of cutthroat trout (e.g., Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*) (Sevon et al. 1997). If introgressive hybrization was suspected, we adopted the philosophy of Dowling and Childs (1992) and scored such populations as Lahontan cutthroat trout. Unpublished reports of genetic studies contracted by NDOW indicate very low levels of introgressive hybridization in Lahontan cutthroat trout from the eastern Lahontan basin (Coffin and Cowan 1995; Sevon et al. 1997).

Because cutthroat trout have good dispersal abilities (Dunham 1996) and apparently persist in even very small habitats (Coffin 1981, 1983; Gerstung 1988; Dunham 1996), we assumed all accessible (i.e., downstream of physical migration barriers) perennial stream habitats above 1,500 m in elevation (see below) historically contained Lahontan cutthroat trout, regardless of current conditions. Lahontan cutthroat trout have been extirpated from over 90% of their original stream habitats in the last 150 years (Coffin and Cowan 1995), and we assumed that most cutthroat absences reflect extinctions that occurred within this time frame.

It was not possible to examine directly the ef-

TABLE 1.—Definition of variables considered in analyses of Lahontan cutthroat trout occurrence.

Variable	Derivation or definition
Total basin area (km^2)	Digitized from U.S. Geological Survey (USGS) topographical maps
Basin shape[a] factor	Square of maximum straight line length of basin divided by total basin area
Elongation ratio[b] (m^{-1})	Diameter of a circle with same area as that of the basin divided by total basin area.
Relief ratio[a] (m^{-1})	Total elevational relief (maximum minus minimum elevation) divided by total basin area.
Average, maximum, and minimum basin elevations (m)	Estimated to nearest 40 m from USGS topographical maps.
Maximum precipitation[c] (cm)	From contour maps of 6-h, 100-year precipitation events.
Nonnative salmonids	Scored 1 if present, 0 if absent.
Fragmentation	Scored 1 if the basin was connected to another with Lahontan cutthroat trout, 0 if not
Latitude, longitude (degrees)	Converted from geographic coordinates given in Nevada Division of Wildlife surveys

[a] Murphey et al. (1977).
[b] Morisawa (1958).
[c] Miller et al. (1973).

fects of land uses (e.g., livestock grazing, dewatering, mining, roads) implicated in the destruction of Lahontan cutthroat trout habitat because they are difficult (and expensive) to quantify (Platts and Nelson 1988; Brussard et al. 1994). In addition, the effects of past land use (i.e., within the last 150 years) may not be observable in the present. Other factors that may cause extirpation of fish populations in the Great Basin include fires (Minshall et al. 1989), floods and associated debris flows (Erman et al. 1988; Strange et al. 1992), droughts and high water temperatures (Keleher and Rahel 1996), freezing in winter (Nelson et al. 1992), interactions with nonnative salmonids (Griffith 1988; Coffin and Cowan 1995), and habitat fragmentation (Rieman and McIntyre 1993, 1995; Dunham 1996). In general, the negative effects of these factors on fish populations are likely to be exacerbated by disruptive land use activities (see Meehan 1991 for example papers).

We focused this exploratory analysis on physical and biotic variables that could be measured from maps or from existing data sets and that might affect fish population persistence (Table 1). Physical and biotic habitat variables measured for each stream basin included several geomorphic descriptors of basin shape previously shown to be related to flood characteristics of arid streams (Morisawa 1958; Murphey et al. 1977; Gordon et al. 1992; Table 1). Basin elevation (maximum, minimum, average) and precipitation characteristics of the stream basins were obtained from topographic and climatological maps (Table 1).

Fragmentation (isolation) and presence or absence of nonnative salmonids were established from NDOW survey records of fish distributions and reviews by agency biologists. No other nonnative, nonsalmonid fishes known from Nevada (i.e., centrachids, ictalurids, or cyprinids; La Rivers 1962) occurred in stream basins considered in this study.

Stream basin areas were estimated by digitizing watershed boundaries on 1:100,000-scale topographic maps (Table 1). The lower (downstream) limit of a stream basin was defined as the point at which a stream joined another of equal ordinal rank (stream order; Horton 1945), or by the 1,500-m elevational contour. Records indicate 1,500 m to be the historical lower elevation limit of stream-living Lahontan cutthroat trout in the Humboldt and Quinn river systems (Snyder 1917; J. Curran, Nevada Division of Wildlife, personal communication). Here, we use the term "historical" in reference to conditions that existed approximately 150 years ago. Watershed boundaries, as defined here, correspond with those identified in the current recovery plan for Lahontan cutthroat trout (Coffin and Cowan 1995).

All statistical treatments of data on stream basins were based on information summarized or collected at this spatial scale. Cutthroat trout occurrence in 119 stream basins was analyzed in relation to physical and environmental habitat variation with multiple logistic regression (Aldrich and Nelson 1984; Hosmer and Lemeshow 1989). All data analyses were conducted with the SAS LOGISTIC procedure (SAS Institute 1995).[3]

Results

Of the 119 stream basins included in this study (Figure 1), 45% were occupied by Lahontan cutthroat trout and 56% were occupied by nonnative salmonids, including brook trout *Salvelinus fontinalis,* rainbow trout, and brown trout *Salmo trutta.* Trout of any species were absent from 25% of the streams sampled. Physical environmental characteristics varied widely among stream basins (Table 2). For example, average elevation was 2,275 m,

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[3] The use of trade or firm names in this paper is for reader information only and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

TABLE 2.—Statistical summary of eight continuous habitat variables (Table 1) used in analyses of Lahontan cutthroat trout occurrence.

Variable	Mean	CV (%)[a]	Range
Total basin area (km^2)	80.3	235.1	2.2–1,721.0
Basin shape factor	4.5	90.4	0.7–34.4
Elongation ratio (m^{-1})	3.3	89.1	0.5–20.7
Relief ratio (m^{-1})	15.6	99.5	0.4–88.4
Average elevation (m)	2,275.0	11.1	1,824–2,860
Maximum elevation (m)	2,807.3	13.2	2,100–3,588
Minimum elevation (m)	1,742.8	12.6	1,500–2,400
Maximum precipitation (cm)	5.1	12.5	4.1–6.1

[a] Coefficient of variation (CV), 100·SD/mean.

and ranged from 1,824 to 2,860 m (Table 2). Stream basin area averaged 80 km^2 and ranged from 2 to 1,721 km^2 (Table 2); however, only 2 of 119 stream basins were larger than 300 km^2.

All variables in the analysis (Table 1) were screened with best subsets logistic regression (SAS Institute 1995). Only habitat fragmentation was significantly related to occurrence of Lahontan cutthroat trout (Wald $X^2 = 29.3$, $df = 1$, $P < 0.0001$). Overall, cutthroat trout occurred in 89% of 47 interconnected stream basins and only 32% of 72 fragmented (isolated) stream basins. Possible interactions between habitat fragmentation and the other variables were examined, but none were significant. The logistic regression model based only on fragmentation correctly classified over 75% of the observations with a probability cutoff of 0.50.

Discussion

Results of this large-scale analysis of Lahontan cutthroat trout occurrence support the conclusions of other, smaller-scale studies (Dunham 1996) and highlight the risk of extinction posed by habitat fragmentation and isolation of local populations in aquatic habitats (Rieman and McIntyre 1993, 1995). Isolation of local populations may increase the risk of extirpation by preventing immigration and recolonization (Stacey and Taper 1992). In addition to isolation, habitat fragmentation reduces the size or area of remaining isolates (Fahrig and Merriam 1994). Reductions in habitat size may lead to losses of habitat complexity and life history variation and reductions in population size, all of which may increase the risk of population extinction (den Boer 1968; Rieman and McIntyre 1993, 1995; Fahrig and Merriam 1994; Schlosser and Angermeier 1995). Thus, habitat fragmentation may increase the risk of local extinctions through isolation and area-related effects, which may not be wholly independent (MacArthur and Wilson 1967).

The lack of any relationship between cutthroat trout occurrence and factors other than habitat fragmentation could mean that those factors do not affect occurrence, but it might mean that our analysis simply could not detect their individual effects (among many), or that they operate on different spatial or temporal scales. Multiple factors such as fires, floods, droughts, extreme temperatures, nonnative species, destructive land use practices, and overexploitation all may affect population persistence of stream fishes. If many of these operate simultaneously, it may be difficult to detect the effect of any one factor unless its influence is very great. Certain agents of extinction may have strong effects in individual basins but show a weak overall effect in an analysis of many stream habitats affected by a variety of factors functioning at different scales (sensu Fausch et al. 1994). If multiple factors act sequentially or simultaneously, factors associated with local extinctions may need to be considered on a case-specific basis. Factors listed above as affecting population persistence also may be agents of habitat fragmentation.

Other work on salmonids has shown occurrence to be related to stream size and basin area (Rieman and McIntyre 1995). Lack of area effects in this study may be due to the difficulty of determining the limits of Lahontan cutthroat trout distributions within drainage basins. We assumed cutthroat trout were not present below 1,500 m in elevation, the apparent lower limit of this species in historical times. Presumably, high summer temperatures excluded cutthroat trout from low-elevation habitats. Today, numerous water diversions and various other forms of habitat degradation have changed stream habitats profoundly in the Lahontan basin. Changes in the distribution of cutthroat trout in response to these impacts have not been uniform. For example, the contemporary lower elevation limit of cutthroat populations in streams ranges from at least 1,650 to 1,950 m (J.B.D., personal observations). Furthermore, seasonal and annual changes in climatic conditions and stream discharge can lead to dramatic population expansions or contractions (Dunham 1996).

For these reasons, our measure of habitat patch size may not have defined population boundaries as accurately as those used in other studies (e.g., Rieman and McIntyre 1995). Consequently, our definition of fragmentation may reflect area as well as isolation effects. In essence, they are the same until a more refined definition of the distribution of local populations is possible. Factors not directly measured in this study also may affect extinction risk for cutthroat trout populations, and we caution that isolation alone is not necessarily a direct agent of extinction. Rather, isolation, by elimination of migration, dispersal, and recolonization, may lead to an irreversible pattern of progressive local extinctions.

Studies of recolonization (Dunham 1996) and the success of transplants following local extinctions (Coffin 1983) provide direct evidence of the importance of habitat connectivity and dispersal to the long-term persistence of Lahontan cutthroat trout populations. For example, severe drought conditions in the late 1980s and early 1990s apparently led to extirpation of Lahontan cutthroat trout from several tributaries and sections of the main-stem Marys River (Dunham 1996). These habitats were rapidly recolonized following the return of cooler, wetter conditions in 1993 (Dunham 1996). In another example, an isolated Lahontan cutthroat trout population extirpated by severe flooding in the 1950s was reestablished by a transplant in 1972 (Coffin 1983). Historically, natural recolonization may have maintained this population when Lahontan cutthroat trout occupied adjacent main-stem river habitats, and when the stream itself was not isolated by water diversions (J.B.D., personal observations).

An alternative mechanism to habitat fragmentation that may produce a pattern similar to that we observed, is spatial autocorrelation of unmeasured habitat characteristics. If similar environmental conditions occur in geographically proximate habitats, the occurrence of Lahontan cutthroat trout may be a product of both among-habitat movement and spatially correlated environments. It is becoming increasingly clear in ecological work that larger-scale patterns in the distributions of animals may emerge both as a result of processes such as extinction and recolonization and through the clustering of populations across large-scale environmental gradients. Further work will be necessary to more clearly define the effects of isolation and spatially correlated habitat characteristics (sensu Harrison and Quinn 1989; Rieman and McIntyre 1996).

In summary, evidence from this and other (Dunham 1996) analyses of local extinctions supports the hypothesis that habitat fragmentation may reduce the long-term viability of Lahontan cutthroat trout populations. In terms of recovery of Lahontan cutthroat trout, much progress may be needed to restore the interconnected populations and stream habitats necessary for long-term population persistence. Management efforts that focus limited resources exclusively on the maintenance of isolated populations may sacrifice long-term population viability for short-term successes.

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