

Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good)

Barbara Johnston and Leonardo Frid

Abstract: Pacific giant salamanders (*Dicamptodon tenebrosus* Good) in the Chilliwack River valley of southwestern British Columbia are at the periphery of their range, and therefore of conservation concern. Although logging is a potential threat to the species, no studies have examined how clear-cutting affects its terrestrial stage. We used radio-telemetry to compare the movements of 35 terrestrial Pacific giant salamanders at sites with three different logging histories: forested, clearcut to the stream margin, and clearcut with riparian buffer strips. The results demonstrate that logging affected movements of the salamanders. Salamanders in clearcuts remained significantly closer to the stream, spent more time in subterranean refuges, and had smaller home ranges than those at forested sites. During a dry year, salamanders in clearcuts were significantly more dependent on precipitation for their movement than salamanders in forested habitats. Salamander movement behavior in riparian buffer strips was not significantly different from that at forested sites but was significantly different from that at clearcut sites. Riparian buffer strips appear to mitigate some of the negative effects of clearcuts on salamander movement.

Résumé : Les salamandres géantes du Pacifique (*Dicamptodon tenebrosus* Good) de la vallée de la Chilliwack dans le sud-ouest de la Colombie-Britannique se retrouvent à la périphérie de leur aire de répartition et, par conséquent, leur conservation suscite des inquiétudes. Bien que la coupe forestière soit une menace potentielle pour l'espèce, personne n'a examiné comment la coupe à blanc affecte le stade terrestre de la salamandre. La radio-télémetrie nous a permis de comparer les déplacements de 35 salamandres géantes du Pacifique terrestres à des sites soumis à des traitements différents de coupe : un site de forêt intacte, un site ayant été coupé à blanc, y compris les rives des cours d'eau, et un site coupé à blanc, mais avec des bandes de protection le long des berges. La coupe forestière affecte les déplacements des salamandres. Par rapport aux animaux au site de forêt intacte, les salamandres dans les zones coupées restent significativement plus près du cours d'eau, elles passent plus de temps dans des refuges souterrains et elles ont des aires vitales réduites. Durant une année sèche, les salamandres des régions coupées dépendaient plus des précipitations pour leurs déplacements que les salamandres en forêt intacte. Le comportement de déplacement dans les bandes de protection ripariennes ne diffère pas de celui observé aux sites forestiers intacts, mais il est significativement différent de celui enregistré dans des zones coupées. Les zones de protection semblent mitiger certains des effets négatifs de la coupe à blanc sur les déplacements des salamandres.

[Traduit par la Rédaction]

Introduction

Amphibian populations have declined worldwide during the last decade (Phillips 1990; Pechman et al. 1991; Blaustein and Wake 1995). Habitat loss and fragmentation are among the leading causes of this trend (Blaustein et al. 1994; Blaustein and Wake 1995). Understanding the impacts of landscape change, such as that caused by logging, would enable managers to direct habitat-conservation efforts to where they are most likely to prevent further amphibian declines.

This study focuses on the Pacific giant salamander (*Dicamptodon tenebrosus* Good), a species at risk in British Columbia (Farr 1989). Canadian populations occur at the northern periphery of the species' geographic range and therefore are of special conservation interest (Lesica and Allendorf 1995). Farr (1989) and Haycock (1991) reported that the main threat to these populations is the intensive logging underway in the Chilliwack River valley, the only locality of the species in Canada. Several studies (Bury 1983; Conner et al. 1988; Corn and Bury 1989) suggest that clearcut logging and road building, which increase sediment deposition in streams, may adversely affect larval Pacific giant salamanders.

Clearcut logging may also negatively affect terrestrial adult Pacific giant salamanders. Amphibians are ectothermic animals with very thin, vascularized skin that is an ineffective barrier to water loss (Zug 1993). These physiological features make most salamanders intolerant of dramatic changes in moisture and temperature (Hutchison 1961; Spotila 1972; Maiorana 1978; Jaeger 1980; Welsh 1990). Clearcut logging drastically alters the microclimatic conditions encountered at

Received 12 March 2002. Accepted 6 November 2002.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on 22 January 2003.

B. Johnston and L. Frid.^{1,2} Department of Zoology,
University of British Columbia, 6270 University Boulevard,
Vancouver, BC V6T 1Z4, Canada.

¹Corresponding author (e-mail: lfrid@essa.com).

²Present address: ESSA Technologies Ltd., Suite 300,
1765 West 8th Avenue, Vancouver, BC V6J 5C6, Canada.

the forest floor. Clearcuts in Oregon and Washington have higher daily average air and soil temperatures, wind velocity, and solar radiation, as well as lower average soil moisture and relative humidity than interior forest habitat (Chen et al. 1993, 1995; Brosnoff et al. 1997). Temperature and moisture conditions encountered in clearcut habitat may exceed the tolerance limits of some terrestrial amphibian species. For example, Dupuis et al. (1995) found that the western redback salamander (*Plethodon vehiculum*) was extremely rare in clearcuts. Numbers of western redback salamanders were extremely low in all managed stands, regardless of age (20–100 years), compared with old-growth stands. Even if environmental conditions are not lethal, an increased risk of dehydration during periods of surface activity in clearcuts may force the salamanders to modify behaviors and spend extended periods of time in moist refuges. Clearcut environments could thereby limit individual fitness and population growth by restricting food intake and reproductive activity (Spotila 1972; Feder 1983).

One management strategy that could reduce the impacts of clearcut logging on terrestrial Pacific giant salamanders is the retention of riparian buffer strips (areas within a defined distance of a stream in which logging activities are restricted) (Bren 1995). Buffer strips effectively reduce the impacts of logging on stream systems by reducing sedimentation and maintaining water quality, stream temperature, amounts of coarse woody debris, and invertebrate community composition (Brown and Krygier 1970; Newbold et al. 1980; Beschta et al. 1987; Budd et al. 1987; Davies and Nelson 1994). In addition, trees retained to form riparian buffer strips represent a source of leaf litter and new coarse woody debris. Trees also provide shade, thereby maintaining soil moisture, relative humidity, and more stable temperatures (Brown and Krygier 1970; Bisson et al. 1987; O'Laughlin and Belt 1995; Brosnoff et al. 1997). Riparian buffer strips have been effective in maintaining populations of some terrestrial mammal (e.g., Cross 1985) and bird species (e.g., Triquet et al. 1990) and likely provide habitat suitable for terrestrial amphibians. Studies which have investigated the efficacy of riparian buffer strips for preserving amphibian species suggest that population densities are higher at sites with buffer strips than at clearcut sites without streamside protection (Dupuis and Steventon 1999; Vesely 1996; but see Kelsey 1995).

Methods commonly used to determine the effects of habitat alteration on a species or community (i.e., comparing population densities or relative abundances in altered and unaltered areas) are not effective for terrestrial Pacific giant salamanders. The relatively sedentary and secretive nature of these animals makes them particularly difficult to find using standard amphibian techniques (pitfall traps, time- and area-constrained searches), and it has proved unfeasible to catch sufficient numbers to make population comparisons (see Kelsey 1995; Vesely 1996). We therefore used radiotelemetry to compare the behavior of terrestrial giant salamanders living in habitats with different harvesting histories, forested and clearcut-logged (with and without the retention of riparian buffer strips), to assess the effects of logging on certain aspects of the animals' ecology. We compared the movements of individuals at forested sites and logged sites to answer the following questions: (i) Do terrestrial Pacific giant salamanders located in clearcut habitat alter their behavior in a man-

ner that may reduce their risk of desiccation? We predicted that in comparison with salamanders located in forested habitat, animals in clearcuts would reduce the amount of time spent on the surface (i.e., increase time spent in refuges and decrease distance traveled on the surface), would be more dependent on precipitation for their activity, and would remain closer to a source of water (stream). (ii) Is the movement of Pacific giant salamanders restricted by clearcut logging? We predicted that animals in clearcuts would have reduced home ranges in comparison with salamanders located in forested habitat. (iii) Do riparian buffer strips reduce the effects on salamander movement associated with clearcuts? We predicted that salamanders in buffer strips would not alter their behavior in the ways outlined above.

Study area

We conducted this study from May to November in 1996–1998 in the Chilliwack and Nooksack drainage basins in southwestern British Columbia, Canada, and northwestern Washington State, U.S.A. This area falls within the Coastal Western Hemlock biogeoclimatic zone (sensu Krajina 1965), with Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red-cedar (*Thuja plicata*) comprising the main old-growth tree species, and salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*), and sword fern (*Polystichum munitum*) dominating the understory. The Nooksack and Chilliwack study areas are separated by approximately 20 km (straight-line distance) over a mountainous ridge. The climatic conditions in the two study areas are very similar, mean annual precipitation being approximately 112 cm at the Nooksack site and 144 cm at the Chilliwack site and average daily maximum/minimum temperatures 14.0/5.0 and 13.8/4.9°C, respectively (Western Regional Climate Center 1998; Environment Canada 1998). We used a total of 12 study sites: 7 forested, 3 clearcut to the stream margin, and 2 clearcut with buffer strips (averaging 20 and 30 m in width) retained on each side of the stream. Each site contained a small stream (1–6 m wide) inhabited by a population of larval Pacific giant salamanders. The physical characteristics of the sites are summarized in Table 1. The stream at one forested site (Tam VSG) was the same as at the downstream clearcut site (Tam VCC). All other sites were on different streams.

Materials and methods

Radio-tagging and tracking

During the first 2 months (mid-May to mid-July) of each field season we captured terrestrial Pacific giant salamanders by searching stream beds and adjacent forest at night with high-powered flashlights and capturing salamanders by hand. We captured a total of 27 salamanders with this technique. In 1998, in addition to night searches we captured four salamanders at one site (Elk) in pitfall traps, as well as three salamanders at a second site (Tam C) and one salamander at a third site (732) by intensively searching the stream during the day. Salamanders were stored in individual containers and transported to the laboratory in a cooler. Following Colberg et al. (1997), we anaesthetized salamanders by immersing them in a 0.6% solution of buffered tricaine methanesulfonate

Table 1. Physical characteristics of the study sites.

Site	Year studied	No. of salamanders tagged	Habitat type	Stand age (years)	Watershed	Altitude (m asl)	Aspect	Avg. slope (deg.)	Tree species composition ^a
Promontory	1996	4	Forested	70	Chilliwack	600	SSW	9	TSHE/THPL/ACMA
Vedder B	1996	2	Forested	30	Chilliwack	300	ESE	10	TSHE/ALRU/THPL
Canyon Creek	1997	2	Forested	117	Nooksack	445	SSE	4	TSHE/PSME/THPL
Glacier Creek	1997	3	Forested	128	Nooksack	415	WSW	11	PSME/TSHE/THPL
Gallop Creek	1997	5	Buffer strip	4 ^b	Nooksack	695	NNW	11	TSHE/ABPR/ALRU
Dry Creek	1997	2	Buffer strip	4 ^b	Nooksack	646	N	19	TSHE/ALRU/THPL
Welcome Pass	1997	2	Clearcut	9	Nooksack	677	S	14	PSME/TSHE/THPL
Tam VSG	1998	1	Forested	50	Chilliwack	400	N	15	TSHE/THPL/PSME
Elk	1998	4	Forested	90	Chilliwack	600	SSW	11	PSME/TSHE/THPL
732	1998	1	Forested	50	Chilliwack	360	N	20	THPL/TSHE/PSME
Tam VCC	1998	3	Clearcut	3	Chilliwack	400	N	12	TSHE/THPL/PSME
Tam C	1998	6	Clearcut	6	Chilliwack	600	SSW	12	TSHE/THPL/PSME

^aABPR, noble fir (*Abies procera*); ACMA, bigleaf maple (*Acer macrophyllum*); ALRU, red alder (*Alnus rubra*); PSME, Douglas-fir (*Pseudotsuga menziesii*); THPL, western red-cedar (*Thuja plicata*); TSHE, western hemlock (*Tsuga heterophylla*). Species are listed in order of dominance.

^bOutside the riparian buffer zone.

(MS 222) and then surgically implanted radio transmitters (Holohil model BD-2GH, mass 1.8 g, 15 × 9 × 4 mm, battery life 3–4 months) into the peritoneal cavity. Salamanders were held in an indoor artificial stream channel at the Cultus Lake laboratory of the Department of Fisheries and Oceans for up to 3 weeks while their incisions healed. Upon recovery, we released salamanders at the location from which they were captured. A total of 35 salamanders ranging in size from 22 to 114 g were radio-tagged over 3 years (17 from forested habitat, 7 from riparian buffer strips, and 11 from clearcuts; see Table 2).

The radio transmitters had a range of approximately 40–60 m, depending on terrain. Using a hand-held directional antenna, we determined salamander locations to an accuracy of ~10 cm. Locations of individuals were usually recorded every second day. We considered an animal to have moved if its location shifted by more than 1 m from its previously recorded position. Refuge duration is defined as the number of days a salamander remained at the same location. Maps of individual salamander movements were drawn by measuring distances and bearings from a fixed point to each recorded location. We calculated the distance to the stream either by direct measurement or by using a map. Mean distances from the stream were not measured for salamanders GLC 35 and GAC 51 because of topographical constraints.

The decision to terminate tracking each season was based on transmitter battery longevity and inactivity of the animals. In 1996, 1997, and 1998, tracking was terminated on 30 October, 10 November, and 28 September, respectively.

Temperature and precipitation

In 1996 we obtained air-temperature and precipitation values from meteorological data collected at the Chilliwack Hatchery (elevation 240 m) about 7 km from the Promontory site (elevation ~600 m) and 21 km from the Vedder site (elevation ~300 m; Table 1). In 1997 and 1998 we installed a weather station at each site consisting of a rain gauge and a temperature data logger (Onset hobo) placed on the forest floor.

Analysis

To test the hypothesis that salamanders in clearcut habitat would alter their behavior in a manner which would reduce the risk of desiccation, we compared a number of different behavioral measures across habitat types (forest, clearcut, and buffered strip). We used individual salamanders as the unit of replication and compared mean movement length (m), mean distance from the stream (m), mean refuge duration (number of days spent at the same location), and mean 95% adaptive kernel home range size (m²) (Kie et al. 1994). The adaptive kernel method calculates the smallest area that contains a specified percentage (95%) of the bivariate probability distribution (Worton 1989). During 1998, an extremely dry and hot year, we also compared the proportions of salamander movements that occurred in the rain at clearcut and forested sites, the two habitat types sampled that year.

Differences in salamander movement patterns between the three habitat types (forest, clearcut, and buffer strip) were analyzed using analysis of variance (ANOVA). All data were log-transformed to meet assumptions of normality and homogeneity between treatment variances. We used independent contrasts to determine whether salamander movements differed (*i*) between forested and buffer-strip sites, and (*ii*) between sites with streamside vegetation (forested or buffer strip) and sites logged to the stream edge. We compared the proportions of movements in the rain by salamanders in clearcuts and salamanders in the forest in 1998 using a Student's *t* test.

Results

Microclimate

The mean daily precipitation for each year was 3.9 cm (1996), 4.4 cm (1997), and 2.5 cm (1998). The mean daily maximum temperature was 19°C (1996) 16°C (1997), and 24°C (1998); 1998 was an abnormally hot and dry year. Surface and soil temperatures were much higher during the day and surface temperatures somewhat lower at night in clearcuts than at buffer-strip or forested sites (Fig. 1).

Table 2. Mean values of the variables entered for each individual salamander; these were the values used in the analysis ($N = 35$).

Salamander	Year	Habitat	Movement length (m)	Distance from stream (m)	Refuge duration (days)	Adaptive kernel home-range size (m ²)	Proportion of movements in the rain
TAM VIS 65	1998	Clearcut	4.55	1.92	3.62	114.3	0.53
TAM VIS 55	1998	Clearcut	10.49	0.03	3.33	293.2	0.43
TAM VIS 57	1998	Clearcut	9.65	21.85	5.27	1 226	0.36
TAM C 9	1998	Clearcut	7.89	3.52	4.86	333.1	0.50
TAM C 41	1998	Clearcut	2.91	0.03	7	12.61	0.13
TAM C 47	1998	Clearcut	8.9	0	5.29	176.3	0.35
TAM C 63	1998	Clearcut	1.61	0.05	13	3.08	0.20
TAM C 69	1998	Clearcut	10.6	1.06	9.36	45.5	0.36
TAM C 97	1998	Clearcut	5.24	0.1	12.25	67.88	0.67
WP 31	1997	Clearcut	6.26	2.2	7.5	195.6	0.63
WP 43	1997	Clearcut	14.04	0.9	4.99	2 002	0.58
TAM VIS 45	1998	Forest	13.57	23.98	5.56	5 778	0.44
ELK 81	1998	Forest	4	13.2	2.75	315.1	0.16
ELK 85	1998	Forest	2.97	4.75	3.83	12.58	0
ELK 91	1998	Forest	3.3	15.61	4.75	75.32	0.14
ELK 54.9	1998	Forest	4.07	1.23	8	73.05	0.33
732 91b	1998	Forest	1.73	0.61	8	3.56	0
GLC 21	1997	Forest	10.36	0.11	8.2	403.3	0.7
GLC 27	1997	Forest	5.76	2.38	4.11	821	0.44
GLC 35	1997	Forest	7.05	na	4.63	5 031.9	0.63
CC 37	1997	Forest	8.52	4.62	5.14	4 057.8	0.76
CC 71	1997	Forest	19.52	66.25	4.43	35 321.3	0.61
V 37	1996	Forest	12.22	0.61	2.73	1 829.3	0.47
V 48	1996	Forest	13.48	0.12	2.63	11 213	0.6
PR 50	1996	Forest	9.2	24.81	4.25	3 705.3	0.67
PR 52	1996	Forest	5.21	13.03	3.96	935.5	0.7
PR 59	1996	Forest	8.23	22.87	3.52	1 550.8	0.58
PR 19	1996	Forest	6.39	8.27	4	866.2	0.33
DC 41	1997	Buffer strip	20.69	2.98	4.64	8 938.1	0.77
DC 59	1997	Buffer strip	8.34	6.15	4.25	4 556.5	0.75
GAC 25	1997	Buffer strip	5.57	0.78	4.71	917.5	0.47
GAC 33	1997	Buffer strip	14.44	9.35	3.58	5 031.9	0.5
GAC 51	1997	Buffer strip	13.54	na	5.47	5 161.6	0.6
GAC 57	1997	Buffer strip	6.51	15.9	3.81	738.4	0.52
GAC 67	1997	Buffer strip	8.67	5.14	3.96	2 444.4	0.5

Movement behavior

In two cases, refuge duration and home-range size, treatment variances were still significantly different after transformation. However, the larger variances were associated with the treatments with larger sample sizes: forest and clearcut. When larger variances are associated with larger treatment samples, the probability of a Type I error is less than α , making the test more conservative (Zar 1996).

Our results were consistent with predictions that salamanders in clearcuts would remain closer to the stream, would remain in refuges longer, and would have smaller home ranges than salamanders in forested habitat (Table 3, Fig. 2). Salamanders in clearcuts with riparian buffer strips behaved similarly to those at forested sites (Table 3, Fig. 2). Mean movement lengths were almost identical across the three habitat types (Table 3, Fig. 2). In 1998, when rainfall was very scarce, salamanders in clearcuts also conducted a higher proportion of their movements in the rain ($40 \pm 6\%$; mean \pm SE) than did

salamanders in the forest ($18 \pm 7\%$) (13 df, $t = 2.4$, $P = 0.03$).

Discussion

Microclimate

Our observations of surface and soil temperatures (Fig. 1) demonstrate that microclimate tends to be more extreme and variable in clearcuts than at either forested or buffer-strip sites. Under such conditions amphibians are more likely to risk desiccation and modify their behavior accordingly. These observations agree with those of others (Chen et al. 1993; 1995; Brosfokske et al. 1997) who have examined the effects of clearcuts on microclimate in detail. While microclimatic conditions at buffer-strip sites were more similar to those at forested sites than were those at clearcut sites, it is important to note that some microclimatic gradients extend up to

Fig. 1. Maximum surface (a) soil (b) temperatures and minimum surface (c) and soil (d) temperatures during August and September 1997 in the three habitat types: clearcut (thin line), buffer strip (thick broken line), and forest (thick solid line).

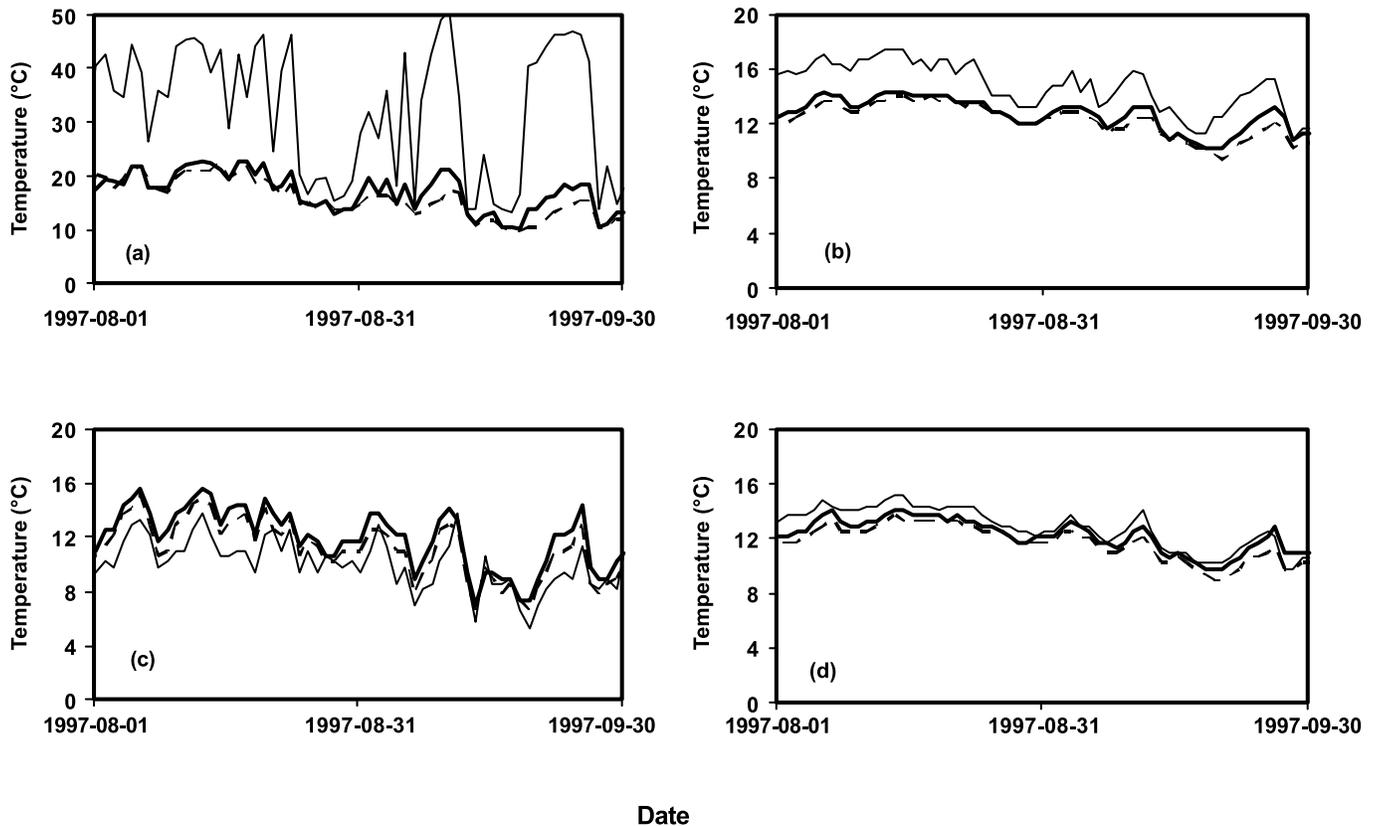


Table 3. ANOVA summary of movement variables across the three habitat types.

Variable	Source	Sum of squares	df	Mean square	<i>F</i>	<i>P</i>
Movement length (\log_{10})	Habitat	0.195	2	0.098	1.388	0.264
	Error	2.252	32	0.07		
Distance from stream (\log_{10})	Habitat	1.778	2	0.889	3.839	0.033
	Contrast 1	0.01	1	0.01	0.043	0.836
	Contrast 2	1.555	1	1.555	6.716	0.015
	Error	6.946	30	0.232		
Refuge duration (\log_{10})	Habitat	0.184	2	0.092	3.734	0.035
	Contrast 1	0.001	1	0.001	0.044	0.834
	Contrast 2	0.179	1	0.179	7.244	0.011
	Error	0.789	32	0.025		
Home-range size (\log_{10})	Habitat	8.569	2	4.285	5.403	0.01
	Contrast 1	1.67	1	1.67	2.106	0.156
	Contrast 2	8.212	1	8.212	10.355	0.003
	Error	25.377	32	0.793		

Note: Contrast 1 represents the difference between forested and buffer-strip habitats and contrast 2 the difference between clearcut habitat and habitats forested to the stream edge. *P* values in boldface type represent statistically significant differences between habitats.

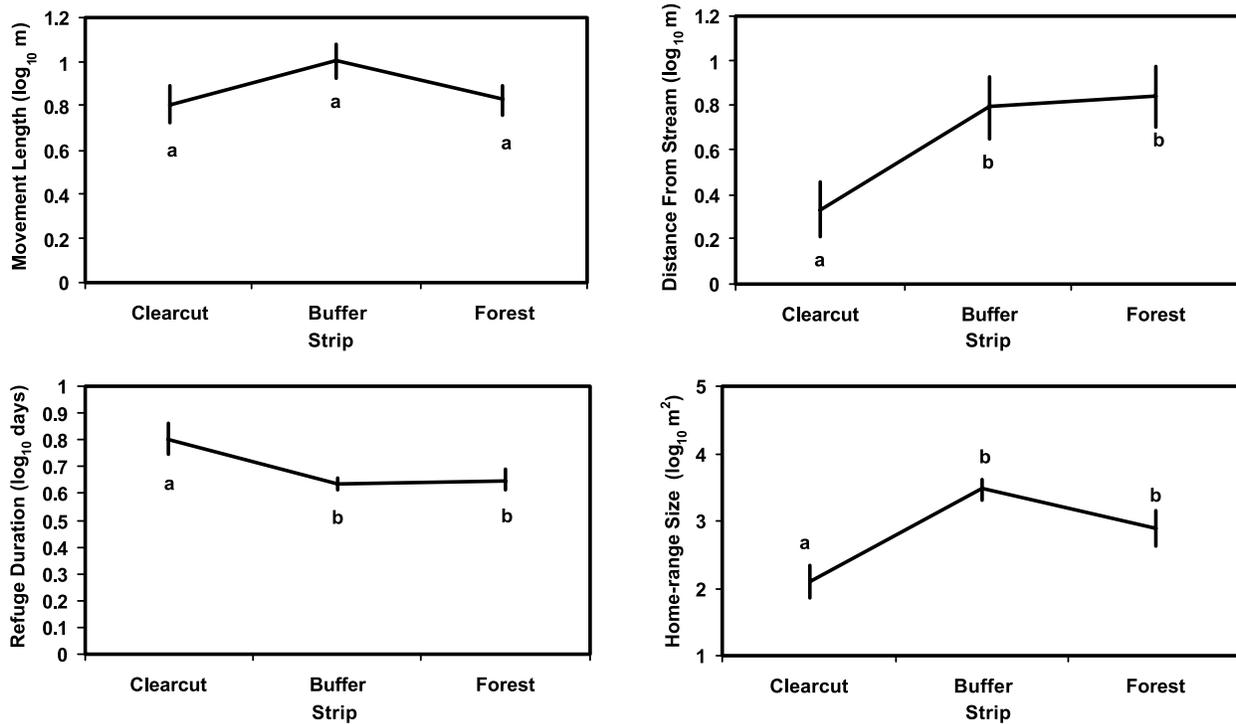
240 m into the forest from the clearcut edge and that in such cases buffer-strip widths up to 300 m may be necessary to maintain natural riparian microclimatic gradients intact (Brosfoske et al. 1997).

The influence of habitat type on behavior

We hypothesized that salamanders inhabiting clearcuts would

alter their behavior in a manner consistent with desiccation avoidance. Explicitly, we predicted that compared with salamanders at forested sites, salamanders in clearcuts would have lower mean movement lengths, stay closer to a source of water, spend more time in refuges, have smaller home ranges, and make a greater proportion of their movements in the rain. Mean distance from the stream, refuge duration,

Fig. 2. Movement length, distance from the stream, refuge duration, and home-range size (mean \pm SE) for Pacific giant salamanders (*Dicamptodon tenebrosus*) in the three habitat types. All four variables are log-transformed to meet the assumptions of ANOVA. Treatments accompanied by the same letter are not significantly different.



and home-range size were consistent with predictions. Contrary to our prediction, however, mean movement lengths were similar across all three habitat types (Table 3, Fig. 1).

Salamanders inhabiting clearcuts remained closer to the stream. This result is consistent with results from other studies of terrestrial amphibians in managed stands (Dupuis et al. 1995; Dupuis 1997). During the unusually dry 1998 field season, most of these animals were found in the stream, whereas salamanders at forested sites often used areas distant from the stream. Because home ranges in clearcuts were limited to near stream habitat, these home ranges were generally more linear and smaller than those in forested habitat. Since amphibians are generally believed to be poor dispersers (Corn and Bury 1989; Sjögren 1991; Petranka et al. 1993; Blaustein et al. 1994), the narrow home ranges observed following clearcut logging could lead to very limited dispersal of terrestrial salamanders between streams after logging.

In addition to being limited to near stream habitat, salamanders in clearcuts in 1998, a particularly dry year, were more dependent on precipitation for their movements than salamanders at forested sites. Salamanders may be limited to moving in the rain during unusually dry years, when the absence of moisture forces them to remain in refuges to avoid desiccation. Dupuis et al. (1995) measured soil moisture in managed stands and old-growth forests and documented noticeable differences in the rate of water loss through the spring and early summer. This suggests that disturbed stands have reduced soil porosity and water-retention capabilities. As in this study, salamander activity was influenced by precipitation during the dry year only (Dupuis et al. 1995).

Changes in behavior that reduce time spent on the surface, such as increased refuge duration or dependence on precipitation, could impact the ability of animals inhabiting clearcut habitat to find food and mates. For example, Fraser (1976) showed that plethodontid salamanders living underground were at an energetic disadvantage compared with those on the surface because availability of prey was limited underground. Similarly, Jaeger (1980) showed that ambient moisture regulated the availability of food for plethodontid salamanders in the eastern U.S.A., and ambient temperature set the metabolic requirements of the salamanders.

The efficacy of riparian buffer strips

We hypothesized that terrestrial Pacific giant salamanders inhabiting riparian buffer strips would not be subject to the same movement reductions as salamanders in clearcuts. Results from the interhabitat comparisons confirm this prediction. We found that terrestrial giant salamanders in riparian buffer strips behaved similarly (distance from the stream, refuge duration, and home-range size) to animals at forested sites and differently from those in clearcuts (Table 3, Fig. 2).

Previous studies examining the effects of riparian buffer strips on amphibian populations have yielded conflicting results. Kelsey (1995) found that even with the retention of buffer strips, the density of *Ascaphus truei* tadpoles was negatively affected by timber harvest. In other studies it was concluded that forested buffer strips maintained both terrestrial (Vesely 1996) and aquatic (Dupuis and Steventon 1999) amphibian population densities higher than those found at sites clear-cut to the stream margin. One study that did not

directly examine riparian buffer strips did show that the terrestrial salamander *Plethodon vehiculum* occurred in evenly distributed clusters throughout old-growth forests on Vancouver Island, but in young and mature second-growth stands the species was largely restricted to riparian zones (Dupuis 1997; Dupuis et al. 1995). This indicates that the riparian zone may act as a refuge and (or) dispersal corridor for some amphibian species in managed stands. Our results also indicate that retaining buffer strips when logging may benefit Pacific giant salamanders.

Acknowledgements

Collection permits (C067840 (1996), C071783 (1997), and C078592 (1998)) were provided by the British Columbia Ministry of the Environment, Lands and Parks. Animal-care protocols (A95-0170 and A94-1582) were also from the British Columbia Ministry of the Environment, Lands and Parks. Financial support for this research was provided by Forest Renewal BC, World Wildlife Fund Canada, and the BC Habitat Conservation Trust Fund as grants to W. Neill and J.S. Richardson, and a National Sciences and Engineering Research Council of Canada scholarship to B. Johnston. We are grateful to W. Neill for his support and advice both in the field and in the revision of the manuscript. We thank J. Curtis, D. Kasimir, M. Krause, B. Matsuda, and D. White for their assistance in the field. K. Mallory and A. Stringer provided assistance with the surgeries. An anonymous reviewer, L. Dupuis, and A. Frid gave useful comments on an earlier version of the manuscript.

References

- Beschta, R.L., Bilby R.E., Brown G.W., Holtby L.B., and Hofstra, T.D. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. *In* Streamside management: forestry and fishery interactions. Edited by E.O. Salo and T.W. Cundy. Contribution 57, Institute of Forest Resources, University of Washington, Seattle. pp. 191–232.
- Bisson, P.A., Bilby, R.E., Bryant, M.D., Dolloff, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koskim, K.V., and Sedell, J.R. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* Streamside management: forestry and fishery interactions. Edited by E.O. Salo and T.W. Cundy. Contribution 57, Institute of Forest Resources, University of Washington, Seattle. pp. 143–190.
- Blaustein, A.R., and Wake, D.B. 1995. The puzzle of declining amphibian populations. *Sci. Am.* **272**: 52–57.
- Blaustein, A.R., Wake, D.B., and Sousa, W.P. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conserv. Biol.* **8**: 60–71.
- Bren, L.J. 1995. Aspects of the geometry of riparian buffer strips and its significance to forestry operations. *For. Ecol. Manag.* **75**: 1–10.
- Brososke, K.D., Chen, J., Naiman, R.J., and Franklin, J.F. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecol. Appl.* **7**: 1188–1200.
- Brown, G.W., and Krygier, J.T. 1970. Effects of clear-cutting on stream temperature. *Water Resour. Res.* **6**: 1133–1139.
- Budd, W.W., Cohen, P.L., Saunders, P.R., and Steiner, F.R. 1987. Stream corridor management in the Pacific Northwest: I. Determination of stream-corridor widths. *Environ. Manag.* **11**: 587–597.
- Bury, R.B. 1983. Differences in amphibian populations in logged and old growth redwood forest. *Northwest Sci.* **57**: 167–178.
- Chen, J., Franklin, J.F., and Spies, T.A. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* **63**: 219–237.
- Chen, J., Franklin, J.F., and Spies, T.A. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Appl.* **5**: 74–86.
- Colberg, M.E., DeNardo, D.F., Rojek, N.A., and Miller, J.W. 1997. Surgical procedure for radio transmitter implantation into aquatic, larval salamanders. *Herpetol. Rev.* **28**: 77–78.
- Conner, E.J., Trush, W.J., and Knight, A.W. 1988. Effects of logging on Pacific giant salamanders: influence of age-class composition and habitat complexity. *Bull. Ecol. Soc. Am.* **69**(Suppl.): 104–105.
- Corn, P.S., and Bury, R.B. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *For. Ecol. Manag.* **29**: 39–57.
- Cross, S.P. 1985. Responses of small mammals to forest riparian perturbations. *In* Riparian ecosystems and their management: reconciling conflicting uses. U.S. For. Serv. Tech. Rep. RM-120. pp. 269–275.
- Davies, P.E., and Nelson, M. 1994. Relationships between riparian buffer widths and the effects of logging on stream habitat, invertebrate community composition and fish abundance. *Aust. J. Mar. Freshw. Res.* **45**: 1289–1305.
- Dupuis, L.A. 1997. Effects of logging on terrestrial amphibians of coastal British Columbia. *Herpetol. Conserv.* **1**: 185–190.
- Dupuis, L.A., and Steventon, D. 1999. Riparian management and the tailed frog in northern coastal forests. *For. Ecol. Manag.* **124**: 35–43.
- Dupuis, L.A., Smith, J.M.N., and Bunnell, F.L. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conserv. Biol.* **9**: 645–653.
- Environment Canada. 1998. British Columbia weather normals 1961–1990. Available at http://www.msc-smc.ec.gc.ca/climate/climate_normals/index_e.cfm (accessed 8 January 2003).
- Farr, A.C.M. 1989. Status report on the Pacific giant salamander (*Dicamptodon ensatus*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont.
- Feder, M.E. 1983. Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica*, **39**: 291–310.
- Fraser, D.F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecology*, **57**: 459–471.
- Haycock, R.D. 1991. Pacific giant salamander *Dicamptodon tenebrosus* status report. Wildlife Branch, British Columbia Ministry of Environment, Lands and Parks.
- Hutchison, V.H. 1961. Critical thermal maxima in salamanders. *Physiol. Zool.* **34**: 92–125.
- Jaeger, R.G. 1980. Fluctuations in prey availability and food limitation for a terrestrial salamander. *Oecologia*, **44**: 335–341.
- Kelsey, K.A. 1995. Responses of headwater stream amphibians to forest practices in western Washington. Ph.D. dissertation, University of Washington, Seattle.
- Kie, J.G., Baldwin, J.A., and Evans, C.J. 1994. CALHOME (California Homerange). U.S. Forest Service, Pacific Southwest Research Station. Available at http://nhsbig.inhs.uiuc.edu/wes/home_range.html (accessed 8 January 2003).
- Krajina, V.J. 1965. Biogeoclimatic zones and classification of British Columbia. *Ecol. West. N. Am.* **1**: 1–17.
- Lesica, P., and Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? *Conserv. Biol.* **9**: 753–760.
- Maiorana, V.C. 1978. Difference in diet as an epiphenomenon: space regulates salamanders. *Can. J. Zool.* **56**: 1017–1025.

- Newbold, J.D., Erman, D.C., and Roby, K.B. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. *Can. J. Fish. Aquat. Sci.* **37**: 1076–1085.
- O’Laughlin, J., and Belt, G.H. 1995. Functional approaches to riparian buffer strip design. *J. For.* **93**: 29–32.
- Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., and Gibbons, J.W. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science (Washington, D.C.)*, **253**: 892–895.
- Petranka, J.W., Eldridge, M.E., and Haley, K.E. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conserv. Biol.* **7**: 363–370.
- Phillips, K. 1990. Where have all the frogs and toads gone? *Bioscience*, **40**: 422–424.
- Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biol. J. Linn. Soc.* **42**: 135–147.
- Spotila, J.R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecol. Monogr.* **42**: 95–125.
- Triquet, A.M., McPeck, G.A., and McComb, W.C. 1990. Songbird diversity in clearcuts with and without riparian buffer strip. *J. Soil Water Conserv.* July–August 1990: 500–503.
- Vesely, D.G. 1996. Terrestrial amphibian abundance and species richness in headwater riparian buffer strips, Oregon Coast Range. M.Sc. thesis, Oregon State University, Corvallis.
- Welsh, H.H., Jr. 1990. Relictual amphibians and old-growth forests. *Conserv. Biol.* **4**: 309–319.
- Western Regional Climate Center. 1998. Washington State, Glacier Ranger Station. Available at <http://www.wrcc.dri.edu/> (accessed 1998).
- Worton, B.J. 1989. Kernel methods for estimation the utilization distribution in home-range studies. *Ecology*, **70**: 164–168.
- Zar, J.H. 1996. *Biostatistical analysis*. 3rd ed. Prentice Hall, Englewood Cliffs, N.J.
- Zug, G.R. 1993. *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, Inc., San Diego.