

# Terrestrial movements of juvenile and adult tailed frogs in relation to timber harvest in coastal British Columbia

Tanya R. Wahbe, Fred L. Bunnell, and R. Bruce Bury

**Abstract:** Tailed frog (*Ascaphus truei* Stejneger) populations are at risk in much of the Pacific Northwest, and recolonization of sites may be slow postlogging. To examine the terrestrial movements of *Ascaphus* in clearcuts and old growth, we employed pitfall traps and drift-fence arrays installed along streams and 100 m into upland habitat. In the fall, we captured frogs farther from streams in old growth than in clearcuts, and more frogs were captured  $\leq 25$  m from streams in clearcuts. Stronger stream affinity in clearcuts was most evident with juvenile frogs, which exhibited more upstream movements than adults. Compared with inland sites where frogs remained close to streams (e.g., 12 m), frogs at our coastal sites were captured at greater distances from streams ( $\geq 100$  m), having lower stream affinity than frogs at inland sites. Long-distance overland movements appear more likely where forested stands are present. Aggregations of *Ascaphus* at individual streams may not represent distinct populations and should not be managed as distinct units. Preserving groups of interconnected streams within watersheds instead of individual streams will improve the conservation status of *Ascaphus*. Population monitoring can ensure conservation measures promote long-term persistence.

**Résumé :** Les populations côtières de la grenouille-à-queue (*Ascaphus truei* Stejneger) sont en péril dans la majeure partie de la région du Nord-Ouest du Pacifique et la recolonisation des sites est lente après la coupe. Pour étudier les déplacements terrestres d'*Ascaphus* dans des parterres de coupe à blanc et des vieilles forêts, les auteurs ont utilisé des pièges fosses et des clôtures de dérivation installés le long de ruisseaux et à 100 m à l'intérieur de la forêt. À l'automne, ils ont capturé les grenouilles plus loin des ruisseaux dans les vieilles forêts que dans les coupes et plus de grenouilles ont été capturées à  $\leq 25$  m des ruisseaux dans les coupes. Les grenouilles juvéniles ont montré une plus grande affinité pour les ruisseaux dans les coupes et elles ont effectué plus de déplacements vers l'amont des ruisseaux que les adultes. Par comparaison avec des sites intérieurs où les grenouilles restaient près des ruisseaux (p. ex., 12 m), les grenouilles de leurs sites côtiers ont été capturées à de plus grandes distances des ruisseaux ( $\geq 100$  m), ce qui suggère qu'elles ont moins d'affinité pour les ruisseaux que les grenouilles de l'intérieur. Les déplacements terrestres sur de longues distances semblent être plus probables quand le couvert forestier est présent. Les rassemblements d'*Ascaphus* dans un ruisseau donné peuvent ne pas correspondre à des populations distinctes et ne devraient pas être gérés comme des unités distinctes. La préservation de groupes de ruisseaux interconnectés dans un bassin hydrographique plutôt que des ruisseaux individuels serait préférable pour améliorer la situation d'*Ascaphus*. Un suivi des populations peut assurer que ces mesures de conservation favorisent la persistance à long terme.

[Traduit par la Rédaction]

## Introduction

Forests are structurally complex ecosystems with greater vertebrate species richness than other terrestrial biomes (Wilson 1988; Bunnell and Kremsater 1990). Timber harvest can significantly alter the structure and function of forests, and in the temperate zone, habitat loss and forest fragmentation are major threats to species (Soulé 1991; Caughley and

Gunn 1996). Habitat structure influences the occurrence and abundance of terrestrial (Ash 1988; deMaynadier and Hunter 1995; Aubry 1997) and stream amphibians (Welsh and Ollivier 1998; Sutherland and Bunnell 2001). However, for most stream amphibians, we have only rudimentary knowledge of their reproductive ecology, diet, growth rates, physiological tolerances, and, in particular, habitat requirements (Corn et al. 2003). Higher temperatures and lower soil mois-

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ture associated with open habitats can be limiting for amphibians, which experience high rates of evaporative water loss (Spotila 1972) and have poorer dispersal abilities than other vertebrates (Sinsch 1990).

Early signs of ecosystem dysfunction usually appear at the level of populations, affecting species with narrow ecological tolerances (Odum 1992). In many forests, amphibians are the most abundant vertebrate group (Burton and Likens 1975; Crisafulli and Hawkins 1998), and some argue they play a key role in ecosystem dynamics (deMaynadier and Hunter 1995). Because of their biphasic life histories (Wilbur 1980), specific habitat requirements (Blaustein et al. 1994), longevity, and strong site fidelity compared with most vertebrates, amphibians are especially sensitive to environmental changes and may serve as valuable indicators of ecosystem dysfunction.

The tailed frog (*Ascaphus truei* Stejneger) is endemic to the Pacific Northwest of North America and is designated "at risk" in coastal British Columbia (British Columbia Conservation Data Centre 2001), Oregon (Oregon Natural Heritage Program 2001), and California (California Natural Heritage Program 2001). It is the only representative of the family Ascaphidae (Nussbaum et al. 1983), and is believed to be the most primitive frog living (Ford and Cannatella 1993). They range from British Columbia to western Montana, between the Pacific Coast and the Rocky Mountains, and southward to northern California (Corkran and Thoms 1996) at elevations ranging from 0 to 2140 m (Leonard et al. 1993; Corkran and Thoms 1996). *Ascaphus* are found in mountainous, coniferous forests in cool, fast-flowing, perennial streams that usually lack fish.

Current *Ascaphus* management guidelines in British Columbia are based on larval habitat data (Ministry of Forests and Ministry of Environment, Lands and Parks 1999). However, available data on the effects of forest practices on larval *Ascaphus* population abundance and density are contradictory or vary by geographic location. While most studies (Bury et al. 1991; Welsh and Lind 1991; Dupuis and Steventon 1999) report negative influences of forest harvesting activities, others (Gilbert and Allwine 1991; Richardson and Neill 1998) have shown no effect or increases in abundance in some areas (e.g., in maritime locations). Still, little is known about the larval population ecology of *Ascaphus*, and even less is known about the transformed frogs, especially in terrestrial habitats. To determine influences of habitat disturbance and to better conserve *Ascaphus* populations, an understanding of both aquatic and terrestrial life stages is necessary.

*Ascaphus* are believed to be sensitive to habitat alteration because of their lengthy larval period of 1–5 years (Wahbe 1996; Wallace and Diller 1998; Bury and Adams 1999; varying with geographic location and elevation), small clutch size of 30–70 eggs (Metter 1967; Leonard et al. 1993), biennial reproduction at high elevation, inland sites (Rocky Mountains, Metter 1967; reproduction may be annual elsewhere, Bury et al. 2001), low recolonization potential (with the exception of Crisafulli and Hawkins 1998), and specialized characteristics of their habitats (Bury and Corn 1988a; Hawkins et al. 1988). *Ascaphus* have a low desiccation tolerance (Claussen 1973) and one of the lowest and narrowest temperature tolerances among anurans (Brattstrom 1963; de Vlaming and Bury 1970).

Despite the linear nature of streams and the ease with which movements can occur near water, *Ascaphus* movements important in dispersal may occur laterally and overland. Patterns of *Ascaphus* movements may vary among regions because of inherent geographic differences, but movements after metamorphosis are poorly documented. While *Ascaphus* exhibit strong site fidelity (20 m around streams) at inland sites (Daugherty and Sheldon 1982), some have been found >100 m from streams during wet weather on the coast (e.g., Welsh and Reynolds 1986; Bury and Corn 1988a). Terrestrial movements by *Ascaphus* may be critical to arrive at new streams and increase the gene pool. Fragmentation may limit movements, and molecular studies suggest that gene flow among *Ascaphus* populations is low (Pauken and Metter 1971; Ritland et al. 2000; Neilson et al. 2001). Movement patterns can represent dispersal ability, recolonization potential, and extinction thresholds (Kramer et al. 1993; Diffendorfer 1998; Fahrig 2001), and these direct measures may be more revealing than molecular techniques.

Our goal was to assess the colonization potential of juvenile and adult *Ascaphus* in clearcuts and old-growth forests. We tested hypotheses based on three predictions. First, amphibians require moist habitats and avoid desiccation. Therefore, we predicted that frogs in clearcuts remain closer to streams than frogs in old-growth forests. Second, as some researchers recorded juvenile movements of at least 75 m from streams during fall (Bury and Corn 1987, 1988b) and a decrease in mobility at the onset of reproductive maturity (Daugherty and Sheldon 1982), we predicted that juveniles undertake most upland movements and that adults move along streams. Third, precipitation and temperature strongly influence amphibian activity (Brattstrom 1963; Bury and Corn 1988b). Because coastal populations experience less thermal stress than inland populations, we predicted that *Ascaphus* in coastal regions move greater distances from streams than those in inland regions.

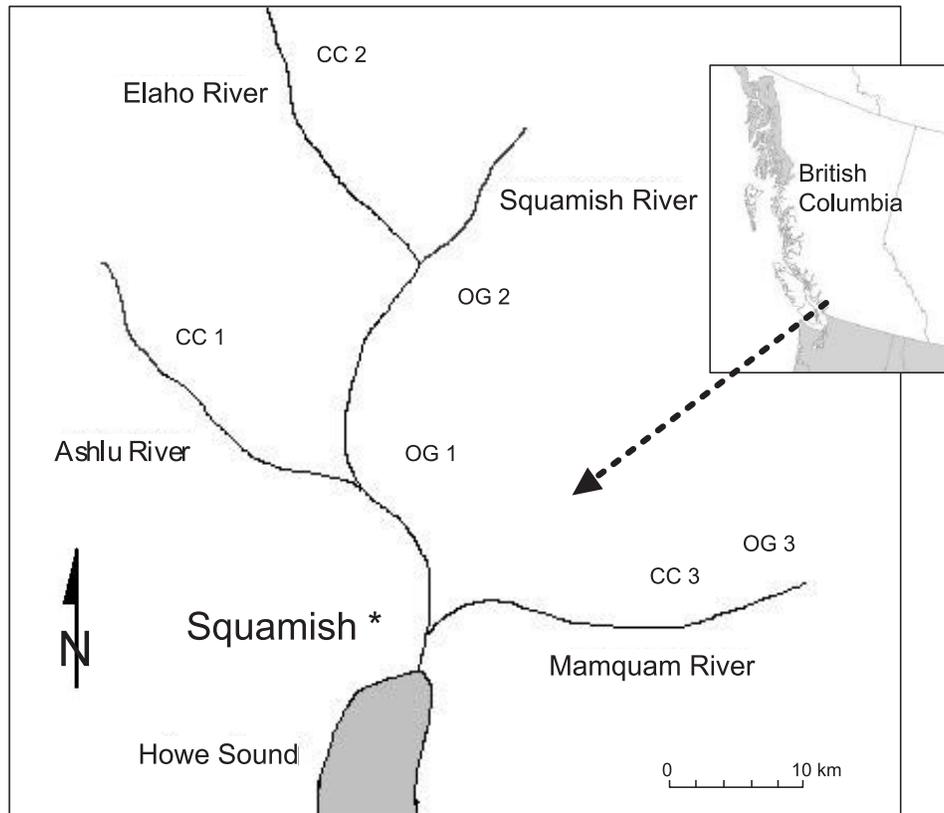
## Materials and methods

### Study area

We examined frog movements near Squamish in southwestern British Columbia (49°N, 122°W), 60 km north of Vancouver in Coastal Western Hemlock and lower portions of Mountain Hemlock biogeoclimatic zones (Meidinger and Pojar 1991). Both zones are relatively moist, with annual precipitation ranging from 1000 to 4400 mm in Coastal Western Hemlock and from 1700 to 5000 mm in Mountain Hemlock (Meidinger and Pojar 1991). Sites were located in four adjacent river basins (Fig. 1) that flow into Howe Sound.

In the upper headwaters of watersheds, we selected a single stream in three old-growth forests (>250 years old) and three recent clearcuts (5 years since logging). These streams were selected after the presence of larval *Ascaphus* in each had been confirmed with 20-min surveys. All streams were 1–3 m wide and fishless. Each site covered about 2.25 ha (Fig. 2) and was surrounded by at least 50 m of contiguous forest, beyond which a clearcut, road, or different forest cover type could be present. Mamquam and Elaho clearcuts were 200 and 500 m downstream from old growth, respectively, while the Ashlu clearcut was 300 m downstream from

**Fig. 1.** Schematic map of study area within British Columbia showing relative positions of the four river basins and the three replicates of each treatment: old growth (OG) and clearcut (CC).



a rocky, unforested ridge. Selected streams were 200–400 m from any adjacent streams.

#### Pitfall trap and drift-fence arrays

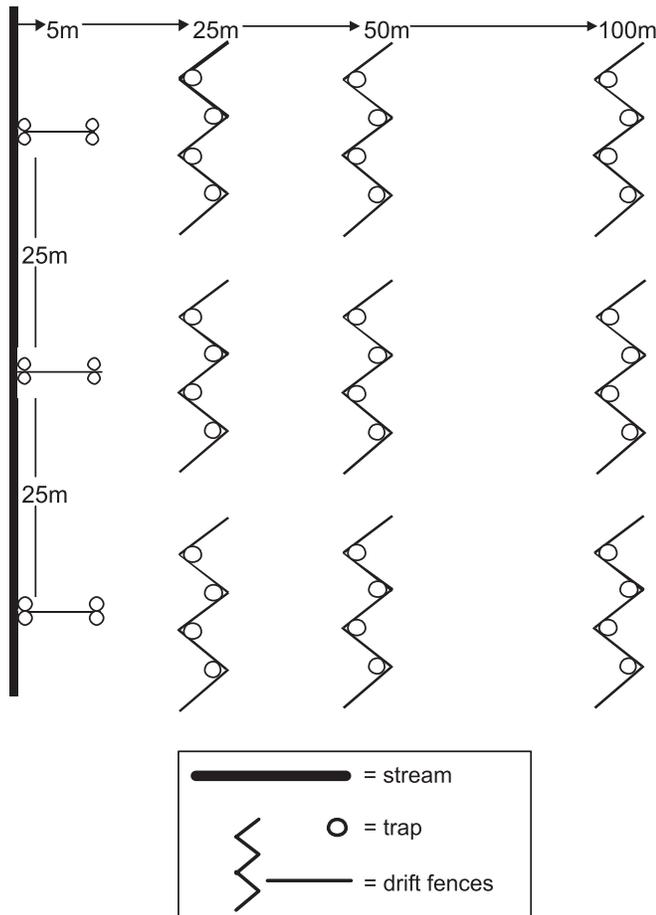
To evaluate frog movements, we installed streamside and upland arrays of pitfall traps with clear, plastic drift fences, adapted from prior designs (Corn and Bury 1990; Corn 1994). Arrays each consisted of four pitfall traps and one or five drift fences (Fig. 2). Traps were constructed of white, smooth-walled polyvinyl chloride sewer pipe, 15 cm in diameter and 40 cm deep. Streamside arrays were designed to detect movements up and down the stream bank. Each array was constructed with a 5 m long drift fence with two traps at each end, installed perpendicular to the stream as close to the water's edge as possible. Upland arrays detected movements towards and away from streams, and included five 5 m long drift fences installed in zigzag formation with one trap at each elbow. Arrays were 20 m in length and parallel to the stream.

At each site, we installed 48 pitfall traps and 240 m of drift fence (total = 288 traps and 1440 m of fence for all sites). Selection of the first streamside array was random, while all others were systematic. The minimum distance of the first array from the nearest logging road was 50 m. In most cases, the first array was upstream from a logging road. In the Ashlu and Mamquam clearcuts, the first arrays were established downstream from logging roads, because upstream forests were not the appropriate size or forest cover type.

We placed a bottomless margarine container at the trap opening, forming a funnel, to keep frogs from hopping or climbing out, and checked traps every 2–3 d for 1- to 4-week periods. To reduce small mammal mortality, we facilitated escape by placing sisal rope in traps, securing it in soil beside the trap (adapted from Wind 1996). Insertion of ropes significantly reduces small mammal mortality (Karraker 2001), while *Ascaphus* are retained in traps. We inclined a cedar shingle against the fence over each trap opening to protect animals from direct sunlight, predation, and rainfall that can flood traps. To prevent desiccation of animals, we placed wet moss in traps, and added fresh water on every visit to maintain moisture.

During rainy periods (mid-September through November), when captures were expected to be high (Bury and Corn 1987), traps were operated almost continuously and were visited frequently. We operated traps 18–30 September and 4–13 October in 1998, 18–25 July, 8–17 August, and 10 September – 1 November in 1999, and 1 September – 9 November in 2000. Unlike fall trapping, we did not operate traps continuously in the summer of 1999: two to three times during July (8 d total), August (10 d), and early September (7 d). At 0 and 100 m from the stream, soil temperature at 15 cm depth (digital thermometer:  $\pm 0.1$  °C) and air temperature in the shade 15 cm above the soil surface (mercury thermometer:  $\pm 0.5$  °C), and a relative measure of soil moisture at 15 cm depth (conductivity meter:  $\pm 0.5$  units) were recorded on each site visit. Soil moisture also was recorded at each capture location. Our conductivity meter had a scale

**Fig. 2.** A trapping grid (representing one experimental unit) showing arrays of streamside and upland pitfall traps and drift fences. Not to scale.



from 0 (dry) to 10 (wet), and Thompson et al. (1996) reported that this device provides stable, reproducible readings.

#### Mark-recapture

We measured, individually marked, and released frogs on the opposite side of the drift fence where they were captured, assuming that was their movement direction. Frogs were classified into two developmental stages based on snout-vent length and morphological features: “juveniles”, most with residual tail present (16.3–27.9 mm snout-vent length) and “adults”, most with secondary sexual characteristics present (28.0–50.1 mm snout-vent length).

We marked frogs using visual implant fluorescent elastomer tags (VIE; Northwest Marine Technologies 2002). This method has no reported effects on mortality or behavior of amphibians (Anholt et al. 1998; Jung et al. 2000; Davis and Ovaska 2001) and is preferable to toe clipping (Clarke 1972). To avoid potentially harmful chemical anesthetics (e.g., tricaine methanesulfonate, also known as MS-222), hyperactive frogs were submerged briefly in ice water to reduce their activity. This likely caused minimal or no stress, as some species of terrestrially hibernating frogs endure freezing of extra-cellular body fluids (Churchill and Storey 1993), and *Ascaphus* are cold-adapted frogs.

Directions of frog movement were categorized as upstream, downstream, upslope, or downslope. Upstream movements were parallel to the stream, against stream flow, and within 5 m of the edge of stream. Downstream movements were parallel to stream, in the direction of stream flow. Upslope movements away from stream were roughly perpendicular to stream and within 100 m of stream edge. Downslope movements towards the stream were roughly perpendicular.

All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. We held the required certificate from the University of British Columbia Committee on Animal Care (No. A0-0110), and the British Columbia provincial permit (No. C088692) necessary for fieldwork on a “Blue-listed” species.

#### Statistical analyses

A single trapping grid consisted of 48 pitfall traps and 240 m of drift fences arranged in trapping arrays. Each trapping grid was treated as an experimental unit for statistical analyses. We installed one trapping grid at each of six sites (three old growth, three clearcut), for a total of six experimental units. We used the statistics package SPSS® for Windows® (SAS Institute Inc. 2003) to run one-way analyses of variance (ANOVAs) on mean values per experimental unit (i.e., six treatment means) for the 254 *Ascaphus* captured during 3 years (1998–2000). Mean distances are calculated based on the average distance from stream across all captures at each site. Recaptures are excluded from analyses. Homogeneity of variances and normality of data were tested before all analyses were performed.

In a separate analysis, interactions among the two treatments, three watersheds, and three years were tested using an ANOVA based on a randomized complete block design with a split-plot year effect. In this mixed-model ANOVA, year and forest cover were fixed factors, and watershed was a random factor. Because interactions among forest cover, year, and watershed were not significant when analyzing mean distances, we pooled watershed and year interaction degrees of freedom into experimental error degrees of freedom to obtain a more precise estimate of variance (Hicks 1982). When differences among multiple means were statistically significant, we used a multiple comparison test (Bonferroni) to evaluate which means differed. All reported *P* values were obtained using statistics tested against a preset significance level of  $\alpha = 0.05$ . Values are reported as the mean  $\pm$  standard error.

When analyzing distance categories, tests for independence ( $\chi^2$ ) were performed on standardized numbers of frogs captured. Numbers of frogs captured were standardized by converting them to numbers of frogs per 100 trap nights, or catch per unit effort (CPUE), to address unequal trapping effort. A trap night is the number of traps in operation  $\times$  the number of nights in operation. Traps full of water, pushed above ground (because of rising water table), or broken were deemed inoperable and were deleted from trap night totals. We ran tests for independence before pooling any data from different sites. Cochran-corrected tests for independence ( $\chi^2_c$ ; Zar 1984) were used for  $2 \times 2$  contingency tables. When CPUE values were analysed, we employed arcsine transformations.

**Table 1.** Number of nights of trapping and number of *Ascaphus* recorded (captured and encountered) in southwestern British Columbia, 1998–2000.

Year	No. of nights	No. of frogs		
		Trapped	Incidental encounters	Total recorded
1998	21	32	13	45
1999	63	128	8	136
2000	70	94	6	100

To assess body condition of individual frogs in old growth and clearcuts, we used a body condition index (BCI). We calculated BCI using observed mass divided by expected mass. Expected mass (predicted  $Y$ ) was obtained from a regression of mass ( $Y$ ) against snout–vent length ( $X$ ). This calculation incorporates length-corrected mass and has been used in studies of whiptail lizards (Dickinson and Fa 2000), terrestrial salamanders (Dupuis et al. 1995), and bears (Catt et al. 2002). BCI calculations were restricted to males and nongravid females to avoid bias created by differences in reproductive status (Stamps 1983).

## Results

### Catch per unit effort

We recognized two trapping periods: summer (July–August) and fall (September–November). Summer trapping occurred only in 1999 and yielded 13 frogs. Summer data are not pooled with fall data for our analyses, and any comparisons between the two seasons should be avoided because of the limited summer sampling period. During the 3 years of fall trapping, no frogs were captured in November during snowfall. We captured the most frogs ( $n = 241$ ) between 26 September and 23 October. In summer, we captured 6 frogs in streamside arrays and 7 in upland arrays; in fall, 134 were streamside, 107 were in upland arrays. We recorded 281 *Ascaphus* from 1998 to 2000: 254 captured, 27 incidental encounters (Table 1).

Of 254 *Ascaphus* captured, 142 were in clearcuts and 112 were in old growth. Results based on statistical analyses represent fall data unless otherwise noted. CPUE was 1.3 times greater in clearcuts than in old-growth forests (Table 2), but the difference between clearcuts and old growth was not statistically significant ( $F_{[1,2]} = 0.109$ ;  $P = 0.772$ ). Distributions of developmental stages differed significantly between clearcuts and old-growth forests ( $\chi^2_{[3]} = 52.30$ ;  $P < 0.001$ ) with 2.9 times more juveniles in clearcuts than in old growth, and 2.3 times more adults in old growth than in clearcuts (Table 2). Juvenile and adult captures also were unevenly distributed across the three watersheds and across the 3 years. The Mamquam watershed yielded three times more adult captures than the Ashlu watershed, and nearly twice as many juveniles were captured in the Elaho watershed compared with Ashlu and Mamquam watersheds. The most adults and juveniles were captured in 1999, and the least were captured in 1998. It later becomes more apparent that relations with forest cover, watershed, and year result from different distribu-

tions in developmental stages captured among watersheds and years.

### Recapture rate

In 3 years, we recaptured 17 frogs (6.7%) of the 254 marked animals. Although none were recaptured in 1998, 6.3% and 9.6% were recaptured in 1999 and 2000, respectively. Recaptured frogs included 10 juveniles and 7 adult frogs captured 4–400 d after initial capture. Recapture rates were 4.5% in old growth and 8.5% in clearcuts.

### Movement patterns: distance from stream

We quantified colonization potential of *Ascaphus* by evaluating their mean distances from streams in old growth and clearcuts. We also evaluated distribution of captures across distance categories. We found a significant difference in the proportion of frog captures across distance categories among old growth and clearcut ( $\chi^2_{[3]} = 23.16$ ;  $P < 0.001$ ). Number of frogs captured within 25 m of streams was not independent of forest cover type ( $\chi^2_{[1]} = 8.04$ ;  $P < 0.005$ ) with more frogs captured within this distance in clearcuts. However, the proportion of frogs captured at distance categories 25–100 m ( $\chi^2_{[2]} = 2.69$ ;  $P > 0.250$ ) and 50–100 m ( $\chi^2_{[1]} = 1.70$ ;  $P > 0.100$ ) were independent of forest cover type.

We failed to detect a difference when examining mean distances from streams in old-growth forests and clearcuts (mixed-model ANOVA:  $F_{[1,2]} = 1.810$ ;  $P = 0.311$ ). However, we detected a watershed (mixed-model ANOVA:  $F_{[2,8]} = 8.440$ ;  $P = 0.011$ ) and year ( $F_{[2,8]} = 7.270$ ;  $P = 0.016$ ) effect on distance from stream. Mean distances from streams in the Ashlu ( $15.15 \pm 4.80$  m) and Mamquam ( $31.53 \pm 9.13$  m) watersheds were two to four times greater than in the Elaho watershed ( $7.72 \pm 6.13$  m), and the difference between Mamquam and Elaho watersheds was statistically significant ( $P = 0.013$ ). During fall, mean distances from streams in 1999 ( $19.56 \pm 9.12$  m) and 2000 ( $28.22 \pm 8.59$  m) were three to four times greater than in 1998 ( $6.62 \pm 4.16$  m), and the difference between 1998 and 2000 was statistically significant ( $P = 0.019$ ).

Because the uneven distribution of developmental stages had a dominating influence on relations with forest cover (Table 2), we examined differences in distance from stream separately for juveniles and adults (Fig. 3a). On average, adults were captured farther from streams ( $28.91 \pm 6.65$  m) than were juveniles ( $17.19 \pm 4.48$  m;  $F_{[1,210]} = 2.296$ ;  $P = 0.029$ ). Juveniles were captured 1.4 times farther from streams in old growth ( $20.01 \pm 9.12$  m) than in clearcuts ( $14.36 \pm 3.05$  m;  $F_{[1,4]} = 0.346$ ;  $P = 0.588$ ). Adults were captured 1.8 times farther from streams in clearcuts ( $37.25 \pm 7.22$  m) than in old growth ( $20.57 \pm 9.98$  m;  $F_{[1,4]} = 1.835$ ;  $P = 0.247$ ). Examining each forest cover type separately, we found no difference between mean juvenile distance ( $20.01 \pm 9.12$  m) and adult distance ( $20.57 \pm 9.98$  m) in old growth ( $F_{[1,4]} = 0.002$ ;  $P = 0.969$ ). However, we found a significant difference between mean juvenile distance ( $14.36 \pm 3.05$  m) and adult distance ( $37.25 \pm 7.22$  m) in clearcuts ( $F_{[1,4]} = 8.527$ ;  $P = 0.043$ ).

We captured 72 females and 180 males in 3 years. Mean distances from streams were  $23.29 \pm 7.80$  m for females and  $16.81 \pm 3.90$  m for males. We found that 29% of mature females and 61% of mature males were captured within 25 m of the stream (Fig. 3b). At streamside, we captured 4.5 times

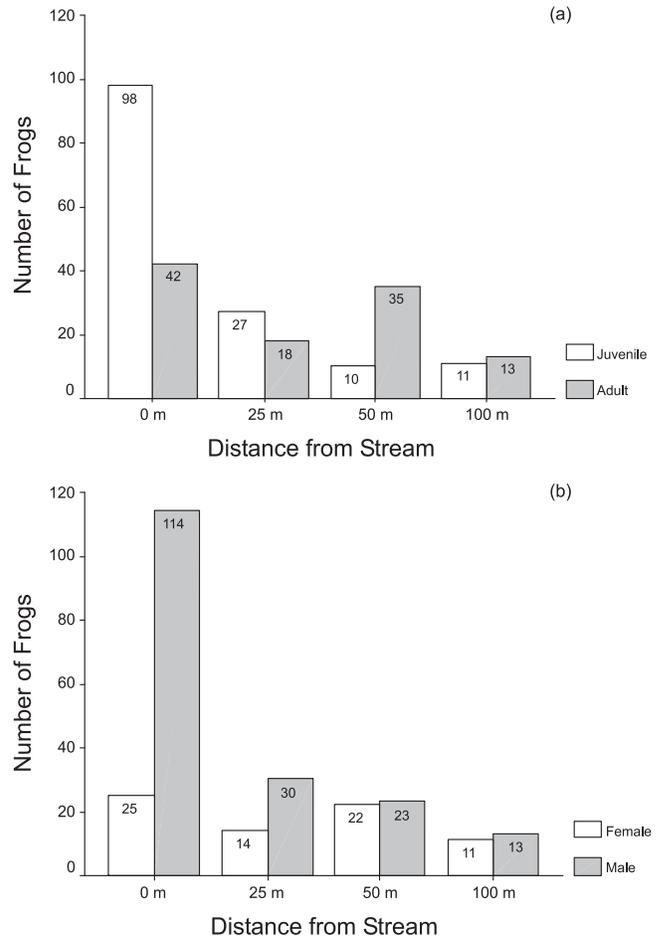
**Table 2.** Total captures, catch per unit effort (CPUE: number of frogs per 100 trap nights (TN)), mean ( $\pm$ SE) distance from stream, mean snout-vent length, individual mass, and total mass by site for juvenile and adult *Ascaphus* at six sites, in fall 1998–2000.

	Juvenile			Adult			Total		
	Clearcut	Old growth	P	Clearcut	Old growth	P	Clearcut	Old growth	P
Captures	109	37	—	33	75	—	142	112	—
CPUE (No./100 TN)	0.70	0.24	—	0.21	0.48	—	0.91	0.72	—
Distance (m)	14.36 $\pm$ 3.05	20.01 $\pm$ 9.12	0.346	37.25 $\pm$ 7.22	20.57 $\pm$ 9.98	1.835	25.81 $\pm$ 6.20	20.29 $\pm$ 6.05	0.037
Snout-vent length (mm)	19.18 $\pm$ 0.31	19.92 $\pm$ 0.02	5.738	37.18 $\pm$ 4.48	38.12 $\pm$ 1.17	0.041	28.18 $\pm$ 4.50	29.02 $\pm$ 4.10	2.405
Individual mass (g)	0.73 $\pm$ 0.08	0.84 $\pm$ 0.02	2.098	5.26 $\pm$ 1.65	5.72 $\pm$ 0.25	0.078	2.99 $\pm$ 1.25	3.29 $\pm$ 1.10	2.015
Total mass <sup>a</sup> (g)	24.08 $\pm$ 6.44	9.35 $\pm$ 2.75	4.428	73.92 $\pm$ 35.96	122.83 $\pm$ 72.02	0.369	98.00 $\pm$ 29.64	132.18 $\pm$ 74.75	0.181

**Note:** All statistical analyses of between-subjects effects were conducted using one-way ANOVAs.

<sup>a</sup>Total mass of *Ascaphus* for each developmental stage and forest cover type.

**Fig. 3.** Number of *Ascaphus* captured at each distance from stream at all sites: (a) juveniles and adults, (b) females and males (juveniles and adults combined). Values within bars represent sample sizes.



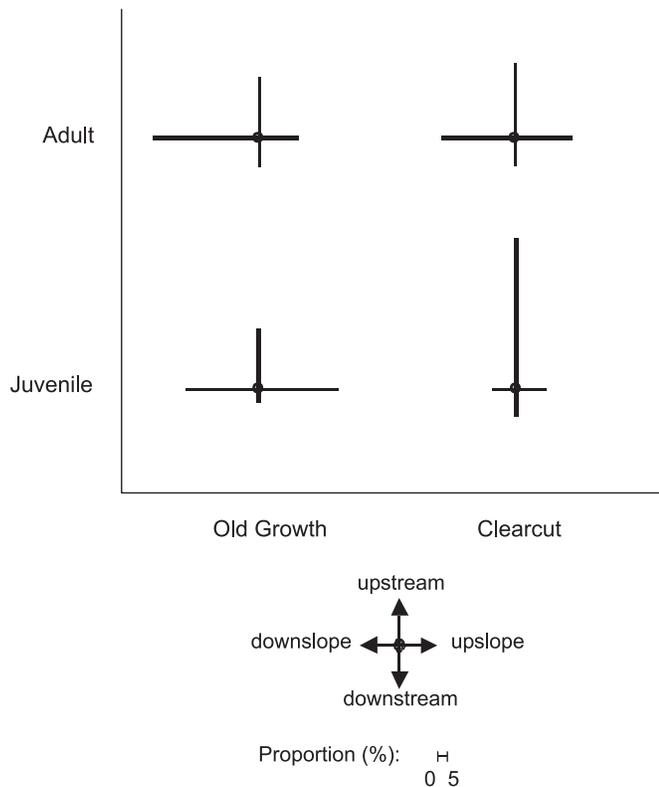
more males than females. Males and females were differentially represented in fall when more males than females were captured. Female captures during the coldest two weeks (24 October – 6 November) matched female captures during the driest months.

**Movement rates and directions**

We estimated movement rates based on distances between initial and subsequent capture. Frogs recaptured in old growth moved an average 2.09 m/d ( $n = 5$ ), and frogs in clearcuts moved 3.36 m/d ( $n = 12$ ). Nine of 12 frogs recaptured in clearcuts were juveniles. More males were recaptured in old growth, and were closer to streams than were females.

There appeared to be no difference in direction of movement between sexes. Although females rarely moved downstream, they were responsible for most downslope movement. For all years combined, movement direction in fall tended to differ between juveniles and adults in old growth and clearcuts (Fig. 4). Adult movement appeared little affected by forest cover type. However, juveniles exhibited stronger stream affinity in clearcuts than in old growth. Combining forest cover types, upstream movement constituted 57% of all juvenile movement, and 28% of all adult movement. Fifteen percent

**Fig. 4.** Relative proportion of *Ascaphus* moving in four directions relative to stream: upstream, downstream, downslope (towards stream), and upslope (away from stream). Legend shows 5% scale for each direction. Fall data only.



of all juvenile movement and 42% of all adult movement was downslope. The apparent differences between forest cover types result primarily from the proportion of developmental stages captured in each forest cover type.

### Body size and condition

We evaluated variation in frog body size between old growth and clearcuts. Differences were small, and none were statistically significant (Table 2). When stages were analyzed separately, juveniles and adults tended to be longer and weigh more in old growth (Table 2). Total mass of frogs in clearcuts (294 g;  $n = 142$  frogs) appeared lower than in old-growth forests (396 g;  $n = 112$ ), primarily because there were more adults in old growth (Table 2). Evaluating stages separately, mean total mass of juveniles in clearcuts ( $n = 109$ ) was 2.5 times greater than in old growth ( $n = 37$ ). Mean total mass of adults in old growth ( $n = 75$ ) was 1.7 times greater than in clearcuts ( $n = 33$ ). Juvenile BCI did not differ between clearcuts ( $0.999 \pm 0.001$ ) and old growth ( $1.040 \pm 0.020$ ;  $F_{1,41} = 4.064$ ;  $P = 0.114$ ). Adult body condition in clearcuts ( $0.999 \pm 0.002$ ) also did not differ from old growth ( $1.001 \pm 0.001$ ;  $F_{1,41} = 1.143$ ;  $P = 0.345$ ).

## Discussion

### Catch per unit effort

Research on the effects of timber harvesting on *Ascaphus* habitat has focused on impacts to streams and riparian zones, but seldom distinguished responses by developmental stage.

In California, Welsh and Lind (2002) reported more *Ascaphus* in streams in late seral forest compared with streams in young forests. In Oregon, Biek et al. (2002) reported *Ascaphus* densities (primarily adults) of 0.11 individuals/m<sup>2</sup> in clearcut streams and 0.21 individuals/m<sup>2</sup> in old growth. Our British Columbia results differ where CPUE of frogs in clearcuts tended to be greater than in old growth. However, we also captured more juveniles (but fewer adults) in clearcuts than in old growth.

The capture of more juveniles in clearcuts may be linked to greater primary productivity (Murphy and Hall 1981; Hawkins et al. 1983), related to increased solar radiation reaching clear-cut streams (see Beschta et al. 1987). Wahbe (1996) and Kim (1999) reported longer and heavier *Ascaphus* larvae in clearcuts compared with old growth in British Columbia. Increased food and temperature could enhance larval growth and, in turn, survival (Sutherland 2000), but the lethal maximum for *Ascaphus* eggs is 18.5 °C (Brown 1975). At least two southwestern British Columbia data sets revealed greater densities of larvae in streams flowing through clearcuts (Richardson and Neill 1998; Wahbe and Bunnell 2003). Further, data from within our study area suggest faster larval growth and earlier metamorphosis in clearcuts (3- to 4-year larval period) compared with a 4- to 5-year larval period in old-growth streams (Wahbe 1996). Therefore, *Ascaphus* in clearcuts may exist at high densities and have short larval periods, which together can lead to an emergence of more metamorphic juveniles, compared with old growth. Although we captured significantly more metamorphs in clearcuts than in old growth, we captured fewer adults in clearcuts. This may suggest lower metamorph survival or adult movement out of clearcuts. In clearcut streams, shorter larval movements than in old growth (Wahbe and Bunnell 2001) may explain more densely distributed larval populations closer to headwaters.

### Recapture rate

Our fall recapture rates on the coast were low (4.5%–8.5%) compared with summer recapture rates inland (33% for juveniles and up to 73% for adult *Ascaphus*, Daugherty and Sheldon 1982; 37.5%, Landreth and Ferguson 1967). The higher rates may result from summer sampling when *Ascaphus* aggregate near streams, increasing capture probability. Our lower rates may reflect capturing more juveniles, which have higher mortality rates (Jones and Raphael 1998), or higher vagility in moist, coastal areas than inland. Recapture rates could also be influenced by site variability, and different sampling designs (e.g., visual encounter surveys) and intensities used.

### Movement patterns: distance from stream

As predicted, we trapped more frogs within 25 m of streams in clearcuts than in old growth. This may suggest stronger stream affinity in clearcuts where preferred microclimatic conditions (e.g., high humidity, cool temperatures) are near streams (Brosofske et al. 1997). Frogs tended to be farther from streams in old growth compared with clearcut sites. For British Columbia Pacific giant salamanders (*Dicamptodon tenebrosus*) in old growth, mean distance from streams was four times greater, refuge duration was 2 d shorter, and home range size was 10 times greater than in clearcuts (radiote-

lemetry; Johnston and Frid 2002). Fewer microclimate constraints in old growth allow stream-breeding amphibians to move greater distances from streams for foraging purposes or dispersal to adjacent streams than in clearcuts.

While patterns are consistent with forest cover reducing anticipated adverse microclimate effects, our microclimate data were similar among forest cover types and could not explain differences in distances frogs moved away from streams. Mean elevation for old growth (717 m) was similar to that of clearcuts (752 m). Mean gradient (hillslope relative to stream) in old growth ( $12^\circ$ ) was equal to that in clearcuts ( $12^\circ$ ). Mean stream aspect in old growth ( $235^\circ$ ) was also similar to that in clearcuts ( $272^\circ$ ). Additionally, soil moisture at increasing distances from stream was not informative for explaining movement patterns.

### Movement rates and directions

Movement rates estimated by successive recaptures are difficult to interpret, because frogs likely did not move consistently in one direction. Other interpretation difficulties stem from low recapture rates, small sample size, and large temporal variation between captures (4–400 d) that may represent daily movement or in some cases, dispersal. We provide an index of relative vagility. Movement rates tended to be higher in clearcuts (3.36 m/d) than in old growth (2.09 m/d). Frogs may move frequently but remain near streams in clearcuts because of increased physiological stress. Most recaptures in clearcuts were juveniles, an exploratory life stage (like some terrestrial mammals and birds; see Sutherland et al. 2000). There also tended to be more male recaptures than females in old growth (but note small sample size), and males tended to be closer to streams, suggesting less movement, than for females. Maxcy (2000) reported greater movement rates for *Ascaphus* in forested stream sites ( $12.27 \pm 3.48$  m/d) compared with stream-buffered sites ( $8.53 \pm 5.01$  m/d) in British Columbia. During summer in Montana (mean annual precipitation = 635 mm; British Columbia: approx. 2500 mm), Daugherty and Sheldon (1982) reported streamside movement rates of 0.34 m/d (within years) and 0.75 m/d (between years). We did not recapture any frogs during summer, but in fall, we recorded a movement rate of 3.0 m/d.

Our results suggest younger frogs perform more overland movements and dispersal than adults do. Bury and Corn (1987, 1988b) captured many recently metamorphosed *Ascaphus* in fall  $\geq 75$  m from streams in pitfall traps set in forested stands. In summer, Daugherty and Sheldon (1982) reported reduced movement at the onset of reproductive maturity, with greater movements in prereproductive frogs and extreme site fidelity in reproductively mature frogs.

Considerable downstream movements by *Ascaphus* larvae occurred over distances up to 64 m in old growth and 3 m in clearcuts within a few weeks (Wahbe and Bunnell 2001). Frogs may move predominantly upstream following metamorphosis to compensate for downstream larval drift. We found that directional movements in clearcuts differed from those in old growth. While most frogs in clearcuts moved upstream, most frogs in old growth moved towards streams. The closest adjacent stream was 200 m, thus frog movements in old growth may represent dispersal from adjacent

streams. In both old growth and clearcuts, upstream movements constituted 57% of all juvenile movements, and 28% of all adult movements. Juveniles clearly exhibited stronger stream affinity in clearcuts, but adults appeared little affected by forest cover. Metter (1964a) observed fewer frogs during summer sampling and speculated that frogs moved upstream for “protection”, presumably in more shaded stream reaches. In clearcuts, frogs may tend to move upstream, because higher elevation sites or steeper gradients in upper stream portions are often less disturbed (hence cooler and more moist upland) because of historical patterns of logging starting at valley bottoms. These upstream movements may also represent movements towards breeding or oviposition sites. Within-stream movements by adults are believed by some to be critical for survival in clearcuts (Adams and Frissell 2001).

Movements toward streams may be for dispersal, breeding, foraging opportunities, or searches for oviposition, overwintering or oversummering sites. Breeding migrations in *Ascaphus* are unreported but hypothesized (Landreth and Ferguson 1967; Brown 1975; Wahbe et al. 2001). Our fall data support speculations by Brown (1975) that adult frogs move to headwaters to breed. Some suggest frogs move downstream to mate (Landreth and Ferguson 1967) or overwinter (Adams and Frissell 2001), but these may be condition-specific responses (e.g., behavioral thermoregulation; Adams and Frissell 2001). We observed stream affinity and upstream movements in mature males during the breeding season and believe these frogs aggregated in search of mature females. Some females may remain beside streams to breed or move towards streams for oviposition, while others may disperse to breed or locate suitable oviposition sites in neighboring streams. All three gravid females captured at streamside moved upstream. Of 15 gravid females captured upslope, 73% moved towards streams. Our data may provide initial evidence suggesting breeding migrations (upland to stream or stream to stream movements) in *Ascaphus*. Because females can store sperm for a year (Metter 1964b) and breed every other year (Metter 1964a), movement through upland forest and later return for oviposition is not unlikely.

Amphibian capture rates vary within and among years because of patterns of precipitation and temperature (Bury and Corn 1987; deMaynadier and Hunter 1998; Aubry 2000). We expected movements to be similarly influenced, and hypothesized that *Ascaphus* in wet regions (coastal British Columbia) would show longer movements than in drier regions (e.g., Idaho). Comparable data are limited, but our results appear consistent with this prediction. *Ascaphus* in coastal British Columbia moved  $\geq 100$  m from streams in both old growth and clearcuts. Few studies of inland populations found *Ascaphus* in upland forest, but in southeastern Washington and northern Idaho (wet and dry seasons sampled), *Ascaphus* moved  $\geq 12$  m from streams (Metter 1964a). It is difficult to make comparisons, because neither area sampled nor sampling method were reported. High site fidelity for inland *Ascaphus* was attributed to warm, dry conditions of the interior that restrict amphibian movements, and suggests low recolonization potential (Daugherty and Sheldon 1982).

Favorable climatic conditions on the coast (e.g., high humidity, extended rainy periods) may enable adults to occupy

larger home ranges or move longer distances than at inland sites. Thermal stress should be minimal on the coast (British Columbia: approx. 2500 mm mean annual precipitation; mean annual temperature = 9 °C) compared with the interior Rocky Mountains (mean annual precipitation = 635 mm; mean annual temperature = 7 °C; Diller and Wallace 1999; Welsh and Lind 2002). Available data suggest greater stream affinity inland than on the coast. Although coastal conditions restrict movements less, we observed stream affinity in clearcuts.

### Body size and condition

Recent evidence suggests growth rate, fitness, and survival of amphibians may be reduced in clearcuts because of lower body condition (Fraser 1976; Kramer et al. 1993) and reduced foraging opportunities (Chen et al. 1993; Jaeger et al. 1995; Brosofske et al. 1997). Chazal and Niewiarowski (1998) reported greater mass loss, lower egg production, and lower mean egg lipid content for mole salamanders (*Ambystoma talpoideum*) in clearcuts relative to forested controls. Grialou et al. (2000) reported western redback salamander (*Plethodon vehiculum*) lengths were skewed toward smaller size classes in clearcuts compared with forests. In contrast, Dupuis and Bunnell (1999) found no relationship between length and forest cover for this species. Thus, effects of forest harvesting practices on amphibian body condition is still unclear.

Despite the presence of larger larvae in clearcut streams (Wahbe 1996; Kim 1999), we recorded larger juveniles in old growth. Smaller metamorph size may lead to reduced fecundity and survivorship, because body size has major influence on an animal's energetic requirements, its potential for resource exploitation and its susceptibility to predators (Wilbur and Collins 1973; Travis 1984; Werner and Gilliam 1984). Amphibian body size is directly related to rehydration and desiccation rates (Ray 1958; Spotila 1972) and an ability to withstand food deprivation.

Our findings suggest aquatic habitat in clearcuts initially may be beneficial to *Ascaphus* larvae, but that terrestrial habitat may not be conducive to long-distance juvenile movements. Clearcuts may provide resistance to amphibian movements (Rothermel and Semlitsch 2002), poor habitat cover and reduced foraging opportunities, increased competition, or shorter active seasons because of temperature increases and declines in relative humidity.

### Conclusion and management recommendations

Timber harvesting reduces habitat patch size, increases population subdivision and isolation via habitat fragmentation (increasing probabilities of local extinction), and removes habitat connectivity, thus reducing dispersal among patches (e.g., Sjögren 1991; Bunnell et al. 1992; Fahrig and Merriam 1994; Nijhuis and Kaplan 1998; Rothermel and Semlitsch 2002). Welsh and Lind (2002) argue that *Ascaphus* populations will continue to decline in the Pacific Northwest in response to anthropogenic disturbance regimes. Our results suggest reduced recolonization potential in *Ascaphus* populations where forest cover has been removed.

Terrestrial habitat use by *Ascaphus* (particularly juvenile frogs) during fall appears more spatially compressed along streams in clearcuts than in old growth. Recent metamorphic wood frogs (*Rana sylvatica*) prefer closed canopies (deMaynadier and Hunter 1999), and we captured juvenile *Ascaphus* farther from streams in old growth than in clearcuts. Adult frogs are considered the most evolutionarily effective migrants (sensu MacArthur and Wilson 1967) because their reproductive value is high, especially for gravid females. We recorded adult *Ascaphus* undertaking more long-distance overland movements than juveniles, and in old growth, we captured twice as many reproductively mature frogs as in clearcuts. It appears there are fewer evolutionarily effective migrants dispersing through clearcuts to adjacent streams.

Aggregations of *Ascaphus* at individual streams may not represent distinct populations, and should not be managed as distinct units. Just as many amphibian species regularly disperse between ponds (Marsh and Trenham 2001), *Ascaphus* may disperse between streams. Thus, structural connectivity between multiple streams within a watershed will probably be a more meaningful unit of management than individual streams with forested buffers. To maintain gene flow, promoting some connectivity between streams may be the single most important issue to address when defining *Ascaphus* conservation strategies.

Amphibians are known to benefit from retention of riparian habitats during logging (Gomez and Anthony 1996; Dupuis and Steventon 1999; Maxcy 2000) because they can ensure moist and less variable microclimatic conditions, particularly in times of drought. Riparian buffers likely serve as movement corridors for juvenile and adult *Ascaphus*, but large openings in adjacent forests may prevent frogs from reaching nearby streams via overland movements. Conservation measures need to promote long-term population persistence (e.g., a partial forest matrix between streams could be retained within each watershed to provide habitat pathways for dispersing frogs). When connectivity between streams cannot be maintained, habitat conservation strategies for *Ascaphus* could be improved by including riparian management areas on multiple adjacent headwaters in areas favoring *Ascaphus*. Reducing distances between mature forest patches would improve the chances of *Ascaphus* moving through harvested watersheds.

Based on available data, and recognizing that uncertainties exist, we recommend monitoring *Ascaphus* populations where a partial forest matrix is retained between streams. Studies could focus on varying the level of harvest within the matrix. Monitoring populations within different management scenarios and evaluating the success of management will allow us to determine if we are indeed achieving our conservation goals.

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