Dispersion of Coastal Tail Frog (*Ascaphus truei*): A Hypothesis Relating Occurrence of Frogs in Non-Fish-Bearing Headwater Basins to Their Seasonal Movements

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Forest Practices Adaptive Management Program

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> Provide science-based recommendations and technical information to assist the board in determining if and when it is necessary or advisable to adjust rules and guidance for aquatic resources to achieve resource goals and objectives. (Forest Practices Rules, WAC 222-12-045)

To provide the science needed to support adaptive management, the FPB made the Cooperative Monitoring, Evaluation and Research Committee (CMER) a participant in the program. The FPB empowered CMER to conduct research, effectiveness monitoring, and validation monitoring in accordance with guidelines recommended in the FFR.

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Proprietary Statement

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Project Summary

Coastal tailed frog (*Ascaphus truei*), one of the best-studied stream-associated amphibians in the Pacific Northwest, is of particular management and conservation interest across its geographic range, largely because of potential sensitivity to forestry practices. This study examined the relationship between the distribution of coastal tailed frog by life stage within and among non-fish-bearing headwater basins on an intrusive basalt lithology in southwest Washington State. We found that the probability of tailed frog occupancy increases with increasing non-fish-bearing basin size/complexity likely because breeding habitat quality increases as a function of basin size. Further, the distribution of different frog life history stages suggests that adult frogs breed in perennially watered reaches but forage higher in the basin at or near stream origin during the non-breeding active season.

Dispersion of Coastal Tailed Frog (*Ascaphus truei*): An Hypothesis Relating Occurrence of Frogs in Non–Fish-Bearing Headwater Basins to Their Seasonal Movements

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ABSTRACT.—The Coastal Tailed Frog is one of the best studied headwater amphibians in the Pacific Northwest, yet we know very little about either its seasonal movements or its distribution within and among headwater basins. During August through October 2000–2002, we studied Coastal Tailed Frogs in 81 headwater basins from managed forests in the Stillman Creek watershed in southwestern Washington State. We found a significant association between tailed frog life stage and their locations along the stream axis: older life stages were located higher in the basin than younger life stages. Data from eight streams sampled in early and late summer 2002 support the hypothesis that adult *Ascaphus truei* move upstream several hundred meters during the low-flow period probably after having moved downstream to breed. We also found little evidence of tailed frog reproduction in small non–fish-bearing basins, which supports the hypothesis that breeding habitat in those basins may be limiting. To test these two hypotheses, we examined *A. truei* occupancy in 65 non–fish-bearing headwater basins ranging in size from first to fourth order in 2003 and 2005. Occupancy increased with basin order, and we found no evidence of reproduction (eggs, larvae, or metamorphs) in first-order non–fish-bearing basins. The length of the dominant stream thread in nearly all first-order basins was shorter than the distance adult *A. truei* moved between early and late summer. We suggest that a headwater stream must remain watered for several hundred meters during the dry season to meet tailed frog breeding requirements. Tailed frogs probably do not reproduce in most first-order non–fish-bearing basins in the Stillman Creek watershed because those basins are too small to reliably provide habitat suitable for oviposition and rearing of their early life stages.

Tailed frogs (genus *Ascaphus*), the sister taxon of all other extant anurans (Ford and Cannatella, 1993), are endemic to the Pacific Northwest (PNW) of North America (Jones et al., 2005). The two species of tailed frog, *Ascaphus montanus* and *Ascaphus truei* (Neilson et al., 2001), are relatively well studied, especially with respect to their response to forest management (Corn and Bury, 1989; Diller and Wallace, 1999; Jackson et al., 2003; Wahbe and Bunnell, 2003). Despite this effort, relatively little work has addressed tailed frog movements, and nearly all such work has focused on whether forest management alters localized movements (i.e., ≤ 100 m) of larvae (Wahbe and Bunnell, 2001) and postmetamorphic life stages (Wahbe et al., 2004; Matsuda and Richardson, 2005). For example, Wahbe and Bunnell (2001) showed that tailed frog larvae moved shorter distances in streams with logging debris than in streams

without debris presumably because the debris acted as a barrier. Wahbe et al. (2004) also found that postmetamorphic tailed frogs remained closer to the stream and seemed less likely to make longer movements in managed forests when compared to older forests. Finally, Matsuda and Richardson (2005) found no difference in movement direction between postmetamorphic tailed frogs from recently harvested versus mature forests. Curiously, we know almost nothing about tailed frog seasonal movements. Indeed, except for Adams and Frissell (2001), who postulated that *A. montanus* may migrate seasonally, no study has addressed how changes in active-season dispersion of tailed frogs may be linked to seasonal patterns in habitat use. In particular, no study has addressed how such seasonal changes in habitat use may influence tailed frog occupancy among non–fish-bearing headwater streams. To address this deficiency, we obtained location data on all *A. truei* life stages on a large number of non–fish-bearing headwater streams, each sam-

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pled over a broad spatial extent, over several years.

MATERIALS AND METHODS

Study Area.—Our study area was the 11,856-ha Stillman Creek watershed in the Willapa Hills, which lies in the Coast Range physiographic province in southwestern Washington State (Franklin and Dyrness, 1988). Igneous basalts and marine sedimentary formations characterize basin geology with basalt formations comprising approximately 80% of the area (Wells, 1981). This basin consists entirely of managed forest < 75 years old and has a generally moderately steep topography (mostly 10–30% slopes). Mean annual precipitation varies from 900 mm at the lowest elevations (250 m) to > 2500 mm at the highest elevations (up to 948 m; Boisfort or Baw Faw Peak; Sumioka et al., 1998). Little of this precipitation falls as snow except at the highest elevations, and there snow rarely persists past May. Temperature data are unavailable for the basin proper, but the two closest stations (Centralia: NCDC COOP Station No. 451276; and Toledo: NCDC COOP Station No. 488500; approximately 25 km to the northwest and east, respectively) report annual means of around 11°C with summer maxima around 34°C and winter minima around −5°C. Both stations are lower in elevation than sampled areas in the Stillman Creek watershed.

This study has two parts, a large-scale study conducted in 2000–2002 and a more focused study done in 2003 and 2005. The early study was designed to determine the distribution and relative abundance of tailed frogs and other instream-dwelling amphibians in headwater streams across managed forest landscapes in southwestern Washington. Although the early study was not focused on tailed frogs per se, it revealed interesting within and among stream occupancy patterns for tailed frogs. Hence, the intent of the second study was to more thoroughly examine these patterns by testing two hypotheses: H_1, Tailed frogs move upstream during the postoviposition period; and H_2, Tailed frogs do not reproduce in small non–fish-bearing headwater basins.

Our sampling addressed only those areas of the watershed above fish-occupied streams (hereafter headwaters) as determined by extensive electrofishing surveys conducted in 1994 (B. Francen, pers. comm.). Stream reaches that comprise a headwater basin, and the basin as a whole, were defined by Strahler (1952) stream order and basin order, respectively. Stream order describes where a particular reach is located within the network (Fig. 1); basin order,

a watershed complexity descriptor, represents the highest order in the basin (i.e., stream order of the reach immediately above fishbearing waters; Fig. 1). Finally, we defined the dominant stream thread (DST) as the string of contiguous reaches starting at the point where fish distribution ends and extending to top of the basin, as defined by the channel head (i.e., the uppermost evidence of a scour channel), following the path of greatest flow. We also recorded the location of the stream origin (O_s) as the uppermost point of surface water at least 100 cm^2 in area (Hunter et al., 2005). The wetted DST length is the total length of the DST minus the length of dry channel. All surveys began at the downstream end of the sample and proceeded upslope. When we encountered a tributary junction during a survey, we followed the reach with the highest flow, estimated visually. Thus, a survey could include up to four different stream orders (Fig. 1).

2000–2002 Study.—In 2000–2002, we selected 131 streams by randomly selecting points where forest roads intersect non–fish-bearing streams on Weyerhaeuser Company land, which makes up approximately 80% of the area of the Stillman Creek watershed. We restricted our selection to streams on basalt substrates (roughly 80% of Weyerhaeuser ownership) because *A. truei* occur more frequently and at higher densities on basalt substrates in managed forests of southwestern Washington (Wilkins and Peterson, 2000), and we wanted to minimize variation caused by geology. We excluded streams in stands < 15 years old because harvest slash prevented effectively sampling the channel (Jackson et al., 2001, 2003), but no other criteria affected stream selection. For this portion of the study, we sampled streams from a road-crossing point upstream to end of channel (i.e., where a scour channel was no longer discernable) or to the next road-crossing point, since the latter might be another random selection. Because we randomly selected streams based on road-crossing points, and some streams had multiple road crossings, we occasionally sampled the same stream from different points. Over the three-year interval, all streams were sampled once during 1 August to 7 October, which represents the low-flow interval of *A. truei* active-season (hereafter low-flow season). In 2002, we also sampled eight of these streams once during May through July. The eight streams sampled in May through July were chosen because downstream starting points were close to (within 50 m of) the fish-bearing stream network. To establish a standard reference point from which to measure frog location, we measured the distance between each animal and the O_s on all streams (Fig. 1)
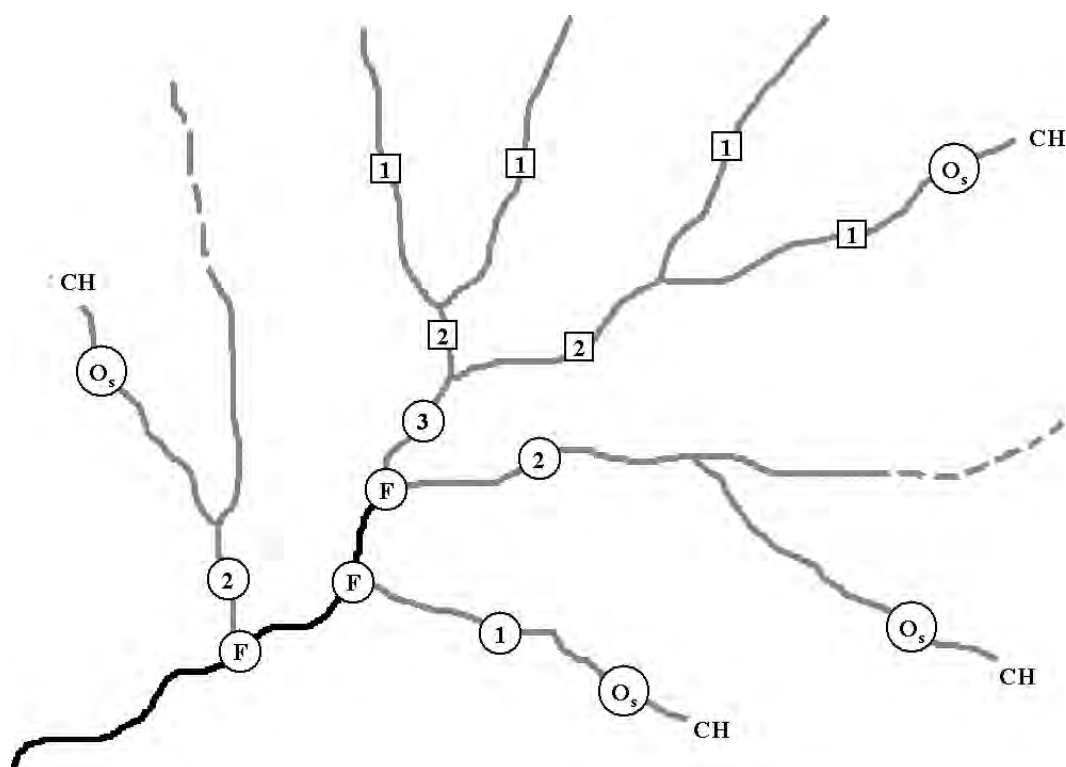
FIG. 1. Diagram of the relationship of non–fishing-bearing basins (gray) to fish-bearing waters (black) showing stream network and basin terminology. For each non–fish-bearing basin, the lower boundary: fish/non–fish-bearing point (F); the stream origin (O$_s$; upstream origin of surface water) for the dominant stream thread (DST); and the basal stream of each non–fish-bearing basin (circled numbers), the basin complexity descriptor, are shown. To illustrate changes in order across the stream network, we also label the order of each stream in the third-order basin (numbers in squares).

during the low period. Locations upstream of the O$_s$ were assigned positive values; those downstream were given negative values.

For the 2000–2002 study, two surveyors conducted a light-touch survey. Light-touch (LT) surveys are a type of visual encounter search whereby surveyors search the streambed and under movable objects on the substrate surface to increase the likelihood of finding frogs. Evaluation of the LT method in streams in the Stillman Creek watershed indicated that channel length surveyed ($>$ 80 m for samples) was longer than the distance required to detect *A. truei* with high confidence (approximately 20 m) when present using the most thorough sampling method available (Quinn et al., in press). We believe that this approach results in an extremely low likelihood of making false negative errors (i.e., failing to find the species when it was actually present). The LT surveys were limited to an area approximating bankfull width, whether or not water was present in the channel. In cases where an upstream road crossing represented the end of the sample, we

continued to walk up-channel (but not survey for frogs) selecting the DST to locate the O$_s$ and channel head. Each tailed frog found was assigned to one of six life stages: egg, first-year larva, second-year larva, metamorph, juvenile, or adult. We distinguished larval year-classes based on the size and hind-limb development criteria of Bury and Adams (1999). Metamorphs had $\geq$ 3 legs and a tail. We distinguished adults from juveniles based on a ''tail'' appendage $\geq$ 1 mm long and the presence of nuptial structures in adult males; females were identified as those individuals $>$ 38 mm snout–vent length (SVL) without these features. We measured size as SVL in millimeters to the nearest 0.5 mm for all life stages except eggs, which were simply tallied. Animal locations were measured to the nearest meter from the O$_s$ with a laser rangefinder or measuring tape. For LT surveys, all cover objects were returned to their original positions, and all animals were handled in situ and released at their capture locations.

2003/2005 Study.—In 2003 and 2005, we selected 65 non–fish-bearing basins across the

entire area subtended by basalt substrates in the Stillman Creek watershed, which included both Weyerhaeuser and Pacific West Timber Company ownerships. For this portion of the study, we sampled the DST that began at the uppermost fish-bearing point (Fig. 1) and concluded at the channel head regardless of road-crossing configuration. We sampled the DSTs of all third- ($N = 13$) and fourth-order ($N = 1$) basins where forest met stand age criteria (see above). Because of the very large number of smaller-order basins (> 500), we sampled a random subset of first-order ($N = 25$) and second-order ($N = 26$) basins. We sampled DSTs in first- and second-order basin from unroaded areas that were not included in study done in 2000–2002 as well as first- and second-order basins from roaded areas. Roads crossed all DSTs from third- and fourth-order basins in the Stillman Creek watershed. Sampling streams unaffected by roads crossings is important because road sediments may affect *A. truei* presence or abundance (Bury and Corn, 1988). In 2003 and 2005, we sampled all streams once during the low-flow season.

During the low flow period of 2003–2005, we used LT to sample the DSTs of 65 non–fish-bearing headwater basins (Fig. 1). We recorded all *A. truei* and measured the distance from the O_s to each animal. Also, we measured the wetted DST length in each basin. As with the 2000–2002 surveys, survey length was long enough (> 100 m for all DSTs) to generally ensure a high degree of confidence in detecting *A. truei* when present (see Quinn et al., in press).

Analysis.—For 2000–2002 data, we used nonparametric statistics to analyze animal locations because a frequency plot revealed that those data were not normally distributed. A distributional plot also revealed that life-stage specific patterns might exist in frog location; hence, we used a Kruskal-Wallis nonparametric ANOVA to identify whether differences in location (i.e., distance from the origin) along the stream axis existed among life stages. This pattern was further explored by examining whether a systematic relationship existed between life stage and frog location for each year using a Spearman Rank correlation (Zar, 1999).

We used a Mann-Whitney *U*-test to compare distances from the O_s of each of second-year larvae and adults between early and late sampling in 2002 (Zar, 1999). We adjusted α to 0.0253 to account for experiment-wise error rates for these two tests. Small sample sizes ($<$ 7) for at least one of the sampling periods (early vs. late) resulted in insufficient power (1-β ≤ 0.4) to compare locations for three life stages (first-year larvae, metamorphs, or juveniles) in 2002 (Zar, 1999).

For analyses involving occupancy, we partitioned data on tailed frog occurrence into two categories, streams with or without evidence of reproduction (i.e., presence of eggs, larvae, or metamorphs or not). We compared tailed frog occupancy in first-order basins with occupancy of first-order reaches from third- and fourth-order basins combined ($N = 18$) using a Fisher's Exact test (Zar, 1999). The idea here was to determine whether the size of the non–fish-bearing basin might affect the occupancy of frogs in streams of comparable order.

For 2003 and 2005 data, we first assessed whether the presence of a road crossing was associated with occupancy patterns by comparing the frequency of *A. truei* occurrence in road- versus non–road-crossed streams using Fisher's Exact test (Zar, 1999). We conducted this comparison for each of all life stages combined and for those life stages implying reproduction for each of first- and second-order basins. Because we found no significant differences in occurrence related to the presence of roads within first- or second-order basins for either life stage combination (Fisher's Exact test: $P > 0.9999$ for all four combinations), we pooled occurrence data from roaded and unroaded basins. We then compared *A. truei* occurrence among stream order categories using a Fisher's Exact test for all life stages and only reproductive stages using a 0.0253 experiment-wise error rate. Again, to identify whether occupancy of first-order streams might be related to the order of the basin in which that stream occurs, we compared occupancy of first-order streams in first-order basins ($N = 26$) to that of first-order streams from all third- and fourth-order basins combined ($N = 14$) using a Fisher's Exact test.

We determined turnover rate in the occupancy of reproductive life stages in basins for which we had repeat visits across the five years we sampled. Turnover rate was defined as the sum of observations noting a change in occupancy (from occupied to unoccupied or vice versa) between repeat visits divided by total number of repeat visit observations. We had 20 sites with repeat visits in consecutive years and 19 and two sites with repeat visits separated by two or three years, respectively. Six sites with repeat visits separated by two or three years also had consecutive year data. For this analysis, we used all repeat visits. For example, a site visited in each of three consecutive years provided two observations on annual turnover (i.e., 2000–2001 and 2001–2002). A site with three visits across four years (e.g., 2000, 2001, and 2005) provided two observations, 2000–2001 and 2001/2005. We calculated annual turnover rate (consecutive year pairs only) and gross
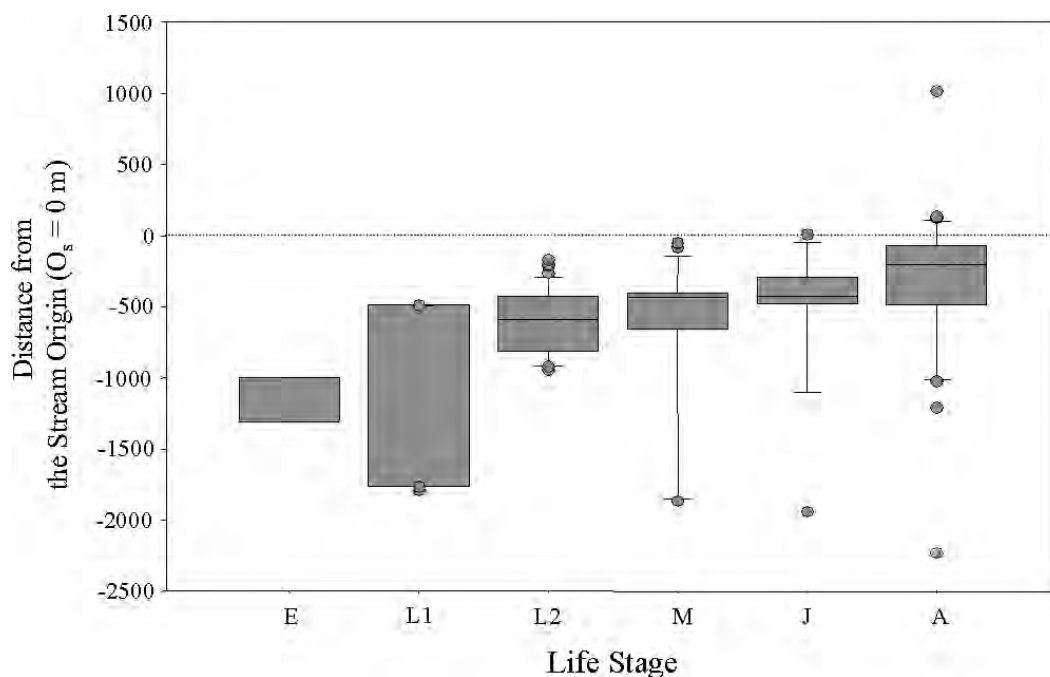
FIG. 2. Location of coastal tailed frogs (*Ascaphus truei*) from 131 headwater streams sampled August through October during 2000–2002 in the Stillman Creek watershed, Washington. Location data are meters either upstream (positive) or downstream (negative) of the stream origin (O_s). Life stages (and sample sizes) are egg masses (E: $N = 2$), first-year larvae (L1: $N = 125$), second-year larvae (L2: $N = 145$), metamorphs (M: $N = 31$), juvenile (J: $N = 13$), and adult (A: $N = 76$). Box plots display the medians (line in boxes), 25th and 75th percentiles (low and upper margin of boxes), 10th and 90th percentiles (lower and upper whiskers), and outliers (points). Where lines or whiskers are not visible, the values are identical to the 25th and 75th percentiles.

turnover rate, which included all sites with repeat visits, consecutive or not.

To index whether the amount of instream habitat differed among basins of different order, we compared the length of their wetted DSTs using a single-factor ANOVA and Bonferroni multiple comparison tests (Zar, 1999). We also compared the wetted DST length of first-order streams in first-order basins to the wetted DST length of first-order streams in third- and fourth-order basins using a *t*-test. To identify whether occupancy was related to wetted DST length, we performed a single-factor logistic regression using wetted DST length as the independent variable and presence (or absence) of life stages indicating *A. truei* reproduction as the dependent variable (Zar, 1999). To determine whether this regression differed significantly from a null model, we performed a drop-in-deviance test comparing this regression model to an intercept-only model (Kleinbaum et al., 2005). We performed cross-validation model assessment (Hosmer and Lemeshow, 2000; Fielding and Bell, 2002) and determined area under the receiver operator characteristic curve (AUC), model sensitivity (% correct presences), and model specificity (% correct absences). This logistic equation was then used to generate probabilities that coastal tailed frogs would reproduce in a basin based on the wetted DST length.

RESULTS

Background.—We recorded 409 frogs in 131 streams during 2000–2002. We recorded *A. truei* in 19% (25 of 131) of streams surveyed and the life stages implying reproduction in 10% (13 of 131) of streams. In descending order of abundance (numbers indicated in parentheses), second-year larvae (145) were most frequently encountered, followed by first-year larvae (125), adults (76), metamorphs (31), eggs (19), and juveniles (13). Most (92%) first-year larvae were found in two clusters of 40 and 75 individuals, each limited to an area ≤ 0.25 m^2. All 19 eggs were from two nests.

Low-Flow Season Dispersion.—We found significant differences in median position along the stream axis among tailed frog life stages in each of the three years (Kruskal-Wallis Test: $H_{2000} = 33, P < 0.0001; H_{2001} = 17, P = < 0.0053; H_{2002} =$
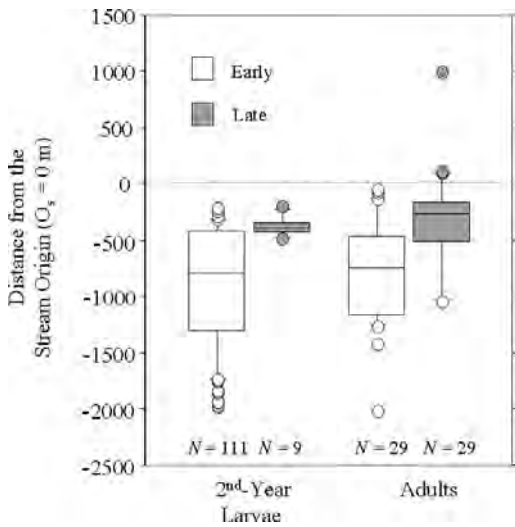
FIG. 3. Location of Coastal Tailed Frog (*Ascaphus truei*) by life stage from eight headwater streams sampled early (May through July) and late (August through October) in the Stillman Creek Basin, Washington, during 2002. Position data (in meters from the stream origin), and box plot characteristics are as in Figure 2. Sample sizes are above the x-axis; data on eggs, first-year larvae, metamorphs, and juveniles are not shown because sample sizes were either small (< 7) or zero in one of the two sample periods.

22, $P = 0.0005$). Older life stages were closer to the O_s in all three years (Spearman Rank Correlation: $\rho_{2000} = 0.793$, $N = 93$, $P < 0.0001$; $\rho_{2001} = 0.478$, $N = 51$, $P = 0.0007$; $\rho_{2002} = 0.247$, $N = 54$, $P = 0.0022$; Fig. 2).

Intraseasonal Changes in Dispersion.—Larvae and adults were each higher in the watershed in late summer as compared to early summer (Mann-Whitney U-test: $P \leq 0.003$ for both; Fig. 3). The median position of adults and second-year larvae in late summer was 406 m and 733 m upstream of their median position in early summer, respectively.

Headwater Basin Occupancy.—In general, we recorded tailed frogs infrequently; in 2000–2002, we found frogs in only 16% (13 of 81) of basins and life stages implying reproduction in only 9% (seven of 81) of basins. We encountered no tailed frog life stages implying reproduction from first-order basins (Fig. 4). Moreover, the proportion of streams occupied with life stages implying reproduction increased with basin order (Fig. 4). Based on life stages implying reproduction, tailed frog occupancy in first-order streams of third- and fourth-order basins (33.3%) was nearly seven times greater than tailed frog occupancy in first-order basins (4.8%; Fisher's Exact test: $P = 0.0350$).
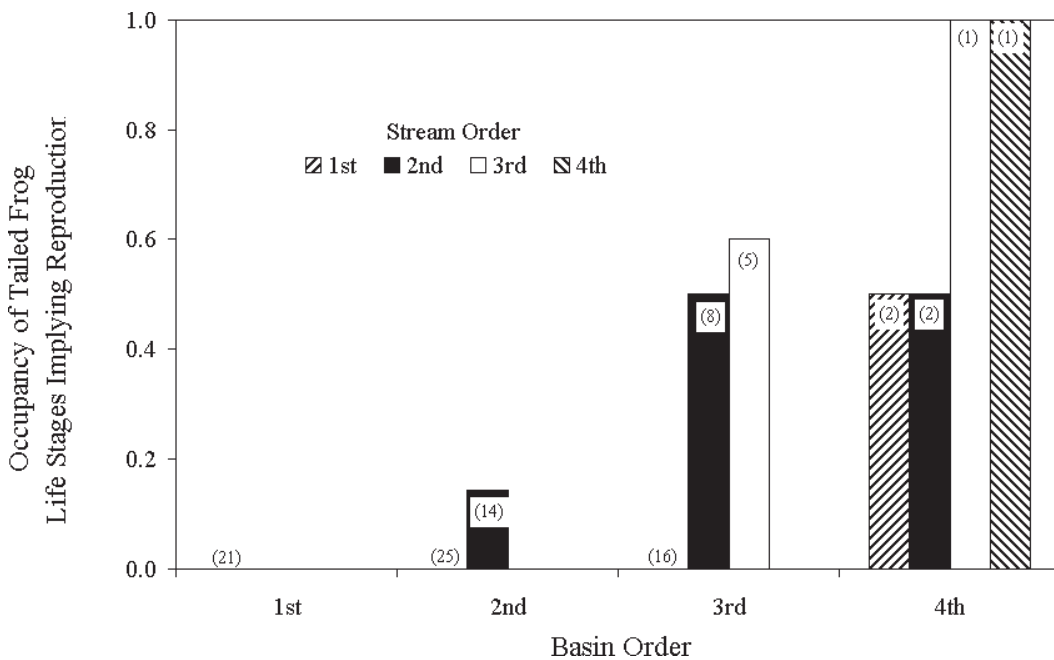

FIG. 4. Proportion of streams occupied by Coastal Tailed Frog (*Ascaphus truei*) life stages implying reproduction as a function of Strahler (1952) stream order within non–fish-bearing basin for the Stillman Creek watershed, Washington, during 2000–2002. Samples size for each stream category is indicated in parentheses.
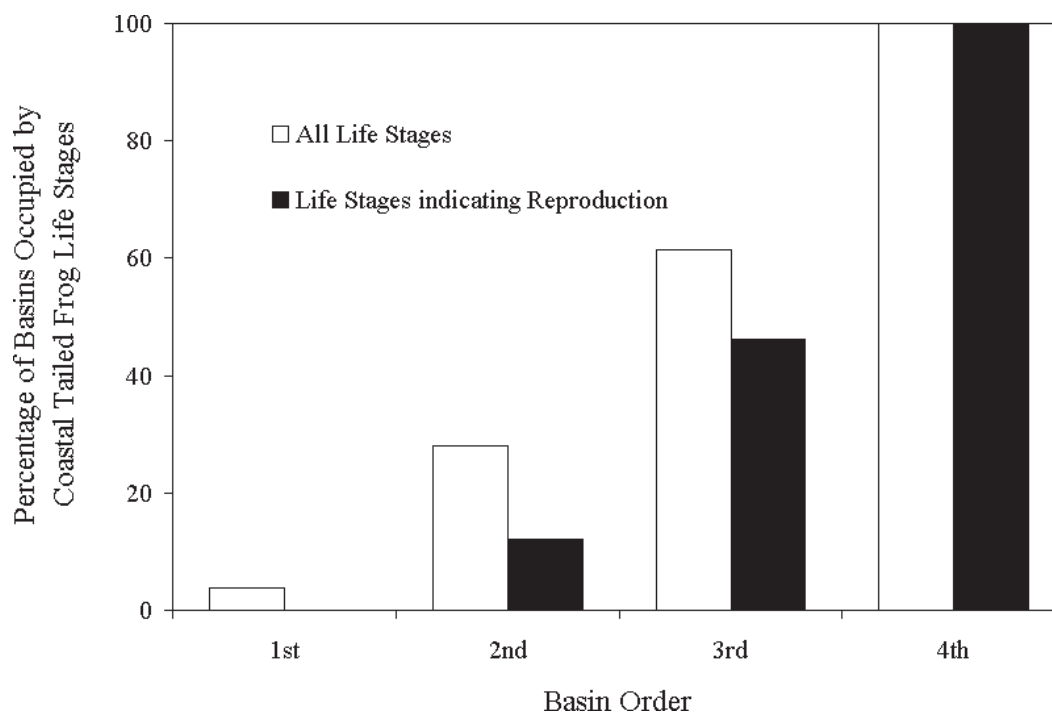
FIG. 5. Percentage occupancy of Coastal Tailed Frog (*Ascaphus truei*) life stages implying reproduction as a function of basin order in the Stillman Creek watershed, Washington, during 2003 and 2005. Sample sizes for basin categories are first ($N = 26$), second ($N = 25$), third ($N = 13$), and fourth ($N = 1$).

In 2003 and 2005, we found *A. truei* in 26% (17 of 65) of basins but life stages suggesting reproduction in only 15% (10 of 65) of basins. We found significant differences in occupancy by basin order for all *A. truei* ($\chi^2 = 17.9$, $P = 0.0004$) and life stages implying reproduction ($\chi^2 = 19.5$, $P = 0.0002$). We found no life stages implying reproduction from first-order basins, but the percentage of basins with life stages implying reproduction increased markedly with increasing basin order (Fig. 5). However, in contrast to data from 2000–2002 based on all life stages, tailed frog occupancy in first-order streams from third- and fourth-order basins (0%) did not differ significantly from tailed frog occupancy in first-order basins (3.8%; Fisher's Exact test: $P > 0.9999$).

Thirty-five basins with 50 repeat visit observations were available to calculate turnover rates. Annual turnover rate, based on 20 basins with 29 repeat visits was 17%. At 18%, gross turnover rate, based on all repeat visit observations, was almost identical.

Wetted DST lengths varied among basin-order categories (ANOVA: $F_{3,61} = 35.094$, $P < 0.0001$; Fig. 6). Differences also existed among the wetted DST lengths for all pairwise comparisons among first- to third-order basins (Bonferroni multiple contrasts: $P \leq 0.0007$ for all combinations); the length of the wetted DST in single fourth-order basin was almost 700 m longer than the median length of the wetted DST in third-order basins. The length of the first-order reach of the wetted DST in third- and fourth-order basins did not differ significantly from the length of the wetted DST in first-order basins (*t*-test: $t_{26,14} = 0.432$, $P = 0.7635$).

We found postmetamorphic *A. truei* in some basins where the wetted DST length was $\leq$ 600 m (Fig. 7A), but the shortest wetted DST length in which we found evidence of *A. truei* reproduction (eggs, larvae or metamorphs) was 687 m (Fig. 7B). Probability of occupancy increased as a function of length of wetted DST, remaining extremely low up to 800 m but increasing sharply thereafter (Fig. 8; drop-in-deviance test: $\chi^2_1 = 24.9$, $P < 0.0001$; coefficients $\pm$ SE: intercept: -4.598 ± 1.084, $P < 0.0004$; wetted length: 0.003 ± 1.084, $P = 0.0004$). Cross-classification validation indicated that 91.3% of basins were correctly classified ($AUC = 0.913$). Sensitivity was 60%: tailed frogs were not observed in four of 10 basins in which they were predicted; specificity was 96.4%: tailed frogs were found in two of 55 where absence was predicted.
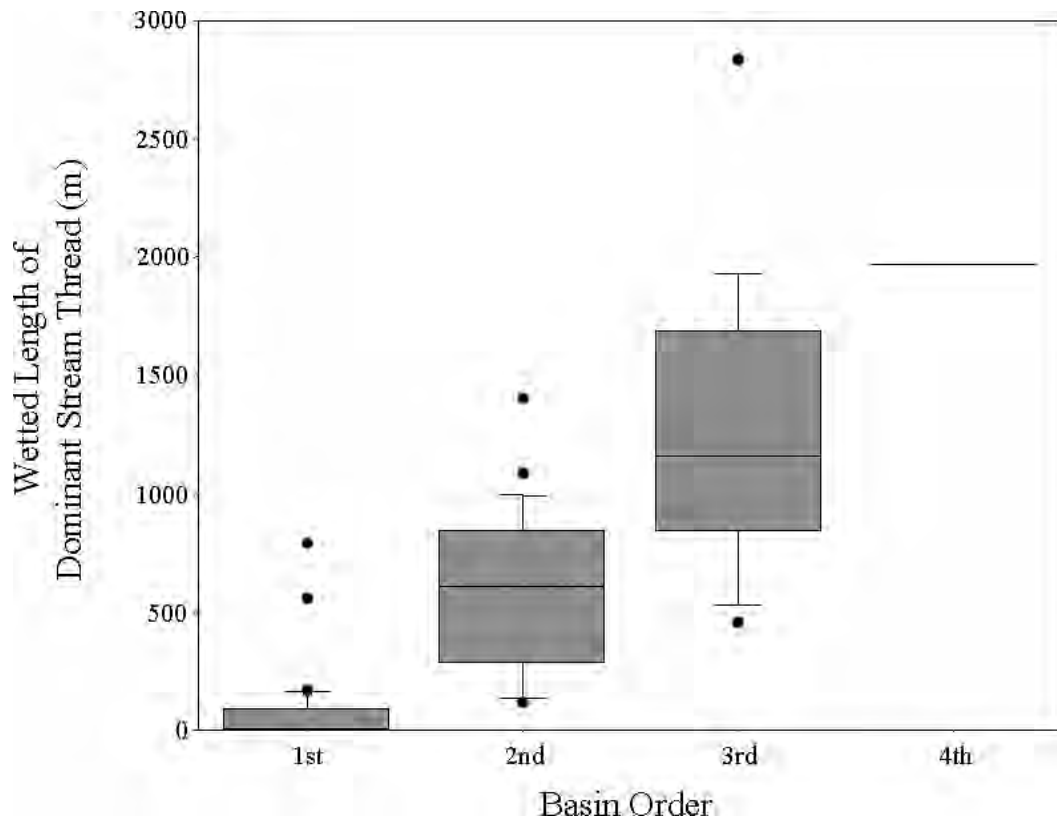
FIG. 6. Variation in wetted length of the dominant stream thread (DST) in 65 basins in the Stillman Creek Basin, Washington, during low flow (1 August to 7 October) for 2003 and 2005. Box plot characteristics are as in Figure 2.

DISCUSSION

Dispersion Implications.—Our results suggest that adult tailed frogs make at least two relatively large-scale movements over the course of a year. Frogs lay their eggs downstream of where they are commonly found in late summer, suggesting that frogs move upstream postbreeding and return downstream to breed, although the exact timing of such movements is unclear. Base on our limited data for 2002, downstream movements do not occur over the early to late summer interval. Limited data indicate that that oviposition occurs in July on the west slopes of the Cascade Mountains (Brown, 1975; Nussbaum et al., 1983); hence, frogs may move downstream immediately before breeding activity and return upstream shortly thereafter.

Why adult tailed frogs move upstream after breeding is unknown, but it may be related to increased food supply. Recent studies of headwater invertebrates indicate that the density and biomass of insects was 2–3 times greater in the nonperennial portions of PNW headwater streams (Muchow and Richardson, 2000; Progar

and Moldenke, 2002). Coastal Tailed Frogs have an invertebrate diet that includes many insects (Gaige, 1920; Fitch, 1936; Bury, 1970; Nussbaum et al., 1983). If seasonally intermittent reaches near the O_s are food rich, moving to such areas may be important to adult tailed frogs, especially females with a high-energy demand in yolking large eggs (Brown, 1989). Upstream movements have been identified in at least one other headwater stream amphibian, but the cause of these movements remains unknown (Lowe, 2003). Lowe observed upstream summer movements in adults and larvae of the headwater salamander *Gyrinophilus porphyriticus* that could not be explained as compensation for passive drift as only a small fraction of the population made significant upstream movements.

We also identified a seasonal shift in the median location of second-year larvae (Fig. 3), but this pattern may not be related to movements per se. *Ascaphus truei* has a two-year larval period in our study area (Bury and Adams, 1999) with second-year larvae typically metamorphosing during summer low flow
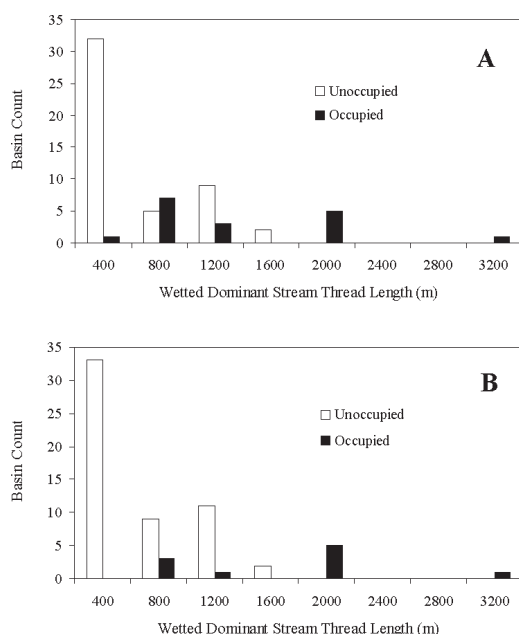
FIG. 7. Coastal Tailed Frog (*Ascaphus truei*) occupancy of non–fish-bearing basins as a function of the wetted length of its dominant stream thread (DST). Labels for length categories are the maximum values for each category. (A) All life stages. (B) Only those life stages indicating reproduction in that basin (i.e., eggs, larvae, or metamorphs).

(Nussbaum et al., 1983). Downstream larvae metamorphosing before upstream larvae could explain the patterns. Besides the shift in position, we noted a large reduction in the number of second-year larvae between early and late samplings presumably resulting from metamorphosis. A second potential explanation has to do with stream-drying patterns. During summer, surface waters in headwater channels become increasingly fragmented in the Willapa Hills study area, resulting in a series of dry and wet reaches (unpubl. data). In cases where fixed groundwater sources maintain flow, the downstream boundaries of wet reaches often move upslope (Hunter et al., 2005), a pattern that we observed in tailed frog-occupied streams. Thus, some tailed frog larvae may move upstream to remain in watered habitat during this period. Marking larvae while tracking surface water patterns will be needed to test alternative explanations, which are not necessarily mutually exclusive.

Little from tailed frog literature relates to the movements we postulate for adult *A. truei*. Upstream (Metter, 1964) or downstream (Landreth and Ferguson, 1967) seasonal moves have been suggested, but careful documentation has been lacking. Furthermore, in an extensive

multiyear study of > 500 marked frogs in Montana, Daugherty and Sheldon (1982) concluded that tailed frogs were sedentary and as adults moved ≤ 60 m. However, Adams and Frissell (2001) pointed out that the annual summer sampling period that Daugherty and Sheldon used may have ended too early to detect seasonal movements. Adams and Frissell (2001) provided evidence of a temperature-influenced downstream move in the fall but in only one of two tributaries of a larger stream. Their results led them to suggest that tailed frog movements might be related to habitat differences between the two tributaries. All aforementioned studies involve populations now part of *A. montanus* (Neilson et al., 2001), which occupy streams that can differ substantially from those where *A. truei* are found, especially given the relatively high water temperatures reported for *A. montanus* habitat (Adams and Frissell, 2001). Notwithstanding these issues, evidence of widespread seasonal movements is lacking for either tailed frog species. Although two recent studies have addressed movement in postmetamorphic *A. truei* (Matsuda and Richardson, 2005; Wahbe et al., 2004), both showed that forestry management may restrict the scale of localized movements, but neither addressed the spatial scale of seasonal movements.

Landscape Occupancy Patterns.—We found a relatively low occupancy rate of *A. truei* across the Stillman Creek watershed, whether the data were evaluated for individual streams (19%) or basins (16% in 2000–2002; 26% in 2003, 2005). Occupancy rates of life stages that suggested reproduction was even rarer, with only 10% of streams and 9% of headwater basins being occupied in 2000–2002, and 10% of headwater basins in 2003 and 2005. We recognize that sampling only during low flow could result in underestimating the frequency of reproduction. Although we cannot address sampling outside the low-flow season, we believe our methods reliably identified streams used for reproduction when reproduction was accompanied by recruitment of first- and second-year larvae. In other words, our methods were rigorous in the sense that we examined the entire length of the DST to evaluate occupancy, as opposed to subsampling only a small part, and we used multiple life stages to infer reproduction (i.e., eggs, first- and second-year larvae, and metamorphs) rather than a single life stage. Moreover, relatively low turnover estimates suggest short-term stability in occupancy rates. Although not designed to address occupancy rates in headwater basins, the only other study that addressed *A. truei* occupancy across a regionally randomized set of streams in southwestern
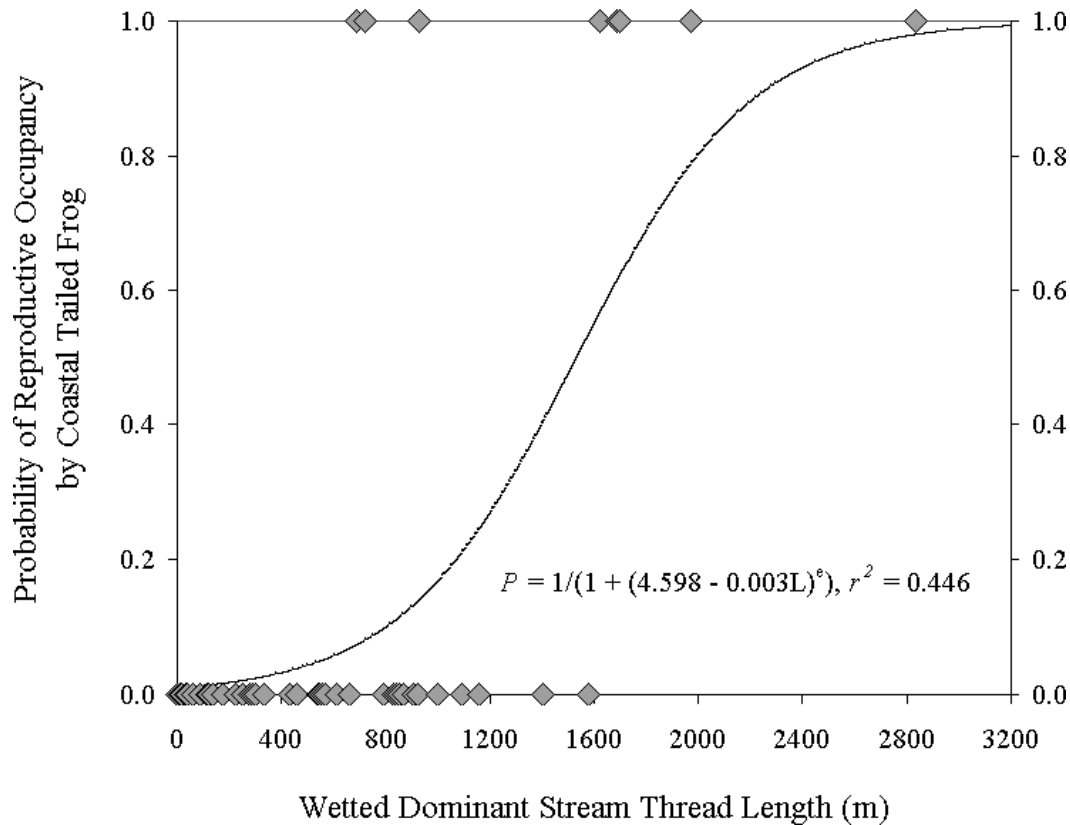
FIG. 8.   Coastal Tailed Frog (*Ascaphus truei*) reproductive occupancy of non–fish-bearing basins as a function of the wetted length of its dominant stream thread (DST). Diamonds indicate occupied (1) or unoccupied (0) basins. The curve describes the probability function generated by the logistic regression (see text for details).

Washington was that of Wilkins and Peterson (2000), who recorded *A. truei* in 13% of 40 non–fish-bearing streams. Low occupancy across this region may be a natural consequence of physical features (e.g., hydrology, geology, and topography) of southwestern Washington State and tailed frog life-history requirements. Larger-order (third or fourth) non–fish-bearing basins are uncommon; only 8% (54 of 642) of such basins are third- or fourth-order in the Stillman Creek watershed. Because a marked reduction in the number of larger-order basins is a general landscape pattern (Hynes, 1970), the low tailed frog occupancy that Wilkins and Peterson (2000) found may indicate that the pattern is regionally widespread.

The basis of the different occupancy patterns we obtained for the 2000–2002 versus 2003–2005 datasets across first-order streams in basins of different sizes is unclear. Although these streams are similar in terms of length, geology, and forest management regimes, first-order streams in larger-order headwater basins had an occupancy rate that was roughly seven times that found in first-order headwater basins in 2000–2002. We did not observe that difference in 2003–2005. In fact, occupancy was near zero regardless of basin size in the latter years. We believe that the difference between datasets reflects the generally higher occupancy of tailed frogs in the down-stream portions of these larger order streams (see Fig. 4). That is, tailed frogs are able to regularly occupy the first-order streams in larger non–fish-bearing basins during wet, but not dry, years. Both 2003 and 2005 were drier than 2000–2002 (Office of the Washington State Climatologist, Annual precipitation data rankings, http://www.climate.washington.edu/precip_rankings.html, 2006) in the late-spring interval, which appears to have a critical influence on summer low flows (Hunter et al., 2005). Verifying this occupancy hypothesis will require understand-ing the relationship between tailed frog distri-bution and interyear variation in surface flows as well as examining the untested assumption that fish-bearing waters, like those immediately downstream of a first-order basin, are unsuitable habitat for tailed frogs.

We found relatively few *A. truei* egg masses, but we believe that tailed frogs oviposit far enough below the stream origin to avoid desiccation of eggs and first-year larvae during summer drying. We suggest that *A. truei* habitat suitability for breeding and early rearing generally declines as one moves upstream of oviposition reaches (i.e., approximately 800 m from O_s). That is, availability and predictability of surface waters declines as one approaches the O_s. In a similar way, the further downstream eggs or first-year larvae occur, the more susceptible those life stages would be to the effects of scour (as a result of sudden high flows) such as mechanical injury or passive drift into fish-bearing reaches where they may fall prey to fish and giant salamanders (*Dicamptodon* spp.). These ideas form the basis of the testable hypothesis: larger non–fish-bearing basins provide higher quality habitat than smaller basins because they better meet the requirements of *A. truei* oviposition and larval rearing.

Our thesis includes the idea that adult *A. truei* move seasonally between reaches with enough flow for oviposition (and development) and suitable habitat in the vicinity of the stream origin for adults. This cycle requires adults to move distances of at least several hundred meters in southwest Washington and is the inverse of the seasonal pattern found in stream salmonids (Groot and Margolis, 1991). We offer these ideas as hypotheses and stress that, although all of them warrant testing, the seasonal movement aspect of our hypothesis is especially in need of verification since we inferred movement from life-stage specific changes in dispersion rather than marked individuals. Tracking marked frogs would be particularly important to eliminate alternative hypotheses explaining the differential distribution of adult frogs we observed between early and late sampling (e.g., detectability changing seasonally because of changes in microhabitat and refuge use by adults). We also emphasize that the these hypotheses were generated from tailed frog work on a basalt geology in a managed forest landscape with precipitation conditions of the interior coastal zone Douglas-fir/western hemlock forest (Franklin and Dyrness, 1988). However, we predict that *A. truei* occupancy will be positively associated with basin size regardless of geology and forestry practices and that similar movement may be expected in basins with similar hydrologies. We recognize that forestry practices may have influenced occupancy in *A. truei*, but it probably does not explain the differential occupancy of *A. truei* we observed with basin size. Because of the general inverse relationship between non–fish-bearing basin size and occupancy, our hypothesis may contribute to a general explanation for low *A. truei* occupancy in coastal and near-coastal landscapes of Washington State. To better understand the putative effects of forest practices on tailed frogs, we suggest that tailed frog studies consider basin size explicitly in their study design.

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