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Activity and Diet in Seepage-Dwelling Coeur d'Alene Salamanders (*Plethodon vandykei idahoensis*)

Abstract

Through 1985 and 1986 activity and diet in a seepage-dwelling population of the Coeur d'Alene salamander (*Plethodon vandykei idahoensis*) were studied in northwestern Montana. Activity was almost entirely nocturnal and had a weak, but significant positive correlation with nighttime substrate temperature. During June, July, and August, activity was periodically reduced and had a weak, but significant negative correlation with daytime substrate temperature and a strong, negative correlation with the number of days since the last rain. *Plethodon v. idahoensis* was active in free water and aquatic prey species were found in its diet. This salamander exploits very wet microhabitat where it is insulated from climatic extremes. These habits may have contributed to the continued survival of *P. v. idahoensis* in a region that once had a milder climate and apparently supported a richer plethodontid fauna.

Introduction

Van Dyke's salamander (*Plethodon vandykei*) is unusual among its congeners in its often close association with free water. Although found in forest debris or damp talus far from such aquatic situations (Slater 1933, Slater and Slipp 1940, Nussbaum *et al.* 1983), it is commonly encountered along streamsides and in the splash-zones of seepages and waterfalls (Nussbaum *et al.* 1983). *Plethodon vandykei* enters streams to avoid capture and has been referred to as the most aquatic *Plethodon* (Brodie 1970).

The ecological importance of this species' preference for very wet microhabitat may vary geographically. It has been implied that such preference reduces competition between the Washington salamander (*P. v. vandykei*) and more terrestrial sympatric *Plethodon* in the mild, damp climate of western Washington (Brodie 1970). In the eastern part of the species' range, the common association of the Coeur d'Alene salamander (*P. v. idahoensis*) with streams and splashzones is probably due to the hydric and thermal stability of these situations (Hynes 1970) in a climate apparently harsher than that associated with other western *Plethodon* (Nussbaum *et al.* 1983). [Since the taxonomy of this species lacks a consensus (Frost 1985), we use the nomenclature of Lowe (1950) which recognizes two subspecies.] Such stability is impor-

tant to plethodontids because they require moist skin for respiration, a trait restricting their surface activity in desiccating conditions (Feder 1983). The ability to be surface-active would appear to be crucial to *Plethodon* since suitable prey may be largely inaccessible below ground (Jaeger 1972, Fraser 1976).

Our study has centered around a seepage-dwelling population of *P. v. idahoensis* in northwestern Montana. Through seasonal censusing, we have attempted to identify and assess environmental factors that limit the surface activity of this salamander in a type of microhabitat with which it is very commonly associated. Our study site and method have permitted observation of the salamander's hydrophilic behavior and we have also analyzed its diet.

Study Site and Methods

The study area is on the north slope of the Cabinet Mountains in Lincoln County, Montana, at 600 m elevation. The six perennial seepages we used occur along an 800 m stretch of an easement cut in 1924 for U.S. Highway 2 and the Northern Pacific Railroad. The easement is approximately 30 m above the Kootenai River along the walls of a steep gorge forested in *Pseudotsuga menziesii*/*Symphoricarpos albus* and *Thuja plicata*/*Clintonia uniflora* habitat types (Pfister *et al.* 1977). Salamanders were first discovered

here in 1962 (Teberg 1964). The springs are of the fracture type (Fetter 1980), with water emerging from tabular beds of Belt quartzite (Winston and Woods 1986). Temperature of emergent water in the springs varies from 4.2°C to 9.4°C annually. The three largest seepages, where we made salamander counts, involve 3 to 9 m high rockfaces down which spring water streams and cascades. The resulting splashzones comprise ~250 m² of vertical, bryophyte-covered rock. At the base of the rockfaces, rubble has accumulated and the splashzones extend horizontally 1 to 3 m. Water from the seepages fills a continuous 1 m wide ditch beside the highway.

Periodic salamander counts were made during 19 all-night and 14 half-night censuses performed from 30 May to 10 November 1985, and from 8 March to 26 October 1986. All-night censuses were conducted to determine qualitatively the diel activity pattern of the salamanders. Counts began 4 hours before sunset and were repeated once every 2 hours until 4 hours after sunrise. Half-night censuses were performed using the same method as above except that counts were terminated 4 hours after sunset.

Seven substrate temperatures were taken during each count using alcohol thermometers. These measurements were made at stations in the seepages established for their proximity to large numbers of salamanders. Three temperatures were taken from the vertical rockfaces, three from substrate at the base of the rockfaces, and one from pooled water in the highway ditch. A mean substrate temperature was calculated for each salamander count.

Starting at sunset, salamanders were counted with the aid of a flashlight. The counting procedure involved walking between 1 and 3 m from the rockface, recording every salamander visible on the ground and on the rockface up to 3 m above ground level. The entire rockface encompassing the three seepages was checked for salamanders. Care was taken to use the same path and method during each count. In all counts except those made during the first census on 30 May 1985, the substrate associated with each salamander was recorded.

For our analysis of salamander activity and distribution within the seepages, data from counts made 4 hours after sunset were arbitrarily used. Census data from 1985 and 1986 were

pooled. Activity levels were compared to mean substrate temperatures from 2 hours before and 4 hours after sunset on the same census visit. Activity levels were also compared to rainfall data obtained from a U.S. Forest Service weather station 10 km from the study site. Spearman rank correlations were calculated with a 1983 SPSS, Inc. software package.

Salamander stomach contents were sampled 10 times from 15 May 1985 to 11 October 1985 and three times in 1986, twice in April and once in May. Two to seven salamanders were collected from each of the six seepages at night, after the last count in a census visit. Following collection, salamanders were kept on ice until their stomach contents were removed, not more than 5 hours later. Salamanders were anesthetized with MS-222 and their stomach contents removed using the flushing method of Legler and Sullivan (1979). We observed no ill effects on salamanders subjected to this procedure, and released each individual at night within 1 m of its site of capture. Prey items obtained from stomach samples were identified using Pennak (1978), Borror *et al.* (1981), and Merritt and Cummins (1984). Stomach content data from 1985 and 1986 were pooled for analysis.

Results

Salamander activity in the Kootenai seepages was reduced in the fall and spring (Figure 1) and had a weak, positive correlation with nighttime substrate temperature ($r_s = 0.3935$, $N = 30$, $P = 0.016$). Much of the spread in a plot of this correlation can be attributed to reduced salamander activity on six summer nights, five in June and July of 1985 and one in August 1986. If these nights are left out of the analysis, the positive correlation between peak salamander activity and nighttime substrate temperature is high ($r_s = 0.7119$, $N = 24$, $P < 0.001$). These six nights were associated with locally high daytime temperatures and the absence of rain. During June, July and August only, peak salamander activity had a weak, negative correlation with daytime substrate temperature ($r_s = -0.4871$, $N = 16$, $P = 0.028$) and a strong, negative correlation with the number of days since the last rain ($r_s = -0.8082$, $N = 16$, $P < 0.001$).

During the last 1985 visit to the site on 10 November, the area within the seepages was

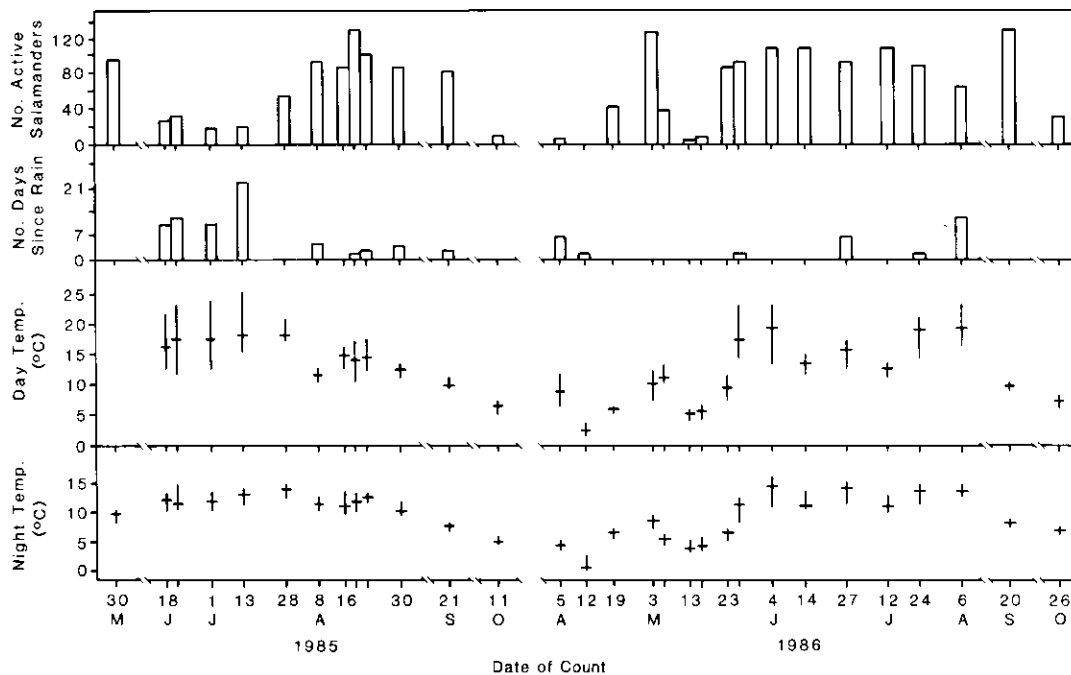


Figure 1. Activity of *Plethodon vandykei idahoensis* 4 hours past sunset and some environmental correlates during ice-free periods in the Kootenai Gorge seepages, Lincoln Co., Montana. Only the first date is given for counts made on consecutive days. Substrate temperature means and ranges represent data taken 4 hours past sunset (night), and 2 hours before sunset (day). No day temperatures were obtained on 30 May 1985.

about 90 percent ice-covered and no salamanders were observed. On 8 March of the following year, when conditions were similar, one salamander was observed at sunset through a hole in the ice where 4.4°C water was flowing over the soil. By 21 March, about 60 percent of the area within the seepages was still ice-bound and four salamanders were counted 4 hours after sunset. All water at the site was completely thawed by 4 April 1986. No visits were made to the site after 26 October 1986, but the seepages were again ice-bound by 25 November (N. Lamorie, pers. comm.).

Salamander activity was almost entirely nocturnal. Five of 11 observations of day-active salamanders occurred while rain was falling from completely overcast skies; during the other six days the sky was clear and no rain had fallen for 24 hours. Salamander activity in 11 of the 19 all-night censuses appeared fairly constant; similar numbers of salamanders were counted both early and late at night. During the other eight all-night censuses, mean substrate temperatures dropped

below 4.0°C and activity was heaviest during early evening, tapering off as temperatures fell.

Of the total number of salamanders ($n = 1950$) observed during this study 4 hours after sunset, 1132 (58.1%) were on vertical rockfaces, 779 (40.0%) were in the rubble at the base of the rockfaces or on various substrates along the side of the highway ditch, 36 (1.8%) had entered the pooled water of the highway ditch, and three (0.2%) were climbing plants. Salamanders observed in the pooled water of the ditch were always within ~10 cm of the pool edge and none were completely submerged. *Plethodon v. idahoensis* must swim voluntarily because individuals were periodically seen on rocks in the middle of the pools. We commonly saw salamanders, especially those on rockfaces, within thin sheets of streaming water (hydropetric areas), but none were observed in rapidly flowing water.

Although we did not mark individuals, our observations indicate a considerable amount of movement by some salamanders. These appeared to travel distances of ~5 m during the night,

crossing the highway ditch and patrolling the edges of its pools. Salamanders remained within the splashzones except on nights when the surrounding ground was saturated by rain. At such times individuals were found up to 10 m from the splashzones and were occasionally observed on the highway.

The prey of *P. v. idahoensis* were mostly insects (Table 1) and many of these were aquatic: immatures of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and many Diptera, as well as Gerridae in all stages of development. Diptera larvae, especially two species of *Caloparyphus* (Stratiomyidae), were numerically and volumetrically the most important prey. Adult salamanders took mostly Diptera larvae (26.1%) and adults (11.8%), Collembola (9.7%), Homoptera (6.6%), Hemiptera (6.6%), Hymenoptera (5.9%), Acarina (5.3%), and Coleoptera adults (4.8%). These prey were found in >20 percent of all adult stomachs except for Homoptera (19.7%) and Hemiptera (13.9%) and comprised 76.8 percent of all items. The numerical importance of Hemiptera was inflated by the appearance of 25 nymphal waterstriders in the stomach of one individual.

TABLE 1. Prey of 122 adult (≥ 4.5 cm SVL) *Plethodon vandykei idahoensis* from the Kootenai Gorge seepages, Lincoln Co., Montana. Percent occurrence denotes the numerical proportion of the total prey (n = 863) ingested.

Prey	Percent Occurrence
COLLEMBOLA	9.7
EPHEMEROPTERA NYMPHS	0.6
PLECOPTERA ADULTS	0.8
PLECOPTERA NYMPHS	2.8
PSOCOPTERA	0.2
HEMIPTERA	6.6
Gerridae	5.4
Other	1.2
HOMOPTERA	6.6
COLEOPTERA ADULTS	4.8
Staphylinidae	2.0
Elateridae	0.7
Cantharidae	0.3
Curculionidae	0.5
Other	1.3
COLEOPTERA LARVAE	1.9
Dytiscidae	1.3
Hydrophilidae	0.3
Other	0.2
TRICHOPTERA ADULTS	3.2
TRICHOPTERA LARVAE	3.5
Rhyacophilidae	0.8

Prey	Percent Occurrence
Limnephilidae	1.0
Lepidostomatidae	0.5
Brachycentridae	0.3
Other	0.8
LEPIDOPTERA ADULTS	0.3
LEPIDOPTERA LARVAE	1.3
DIPTERA ADULTS	11.8
Chironomidae	3.7
Mycetophilidae	1.7
Other	6.4
DIPTERA LARVAE	26.1
Tipulidae	4.9
Psychodidae	4.9
Dixiidae	0.5
Chironomidae	6.0
Stratiomyidae	8.1
Other	1.7
HYMENOPTERA ADULTS	5.9
Ichneumonidae	2.7
Formicidae	1.6
Other	1.6
DIPLOPODA	0.3
ACARINA	5.3
ARANEA	3.4
PHALANGIDA	0.1
GASTROPODA	2.1
Lymnaidae	1.2
Other	0.9
OLIGOCHAETA	2.7

Discussion

Our observations of *P. v. idahoensis* in hypopetric areas and in pooled water indicate this salamander is well adapted to life in splashzones. This adaptation is reflected in the importance of semiaquatic and aquatic prey in the salamander's diet (Table 1). The ability of *P. v. idahoensis* to live in very wet microhabitat, such as that of the Kootenai seepages, enables it to occupy equable conditions in a relatively severe climate. Plethodontids are restricted in activity, and thus in their foraging ability, by low humidity, low substrate moisture, and high temperatures (Feder 1983, Feder and Londos 1984, Keen 1984). Seepage areas provide cool water (Hynes 1970) and splashzones moisten substrates while providing locally high humidity (Huheey and Brandon 1973). Conditions in the Kootenai seepages that are favorable to plethodontids center around local bedrock fracturing. This fracturing not only results in the emergence of spring water (Fetter 1980), but also provides daytime retreats for the salamanders and is apparently deep enough for refuge from freezing during winter.

Despite favorable conditions within the seepages, salamander activity is reduced during cold weather. In late fall, winter, and early spring, movement out of fractures may be restricted by the ice that covers seepage surfaces. At other times activity appears to be reduced by substrate temperatures dropping to -4°C . Periods of these low, nonfreezing temperatures occur primarily in April, May, October, and November. The thermal stability of spring water (Hynes 1970) probably enables seepage-dwelling *P. v. idahoensis* to be active on colder nights than *P. v. idahoensis* residing in other types of microhabitat.

Thermal and hydric stability result in greater midsummer activity of *P. v. idahoensis* in the splashzones of seepages and waterfalls than in other situations. Nussbaum *et al.* (1983) reported that forest and talus populations remain largely underground from June to September, a pattern typical of plethodontid salamanders in western North America (Houck 1977). Reductions in salamander activity during the summer months do occur in the Kootenai seepages and are accompanied by high daytime temperatures and lack of rain (Figure 1). These reductions are periodic, however, and activity can be observed throughout the summer. The annual activity cycle of seepage-dwelling *P. v. idahoensis*, thus appears to be more similar to the cycle of eastern plethodontids (Taub 1961, Houck 1977) than to that of most western forms.

Midsummer reductions of salamander activity in the seepages may stem from a heating of substrates during the day, which forces salamanders into the deeper fractures of the rockface. This factor does not greatly affect the number of night-active salamanders on a short term basis, as indicated by the weak correlation between daytime substrate temperatures and summer salamander activity. Over a long period of little rain and high daytime temperatures, however, it appears that the salamanders move underground and relatively few emerge at night. Evidence for such movement includes the negative correlation of summer salamander activity to lack of rain, the high daytime substrate temperatures associated with periods of little rain (Figure 1), and the report by Lynch (1984) that in midsummer, salamanders in the Kootenai seepages are relatively difficult to find under surface debris during the day. Vertical migration of North American plethodontids to avoid heat has been

recorded in field experiments (e.g., Taub 1961), but such behavior is rarely observed in the field because these salamanders may only infrequently encounter unsuitably high temperatures in the moist situations they inhabit (Feder 1983).

Nocturnal activity such as we observed in *P. v. idahoensis* is common in plethodontids (Hairston 1949) and is probably associated with endogenous rhythms (see Ralph 1957, Adler 1970). These rhythms enable organisms spending a portion of their day underground to emerge at appropriate times without environmental cues (Enright 1970). Selection for nocturnal activity may come from daytime predators (Semlitsch and Pechmann 1985) such as birds, which can be efficient at capturing salamanders (Brandon and Huheey 1975, Wilson and Simon 1985). Plethodontids can also avoid heat or desiccation via nocturnal activity (Feder 1983), and under favorable conditions of light, temperature, and moisture some species may be active during the day (Hairston 1949). However, in the Kootenai seepages we observed little diurnal activity, even on cloudy, cool days.

Conditions within splashzones that provide suitable habitat for *P. v. idahoensis* also help sustain populations of the invertebrates upon which salamanders feed (Hynes 1970, Huheey and Brandon 1973, Keen 1979). That we observed *P. v. idahoensis* partly submerged in standing water, plus the occurrence of waterstriders and Collembola in the diet, indicate this salamander is able to forage upon neustonic organisms (Scott 1956, Usinger 1956). It is unclear how the salamander takes benthic prey but most of these were apparently captured in hydropetric areas or in the highly saturated soil within the splashzones. Such areas support populations of snails and oligochaetes, as well as the immatures of some Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and Diptera (Hynes 1970, Pennak 1978, Teskey 1984). Some of the aquatic organisms in the diet of *P. v. idahoensis* may represent instances of these invertebrates leaving the water. A few benthic insects, such as the larvae of some Trichoptera, are known to emerge from water to forage (Erman 1981) and many immature aquatic insects leave the water before transforming into adults (Hynes 1970). The majority of the Plecoptera nymphs taken by salamanders in this study were in their last instar and were, therefore, likely captured on land prior to their final molt (see Hynes 1976).

The diet of *P. v. idahoensis* in the Kootenai seepages is unusual for that reported in western *Plethodon*. The diets of the Del Norte salamander (*P. elongatus*), the Larch Mountain salamander (*P. larselli*), the Jemez Mountains salamander (*P. neomexicanus*), the Siskyou Mountain salamander (*P. stormi*), and the western red-backed salamander (*P. vehiculum*), lack aquatic prey (Dumas 1956, Bury and Johnson 1965, Altig and Brodie 1971, Reagan 1972, Nussbaum *et al.* 1983), probably because of the terrestrial habits of these species. Of all western *Plethodon* only Dunn's salamander (*P. dunni*) is commonly present in microhabitat similar to that of *P. vandykei*. The former has been collected in water-soaked areas and along streamsides (Stebbins 1951, Dumas 1956, Brodie 1970), and like *P. vandykei* (Brodie 1970), may take to water to avoid danger (Stebbins 1951). Reports on the diet of *P. dunni* by Dumas (1956) and Altig and Brodie (1971) do not mention aquatic prey. While this may indicate less aquatic habits for *P. dunni* than *P. vandykei*, it is possible that the salamanders used in these two studies were from populations not associated with free water.

There is a strong resemblance between the diet of *P. v. idahoensis* in the Kootenai seepages and that of adults of some species of *Desmognathus* that live in similar microhabitat in eastern North America (Burton 1976, Keen 1979). This similarity probably stems from a shared propensity for entering water (see Bishop 1943, Hairston 1949), at least to the extent required to take neustonic and hydropetric prey. *Plethodon v. idahoensis* may thus be regarded as an ecological counterpart to the desmognathine and hemidactyliine plethodontid species that occupy a semi-

aquatic adaptive zone (Wake 1966) unexploited by most *Plethodon*.

Given the paucity of behavioral and dietary information on hydrophilic species of *Plethodon* such as *P. dunni*, it is unclear whether the extremely close association between *P. vandykei* and free water is unique for the genus. However, *P. vandykei* has a unique disjunct distribution (Nussbaum *et al.* 1983) which may attest to the importance of such an association. It is possible that an ability to reside in the insulation of very wet microhabitat has contributed to the persistence of this salamander in the northern Rocky Mountains; a region with severe winters and dry summers (Baily 1980, Nussbaum *et al.* 1983), where drastically changing environmental conditions presumably eliminated an earlier, richer plethodontid fauna (Thurrow 1968, Tihen and Wake 1981).

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