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Biogeographic Analysis of the Coeur d'Alene Salamander *(Plethodon idahoensis)*

Abstract

We constructed a map comparing the U.S. geographic range of the Coeur d'Alene salamander (*Plethodon idahoensis*) with climatic and geological variables. Lilac bloom dates were used to approximate 1,100-1,800 m upper altitudinal limits for the salamander. *Plethodon idahoensis* occupies temperate regions of the northern Rocky Mountains with at least 50 cm average annual precipitation, and appears to be geographically restricted by unconsolidated geological deposits. Our map identifies regions potentially inhabited by *P. idahoensis*, and may therefore be useful in future study and protection of this species.

Introduction

The Coeur d'Alene salamander (*Plethodon idahoensis*) is a terrestrial amphibian inhabiting northern Idaho, northwestern Montana, and southeastern British Columbia; it is the sole lungless salamander (Plethodontidae) of the northern Rocky Mountains (Nussbaum et al. 1983, Holmberg et al. 1984). Although the species' geographic range has been largely defined (Orchard 1991, Wilson et al. 1997), much of the area inhabited by *P. idahoensis* remains unsurveyed. Little is known of specific factors that influence the salamander's occurrence, and potential habitat has not been identified.

We used cartographic methods (Lynch 1981) to compare the distribution of *P. idahoensis* with variables known to influence occurrence of other terrestrial salamanders. These include levels of precipitation and annual duration of cold weather, which affect foraging (Lynch 1981) and reproduction (Houck 1977), and the presence of rocky microhabitat, which can affect availability of shelter and nesting sites (Bury et al. 1991). Our objective was to produce a map that identifies limiting factors and reveals regions potentially inhabited by *P. idahoensis*.

Methods

We compiled localities from museum and field surveys of Wilson et al. (1997). These are listed with the Idaho Natural Heritage Program, Boise, and the Montana Natural Heritage Program, Helena. Localities were plotted on U.S. Geological Survey topographic maps (1:500,000 scale) to provide a base for environmental factors. We transferred the isohyet of lowest value encompassing all populations from average annual precipitation maps (USDA Soil Conservation Service 1965a, 1965b, 1965c; Pacific Northwest River Basins Commission 1969) to outline regions having at least the minimum average precipitation in which the salamander occurs.

Because annual temperature variation has not been directly measured and mapped in the northern Rockies, we used the average first bloom date of the common purple lilac (*Syringa vulgaris*) to index regionally the duration of cold weather (Caprio 1966, 1970). Locality elevations were obtained from U.S. Geological Survey topographic maps (1:24,000 scale). To reveal how cold may affect the salamander's distribution we examined bloom dates for high-elevation localities, and assumed the latest date among all localities represented an annual temperature regime near a lower tolerance limit for the species. To our base map, we then transferred published isophenes depicting geographic variation of this bloom date relative to elevation (Caprio 1966). We used these isophenes to draw topographic contours on the base map denoting variation in the altitudinal limits of the salamander.

Regions underlain by unconsolidated Quaternary deposits (aeolian, alluvial, glacial, and lacustrine) were transferred to our base map from geologic maps (Ross et al. 1958, Huntting et al. 1961,

Bond and Wood 1978, Walker and Macleod 1991). These represent areas in which rock outcrops and rocky colluvium are rare. A final map showing localities, climatic regions, and unconsolidated deposits was produced with NIH Image 144b and Deneba CANVAS 3.0 computer programs.

Results

The minimum average annual precipitation associated with *P. idahoensis* is 50 cm for a locality on the Clark Fork River, Montana (47°, 23', 23" N; 115°, 48', 32" W; 760 m elev.). The Columbia Plateau and drainages of the Salmon, Bitterroot, and Flathead Rivers receive less than this amount and circumscribe the salamander's U.S. distribution (Figure 1). Except along the southern extent of the species' occurrence these lowlands are also underlain by unconsolidated Quaternary deposits. Unconsolidated deposits flanking the Selkirk Mountains are within the climatic range of the salamander and bound the northwestern limit of its U.S. distribution.

The latest average annual *S. vulgaris* bloom date for any locality is 14 June for a site in the Kootenai River drainage, Montana (48°, 39', 36" N; 115°, 39' W; 1,300 m elev.). This date projected to other sections of the region predicts an upper altitudinal limit for *P. idahoensis* that varies from 1,100 m on the northwest tip of the Idaho Panhandle to 1,800 m at the southern end of the species' geographic range. Regions above these presumptive limits are prominent at the northern, eastern, and southern margins of the salamander's distribution; and form the crest of the Bitterroot Range, which separates Montana populations from those in Idaho.

In Montana, *P. idahoensis* occupies narrow corridors of suitable climate in the Kootenai and Clark Fork River drainages. On the west slope of the Bitterroot Range of Idaho, the salamander occurs only sparsely across a continuous region of favorable conditions. Most Idaho localities occur upslope in canyons draining the Bitterroots.

Discussion

Climatic regions suitable for *P. idahoensis* encompass the disjunct coastal forest province of the northern Rockies (Heusser 1983, Cooper et al. 1991). The salamander is associated with this province, except for its apparent absence from the Selkirk Mountains. Projected upper altitudinal limits of *P. idahoensis* correspond with the transition from temperate to subalpine communities (Krajina 1969, Arno 1979, Habeck 1987). The Bitterroot Range, with its comparatively low elevations and strong maritime climate (Cooper et al. 1991), contains most potential habitat for the species.

Plethodon idahoensis localities are most abundant in Bitterroot uplands where near-coastal (75-140 cm) annual precipitation levels exist (USDA Soil Conservation Service 1965a). These uplands also support the region's greatest diversity of coastal disjunct plants, invertebrates and amphibians (Nussbaum et al. 1983, Johnson 1987, Lorain 1988). Populations of *P. idahoensis* in xeric surrounding areas occupy favorably moist microhabit (Wilson et al. 1997).

The lack of populations in climatically suitable areas of the Selkirk lowlands indicates that unconsolidated deposits limit distribution of *P. idahoensis*. Such deposits likely influenced the salamander's current geographic range by limiting post-Pleistocene dispersal (Lynch 1984). The absence of *P. idahoensis* from mountains east of the Bitterroot Range, for example, is correlated with widespread occurrence of glacio-alluvial barriers in intervening valleys. Although alluvial deposits restrict dispersal by *Plethodon*, rocky uplands paralleling a river can provide dispersal corridors (Thurow 1968). Both the Kootenai and Clark Fork Rivers trend northward and thus helped effect the latitudinal breadth of the salamander's present distribution. All known Canadian populations are in the Kootenai drainage (Orchard 1991).

Syringa vulgaris phenological data are not available for Canada, so we did not include Canadian lands in our analysis. However, if isophenes published for the U.S. (Caprio 1966) are projected onto Canadian topographic maps, an upper altitudinal limit for *P. idahoensis* of 750 m is indicated for the northern end of the Kootenai Valley, 200 km north of the U.S.-Canadian border. This valley receives sufficient precipitation for *P. idahoensis* along its entire length (Farley 1979) and is worthy of more surveys.

Plethodon idahoensis is most closely related to Van Dyke's salamander (*Plethodon vandykei*) of western Washington. There has even been debate as to whether the two forms actually comprise a single species (Howard et al. 1993). Although *P. idahoensis* occupies drier habitats, both species

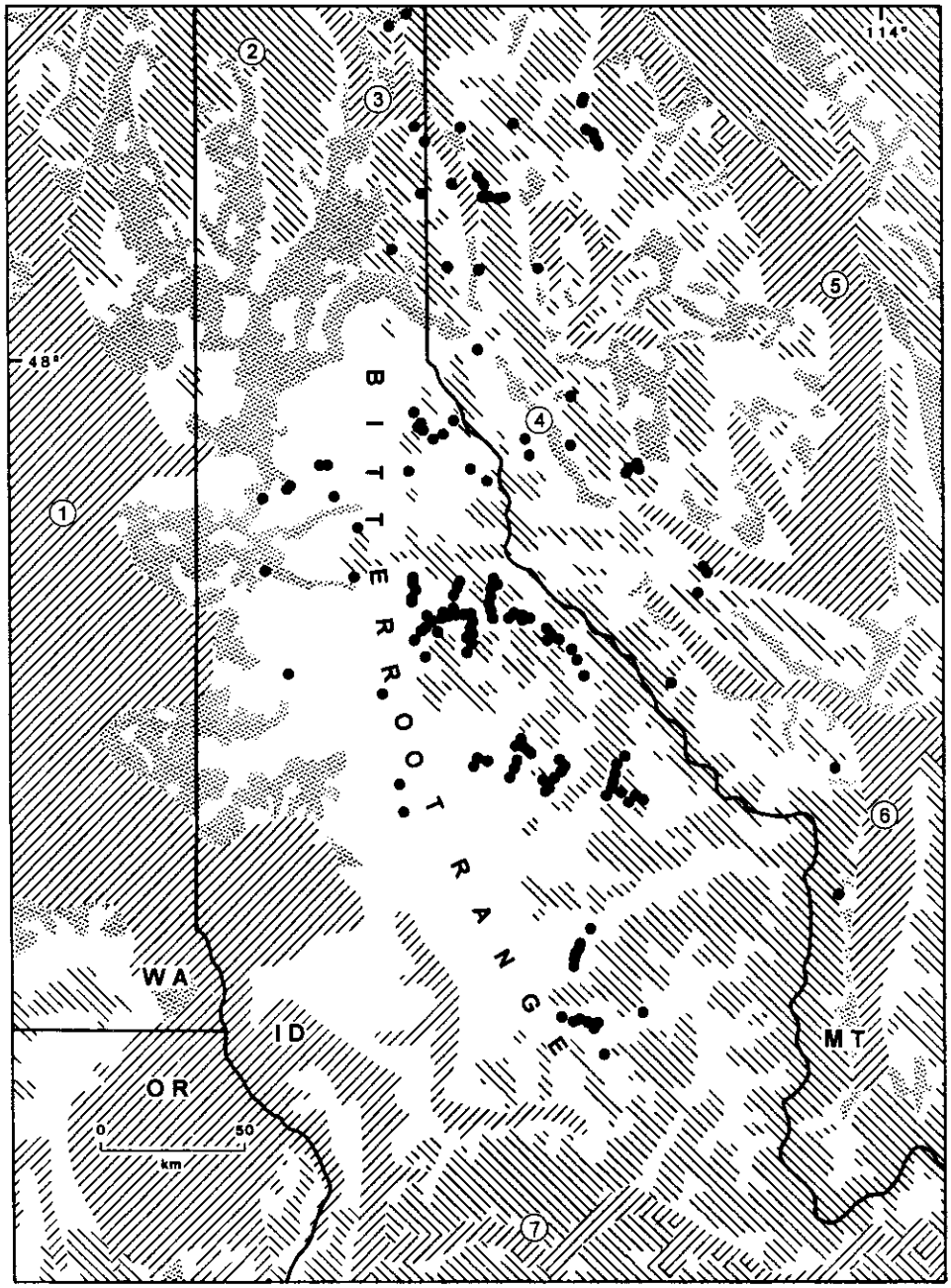

Figure 1. The U.S. distribution of *Plethodon idahoensis* relative to three environmental factors. Closed circles represent localities. Regions with less than 50 cm average annual precipitation are represented by hatching directed upward to the right. Hatching directed upward to the left delimits regions with average *Syringa vulgaris* bloom dates later than 14 June. Stippling indicates unconsolidated Quaternary deposits. For visual clarity, unconsolidated deposits are depicted only within the climatic range of the salamander, and the following geographic features are represented by numbers: Columbia Plateau (1), Selkirk Mountains (2), Kootenai River (3), Clark Fork River (4), Flathead Valley (5), Bitterroot Valley (6), Salmon River (7).

inhabit temperate mesophytic forests and have similar upper altitudinal limits (Wilson et al. 1995). Paleobotanical evidence (Detling 1968, Daubenmire 1975) and molecular estimates of the timing of speciation in Pacific Northwest amphibians (Highton and Larson 1979, Daugherty et al. 1983) suggest that vicariance of *P. idahoensis* and *P. vandykei* originated during a pre-Pleistocene xerification of the Columbia Plateau. This event, which resulted from development of the Cascade Mountains rainshadow (Smiley 1963), also helped to isolate other elements of the Rocky Mountain disjunct coastal biota (Daubenmire 1975, Johnson 1987).

Speculations of more recent occurrence of *P. idahoensis* or *P. vandykei* on the Columbia Plateau or in uplands to the north (Savage 1952, Wake 1966, Howard et al. 1993) are not supported by our analysis. These regions are largely outside of the geological and climatic ranges that presently favor occurrence by either species (Pacific Northwest River Basins Commission 1969, Farley 1979, Wilson et al. 1995) and were dominated by sagebrush steppe with subalpine arboreal elements during Pleistocene glacial maxima (Barnosky et al. 1987).

Our study suggests that *P. idahoensis* is restricted to Rocky Mountain regions north of the Salmon River. Isolated populations may yet be encountered in the Bitterroot Range and in mountainous regions west of the Flathead Valley of Montana. Much of the southern Bitterroots is inaccessible by road and has been inadequately searched. By identifying potential habitat in these and other areas we hope to facilitate future surveys and thus enable protection and further study of this unique species.

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Literature Cited

Arno, S.F. 1979. Forest regions of Montana. USDA For. Serv. Res. Pap. INT-218. Interm. For. Range Exp. Sta., Ogden, UT. 39 p.

Barnosky, C.W., P.M. Anderson, and P.J. Bartlein. 1987. The northwestern U.S. during deglaciation: vegetational history and paleoclimatic implications. *In* W.F. Ruddiman and H.E. Wright, Jr. (eds.), North America and adjacent oceans during the last deglaciation. Geol. Soc. No. Am. Boulder, CO. Pp. 289-321.

Bond, J.G., and C.H. Wood. 1978. Geologic map of Idaho. Idaho Dept. Lands, Bureau Mines and Geol., Moscow.

Bury, R.B., Corn, P.S., and K.B. Aubry. 1991. Regional patterns of terrestrial amphibian communities in Oregon and Washington. *In* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M. H. Huff (eds.), Wildlife and vegetation of unmanaged Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. Pac. Northw. Res. Sta., Portland, OR. Pp. 341-350.

Caprio, J.M. 1966. Pattern of plant development in the western United States. Mont. Agr. Exp. Sta. Bull. 607:1-42.

_____. 1970. Areal and temporal variations in developmental phases of *Syringa vulgaris* L. throughout the western United States. Utah State University, Logan. Ph.D. Dissertation.

Cooper, S.V., K.E. Neiman, R. Steele, and D.W. Roberts. 1991. Forest habitat types of northern Idaho: a second approximation. USDA For. Ser. Gen. Tech. Rep. INT-236. Interm. For. Range Exp. Sta., Ogden, UT. 143 p.

Daubenmire, R. 1975. Floristic plant geography of eastern Washington and northern Idaho. J. Biogeog. 2:1-18.

Daugherty, C.H., F.W. Allendorf, W.W. Dunlap, and K.L. Knudsen. 1983. Systematic implications of geographic patterns of variation in the genus *Dicamptodon*. Copeia 1983:679-691.

Detling, L.E. 1968. Historical background of the flora of the Pacific Northwest. Univ. Or. Mus. Nat. Hist. Bull. 13:1-57.

Farley, A.L. 1979. Atlas of British Columbia. University of British Columbia Press, Vancouver, BC.

Habeck, J.R. 1987. Present-day vegetation in the northern Rocky Mountains. Ann. Missouri Bot. Garden 74:804-840.

Heusser, C.J. 1983. Vegetational history of the Northwest including Alaska. *In* S.C. Porter (ed.), Late-Quaternary environments of the United States. Vol. 1. University of Minnesota Press. Minneapolis. Pp. 239-258.

Highton, R., and A. Larson. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. Sys. Zool. 28:579-599.

Holmberg, R.G., N.P.D. Angerilli, and L.J. LaCasse. 1984. Overwintering aggregations of *Leiobunum paessleri* in caves and mines (Arachnida, Opiliones). J. Arachnol. 12:195-205.

Houck, L.D. 1977. Life history patterns and reproductive biology of neotropical salamanders. *In* D.H. Taylor and S.I. Guttman (eds.), The reproductive biology of amphibians. Plenum Publishing Corp., Chicago, IL. Pp. 43-72.

Howard, J.H., L.W. Seeb, and R.L. Wallace. 1993. Genetic variation and population divergence in the *Plethodon vandykei* species group. Herpetologica 49:238-247.

Huntting, M.T., W.A.G. Bennet, V.E. Livingston, Jr., and W.S. Moen. 1961. Geologic map of Washington. Wash. Dept. Conserv., Div. Mines and Geol., Olympia.

Johnson, P.J. 1987. Larval taxonomy, biology, and biogeography of the genera of North American Byrrhidae (Insecta: Coleoptera). University of Idaho, Moscow. M.S. Thesis.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. *In* V.J. Krajina and R.C. Brooke (eds.), Ecology of western North America. Vol. 2. Dept. of Bot., Univ. British Columbia, BC, Canada. Pp. 1-146.

Lorain, C.C. 1988. Floristic history and distribution of coastal disjunct plants of the northern Rocky Mountains. University of Idaho, Moscow. M.S. Thesis.

Lynch, J.F., Jr. 1984. Reproductive ecology of *Plethodon idahoensis*. University of Idaho, Moscow. M.S. Thesis.

Lynch, J.F. 1981. Patterns of ontogenetic and geographic variation in the black salamander, *Aneides flavipunctatus* (Caudata: Plethodontidae). Smithson. Contrib. Zool. 324:1-53.

Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University of Idaho Press, Moscow.

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Orchard, S.A. 1991. Amphibian population declines in British Columbia. *In* C.A. Bishop and K.E. Pettit (eds.), Declines in Canadian amphibian populations: designing a national monitoring strategy. Can. Wildl. Serv. Occ. Pap. 76. Can. Wildl. Serv., Ottawa, Ontario. Pp. 10-13.

Pacific Northwest River Basins Commission. 1969. Climatological handbook, Columbia Basin states precipitation, vol. 2. Env. Sci. Serv. Admin., Washington, DC.

Ross, C.P., D.A. Andrews, and I.J. Witkind. 1958. Geologic map of Montana. Mont. Bureau Mines and Geol., Helena, MT.

Savage, J.M. 1952. The distribution of the Pacific giant salamander, *Dicamptodon ensatus*, east of the Cascade Mountains. Copeia 1952:183.

Smiley, C.J. 1963. The Ellensburg flora of Washington. Univ. Calif. Publ. Geol. Sci. 35:159-276.

Thurow, G.R. 1968. On the small black *Plethodon* problem. West. Ill. Univ. Ser. Biol. Sci. 6:1-48.

USDA Soil Conservation Service. 1965a. Map of mean annual precipitation, State of Idaho. U.S. Weather Bureau Riv. Forecast Center, Portland, OR.

_____. 1965b. Map of mean annual precipitation, State of Oregon. U.S. Weather Bureau Riv. Forecast Center. Portland, OR.

_____. 1965c. Map of mean annual precipitation, State of Washington. U.S. Weather Bureau Riv. Forecast Center, Portland, OR.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. Calif. Acad. Sci. 4:1-111.

Walker, G.W., and N.S. Macleod. 1991. Geologic map of Oregon. USDI, U.S. Geol. Survey Publ., Washington, DC.

Wilson, A.G., Jr., J.H. Larsen, Jr., and K.R. McAllister. 1995. Distribution of Van Dyke's Salamander (*Plethodon vandykei* Van Denburgh). Am. Midl. Nat. 134:388-393.

Wilson, A.G., E.M. Wilson, C.R. Groves, and R.L. Wallace. 1997. Distribution of the Coeur d'Alene Salamander (*Plethodon idahoensis* Slater and Slipp). Gr. Basin Nat. 57:359-362.