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Evaluating Residual Tree Patches as Stepping Stones and Short-Term Refugia for Red-Legged Frogs

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ABSTRACT Temperate pond-breeding amphibians are vulnerable to forest fragmentation because they must access upland terrestrial sites during the nonbreeding season but are prone to desiccation in hot, dry environments without canopy cover. Harvesting techniques that retain live trees in the cut block are advocated for sustaining forest biodiversity, but the effects of these practices on amphibians are unknown. We studied red-legged frogs (*Rana aurora*) in movement trials to assess: 1) how short-term use of residual trees was affected by tree patch size, streams, and neighborhood features; 2) whether residual tree patches were used as stepping stones in negotiating cut blocks; 3) the effects of patch size and patch proximity in altering movement paths; and 4) the effects of retention level and patch size on interpatch distance. Residual tree patches were potentially valuable short-term refugia but their value was size dependent. Virtually all frogs released at the base of single trees or inside small tree clusters left within 72 hours, but the proportion leaving decreased curvilinearly with increasing patch size. Frogs were less likely to leave tree patches with a running stream or where neighborhood stream density was high. Residual tree patches did not systematically alter movement paths. Frogs intercepted residual tree patches mostly at random and had to be within 5–20 m of a tree patch before moving to it in greater proportions than expected by chance. However, amphibian movements were biased toward large (0.8 ha) patches and away from small (0.3 ha) patches 50 m away. Our results indicated that residual trees should not be retained singly but should be aggregated in groups between 0.8 ha and 1.5 ha, preferably in stream locations. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1836–1844; 2007)

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Structural or variable-retention harvesting that retains green trees in the harvested area is replacing clear-cut logging as the standard silvicultural practice in many temperate and boreal forests (Franklin et al. 1997, Mitchell and Beese 2002). The shift from clear-cut logging is occurring because many resource practitioners now believe that ecologically sustainable forestry can best be achieved by having timber removal approximate natural disturbance regimes (Franklin et al. 2002). Habitat loss and habitat fragmentation cannot be addressed by focusing exclusively on ecological reserves, which typically cover much less area than the nonreserve matrix or harvested area in most temperate forests (Lindenmayer and Franklin 2002). To be effective, conservation strategies must also emphasize harvested areas (Lindenmayer and Franklin 2002). Structural retention harvesting retains late-seral attributes such as large living trees, snags, and downed wood material, and provides critical habitat to organisms that would normally be lost immediately after clear-cutting (Rodewald and Yahner 2000, Schieck and Hobson 2000, Tittler et al. 2001). Additionally, residual structures in the matrix may facilitate landscape connectivity for organisms, thereby preventing populations in reserves from becoming isolated and fragmented (Burkey 1989).

Variable-retention harvesting, which is a systematic approach to structural retention harvesting, exists in many forms in order to mimic the complex outcomes of natural disturbance regimes as well as meet a diverse array of forest management objectives (Franklin et al. 1997). The amounts, types, and spatial arrangement of both live and dead residual

structures vary widely from one form to another. In dispersed retention, single residual structures are distributed uniformly over the harvested area, but in aggregated retention, residual structures are concentrated in small intact areas of forest within the harvested matrix. There are many tradeoffs between each approach with, for example, dispersed retention accommodating territorial behavior in animals but lacking the niches provided by the intact soil, understory, and overstory layer in aggregated retention. Residual structures for any given retention level are more closely spaced in dispersed than in aggregated retention, but the microclimate in aggregated retention more closely resembles that of the original forest. The variability of structural retention harvesting, coupled with its short implementation history, mean that the key issues of what structure to retain, how much to retain, and how to distribute the structures across space have received limited empirical assessment despite its widespread application (Lindenmayer and Franklin 2002). Amphibian response to variable-retention harvesting is virtually unknown. Research on biodiversity response has focused primarily on stand structure (Sullivan et al. 2001), vascular plants (Halpern et al. 2005, Nelson and Halpern 2005), small mammals (Moses and Boutin 2001, Sullivan and Sullivan 2001), and avian communities (Merrill et al. 1998, Rodewald and Yahner 2000, Schieck and Hobson 2000, Tittler et al. 2001).

Temperate pond-breeding amphibians are highly vulnerable to forest fragmentation (Skelly et al. 1999; Marsh and Trenham 2001; Semlitsch 2000, 2002) and should benefit from a silvicultural regime that helps to maintain landscape connectivity. Although pond-breeding amphibians repro-

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duce in water, they inhabit upland, terrestrial sites during the nonbreeding season (Dodd 1996, Dodd and Cade 1998, Lamoureux and Madison 1999) and a terrestrial network that links both seasonal sites and sub-populations is critical to their conservation (Marsh and Trenham 2001, Semlitsch 2002). Isolation effects for pond-breeding amphibians are more strongly dictated by the distribution of terrestrial habitats than by the distribution of breeding ponds (Semlitsch 1998, Marsh and Trenham 2001, Pope et al. 2000), with traditional clear-cuts acting as strong barriers to anuran movements (Chan-McLeod 2003).

The red-legged frog (*Rana aurora*) epitomizes temperate pond-breeding anurans that inhabit upland areas during the nonbreeding season but inhabit marshes, ponds, lake edges, and slow streams while breeding (Corkran and Thoms 1996). Both the postbreeding habitats and the overwintering sites may be located in upland habitats far from the aquatic breeding sites (Licht 1969), sometimes at considerable distances from water.

The red-legged frog also epitomizes the plight of declining amphibians worldwide. The northern sub-species of the red-legged frog (*R. a. aurora*) is blue-listed in British Columbia, Canada, and has been designated a species of special concern by the Committee on the Status of Endangered Wildlife in Canada. The Californian sub-species (*R. a. draytoni*) is a species of special concern in California, and has been designated as a federally threatened species by the United States Fish and Wildlife Service.

In general, amphibians require moist and shady conditions. We expect that amphibian movement through harvested areas will be facilitated by green trees retained by variable retention harvesting. We predict that: 1) red-legged frogs, which are averse to crossing cutover areas, will be more likely to use residual trees as stepping-stones through a harvested area if the distance to the residual tree is short; 2) red-legged frogs will be less likely to move to small residual tree patches than to large patches, because large patches will be more easily perceived and will provide a more hospitable climate; 3) the usefulness of residual trees as short-term refugia will depend on tree patch size, which strongly dictates microclimatic conditions and the relative influence of edge effects from the adjacent cut matrix; and 4) the use of a given residual tree patch will increase if nearby features, such as neighboring green trees and streams, act to funnel amphibians to the tree patch. Because there is a direct tradeoff between the number and the size of tree patches that can be retained for a given retention level, we expect that there will be an optimal harvest configuration that will balance the trade-off between the distance that a frog must travel in the matrix before reaching cover, and the quality of that cover.

Our study objectives were to quantify the short-term use of residual trees and residual tree patches by frogs, and to determine whether residual trees and tree patches facilitate the movement of frogs through cut blocks. We specifically addressed the following questions: 1) How is short-term use of residual trees by frogs affected by patch size, the presence

or absence of a stream within the patch, and proximity to neighboring features (residual trees, residual tree patches, streams)? 2) Do frogs use residual tree patches as stepping stones in their movement through the cut-block? 3) Will a frog choose the largest residual tree patch if it is located at equal distances from various sized patches? 4) How close does a residual tree patch have to be before it will measurably influence frog movement? 5) What is the mean interpatch distance that a frog would have to cross for a typical variable-retention cut block and how would this be affected by retention level and patch size?

STUDY AREA

We conducted our study in the forests of the Coastal Western Hemlock biogeoclimatic zone north of Campbell River (50°8'N–50°28'N, 125°15'W–126°22'W) on Vancouver Island, British Columbia. Western hemlock (*Tsuga heterophylla*) was the dominant tree species in the study area, occurring in pure or mixed-conifer stands with minor components of amabilis fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*). Dominant understory vegetation included regenerating trees, salal (*Gaultheria shallon*), false azalea (*Menziesia ferruginea*), Alaskan blueberry (*Vaccinium alaskaense*), oval-leaved huckleberry (*V. ovalifolium*), dull Oregon-grape (*Mahonia nervosa*), sword-fern (*Polystichum munitum*), and bracken fern (*Pteridium aquilinum*). A well-developed moss layer consisted primarily of step moss (*Hylocomium splendens*) and lanky moss (*Rhytidiadelphus loreus*). Mean rainfall for the summer months averaged 39.5–49.3 mm per month accumulated over 8–11 days with measurable rainfall (Environment Canada 2006). The mean daily maximum temperature for July and August was 23.1° C while the mean daily minimum was 10.2° C.

The experimental sites were comprised of cut blocks that had been recently harvested by Weyerhaeuser Ltd. in the variable-retention method (Mitchell and Beese 2002). More than half the total area of the cut block was within at least one tree height of the base of a tree or group of trees, and all areas of the cut block were minimally within 2 tree heights of the base of a tree or group of trees. The level of tree retention was typically between 5% and 30%.

METHODS

Experimental Design

Short-term use of residual trees and tree patches.—We selected 20 residual trees and tree patches as release points for radiocollared frogs using the following criteria: 1) canopy areas above release points spanned the range of residual tree canopies created by standard variable-retention harvesting operations (0.07–2.7 ha), 2) 10–20% of green trees were retained in the variable-retention cut block, 3) site was <400 m elevation with <10% slope, and 4) the cut block was harvested within the last 2 years. We released 200 frogs (10 frogs at each of the 20 release points) at either the center of the tree patch or at the base of individual trees, and monitored them to see whether and when they left the tree

cover. We terminated the trials either when the frog left the patch or after 72 hours. We measured from the ground or from ortho-rectified (20-cm pixel) photographs the area occupied by the tree crown or tree patch, the distance to the nearest single tree, the distance to the nearest tree patch, the distance to the nearest stand of mature forest, and stream density inside 3 concentric circles (with 50-m, 100-m, and 150-m radii) centered around each release point. We recorded the presence of a stream or wetland in cut-over areas, at the base of individual trees, or inside tree patches.

Movements through variable-retention cut blocks.—We conducted 3 trials to evaluate movement behavior in the cut blocks. In trial 1, we assessed whether frogs used residual trees or residual tree patches as stepping stones when moving through variable-retention cut blocks. We released 80 frogs, 10 each in 4 randomly located residual tree patches and at 4 randomly located points in the harvested matrix. We released each frog individually and did not run trials concurrently for multiple frogs at the same release point. Following release, we monitored 24 (30%) frogs (3 frogs at each of 8 sites) every second hour for the first 24 hours and monitored 56 (70%) frogs (7 frogs at each of 8 sites) daily for up to 6 days. We analyzed the movement paths of all frogs for deliberate movements toward or away from residual trees, residual tree patches, roads, and streams. In trial 2, we evaluated whether frogs preferentially moved toward the largest tree patch if given a choice of various-sized patches. We selected 4 release points using the following criteria: 1) the release point was at the center of, and equidistant to, 3 surrounding tree patches of differing sizes; 2) the distance from the release point to each of the 3 surrounding tree patches was approximately 50 m; and 3) size differences between successively larger tree patches averaged $>2,000 \text{ m}^2$. Tree patches surrounding the 4 release points averaged $3,539 \text{ m}^2$ for the small patch, $5,888 \text{ m}^2$ for the medium patch, and $8,173 \text{ m}^2$ for the large patch. We released 28 frogs (7 frogs at each of the 4 release points), and monitored their movement. In trial 3, we quantified how close a residual tree patch had to be before it measurably influenced the direction of the frog's movement. We released 10 frogs at each of 5 distances (5 m, 10 m, 20 m, 30 m, and 40 m) from a tree patch. We also released 10 frogs at each of 4 distances (20 m, 40 m, 60 m, and 80 m) from a second tree patch. We monitored the proportion of frogs moving toward the patch for each release distance.

Field Methodology

We captured and fitted red-legged frogs with radio-transmitters (E362 from Sirtrack Ltd., Havelock North, New Zealand; BD-2 and BD-2a from Holohil Systems Ltd., Carp, ON, Canada) using the method of Chan-McLeod (2003). We transported frogs to the experimental sites and returned them to their respective capture locations following movement trials conducted between May and September in 2000 and 2001. We followed the guidelines of the Declining Amphibian Populations Task Force Field Code of Practice for handling amphibians. Our experimental protocol and handling procedures conformed to the

standards of the University of British Columbia Committee on Animal Care and we obtained a sundry permit from the British Columbia Ministry of Water, Lands, and Air Protection for amphibian capture. We released frogs and monitored their movements using the method of Chan-McLeod (2003)

Effects of Tree Patch Size and Retention Level on Interpatch Distance

To determine the mean inter-patch distance that a frog would typically have to cross when moving through variable-retention cut blocks, we simulated the effects of tree patch size and retention level on the mean distance between patches for a hypothetical, square, variable-retention cut block measuring 40 ha in size. We placed residual tree patches randomly using 4 retention levels (10%, 20%, 30%, and 40%) for each of 5 patch sizes (0.1 ha, 0.5 ha, 1 ha, 1.5 ha, 2 ha). We computed the mean interpatch distance for each scenario by averaging the distances between each tree patch in the cut block and 4 of its nearest neighbors. We assumed that the cut block was bordered by mature forests on all sides. Thus, the closest neighbors for residual tree patches at the edge of the cut block might include the surrounding forest. We simulated each scenario 200 times. We repeated the exercise twice, once for circular tree patches and once for rectangular tree patches with 3:1 dimensions.

Data Analyses

Prior to statistical analyses, we evaluated variables for normality using the Shapiro-Wilks test and for homogeneity of variance using Levene's test. In the case of nonnormal data, we first attempted curvilinear regression with transformed variables before using nonparametric approaches.

We conducted forward stepwise regression to assess the effects of patch size and neighboring features on the short-term use of residual trees and tree patches. The dependent variable was the proportion of frogs that left the residual tree or tree patch by the end of the 72-hour trial period. We used the following independent variables: canopy area of the residual tree or tree patch, distance to the nearest stream, distance to the nearest neighboring patch, distance to the nearest individual tree, distance to the nearest mature forest, and stream densities within 50 m, 100 m, and 150 m.

We used the complete movement path as the basic unit of analyses for all movements (Turchin 1998). We used a kinematic approach in trial 1 to resolve issues of autocorrelation and unidirectional persistence (Okubo et al. 1977, Parrish and Turchin 1997) for the 24 frogs that were monitored at 2-hour intervals. We selected the scale for analyzing movement data by determining the point at which there was no autocorrelation in the discrete acceleration of frog movements. We used the standard autocorrelation function for continuous variables to scan for potential incidences of first- or higher order autocorrelations. We used the Durbin-Watson statistic to confirm significant incidences of autocorrelation in data with correlation

coefficients of >0.49 . We analyzed our data at the scale of observation when significant autocorrelation was not detected in discrete acceleration. We analyzed only data collected during the active window (0000–1400 hr) of the primarily nocturnal red-legged frog. We plotted the x and y components of discrete acceleration against the independent variables (distances to the closest stream, road, single tree, and tree patch). Positive acceleration values implied attraction and, hence, attraction towards the focus, while a negative projection implied repulsion or acceleration away from it (Turchin 1998).

We identified independent movement paths following the method of Turchin et al. (1991) for all trials in which frogs were monitored at >2 -hour intervals. Movement data for these trials were not appropriate for kinematic analysis because of the course scale of observation. Following Turchin et al. (1991), we combined n steps into a single move if the $n - 1$ intermediate positions were within a specified distance (x) of the line connecting the first and the last steps in the path. We used an x -value of 5 m as this was the point when serial correlation disappeared for frog movement data (Chan-McLeod 2003). For trial 1, we identified deliberate movements toward or away from individual tree patches using Lehman and Lienert's (1980) binomial test against sectoral preference of circular observations. For trial 2, we used the Mann-Whitney test to contrast the observed and expected proportions of movements toward the open matrix and the small, medium, and large patches. The expected probability of moving in any given direction was randomly based. For a given tree patch, the randomly based expectation of moving toward that patch was equal to the angle subtended from the frog to the patch, divided by 360 degrees. For trial 3, we used the binomial test against sectoral preference of circular observations (Lehman and Lienert 1980) to compare the expected versus the observed numbers of frogs that moved toward the tree patch for each release distance, using the same method as for trial 2.

RESULTS

Short-Term Use of Residual Trees and Tree Patches

Fifty-five percent ($n = 109$) of the 198 frogs released at the base of individual trees or in the middle of residual tree patches left before the end of the trial. Fewer frogs left on each successive day: 50.7% of the total departures occurred on the first day, 28.4% occurred on the second day, and 20.7% occurred on the third day.

Tree patch size ($P = 0.004$) and stream density within a 100-m radius of the release point ($P = 0.001$) affected the proportion of frogs that left before the end of the trial period. Frogs were less likely to leave tree patches that were large and where the neighboring stream density was high ($F_{2,17} = 19.02$; $R^2 = 0.69$; $P < 0.001$). The presence of a stream within the tree patch, and the distances to the nearest tree patch, individual tree, or mature forest were not selected when tree patch size and stream density were already entered into the model. However, univariate analysis indicated that

the presence of a stream within the tree patch affected the proportion of frogs that left before the end of the trial ($F_{1,18} = 16.06$; $r^2 = 0.47$; $P < 0.001$).

The negative relationship between the proportion of frogs that left before the end of the trial (y) and tree patch size (x) was curvilinear for patches without running streams (Fig. 1; $F_{2,13} = 14.60$; $R^2 = 0.69$; $P < 0.001$; $\log y = 0.1947164 - 0.0764003 \times \log x - 0.0000439 \times x$). Virtually all frogs released at the base of individual trees or inside small tree clusters left before the end of the trial. From the fitted regression, half of all frogs released inside tree patches measuring 5,000 m² were expected to leave before the trial concluded. Although the proportion of frogs departing declined rapidly with increasing patch size, there were frogs departing from even the largest tree patches that did not have running streams. In 2 cases where all frogs remained for the duration of the trial, the release points were inside patches with wet streams. For these patches, the relationship between the proportion of departing frogs and patch size was linear (Fig. 1; $F_{1,2} = 1,130$; $r^2 = 0.99$; $P < 0.001$; $y = 0.612858 - 0.0000748 \times x$). The x -intercept for this line (i.e., the smallest patch size at which zero departures was exp) was 0.82 ha.

Movement Through the Variable-Retention Cut Blocks

Trial 1: residual trees as stepping stones.—Kinematic analyses indicated that the movement directions of 24 red-legged frogs released inside variable-retention cut blocks were not influenced by the location of block features. There were no apparent relationships between the frog's discrete acceleration and its distance to the nearest stream, road, residual single tree, or residual tree patch.

The movement paths of red-legged frogs monitored for up to 6 days also did not show a measurable attraction to residual tree patches ($Tn_{64} = 0.899$; $P = 0.186$). Although a few individuals apparently moved from tree patch to tree patch, the majority of movement paths did not show such a pattern. For many animals, the movement direction did not intersect tree patches despite an obvious directional persistence.

Trial 2: effect of patch size on movement path.—Different proportions of frogs moved toward the small, medium, and large tree patches ($T_3 = 8.382$; $P = 0.039$; Fig. 2). The proportion of frogs moving toward the small tree patch was less than that expected under random movement directions ($U_1 = 100.0$; $P = 0.046$), whereas the proportion of frogs moving toward the large tree patch exceeded random expectations ($U_1 = 5.0$; $P = 0.003$). The proportions of frogs moving toward the medium patch ($U_1 = 70.0$; $P = 0.675$) and the matrix ($U_1 = 84.0$; $P = 0.249$) did not differ from random expectations.

Trial 3: effect of patch proximity on movement path.—Frogs moved toward the tree patch in higher proportions than expected only at the release points closest to the patches ($P = 0.002$, Fig. 3a; $P = 0.047$, Fig. 3b). The observed and expected number of frogs moving toward the tree patch did not differ ($P > 0.05$) for any of the other release points.

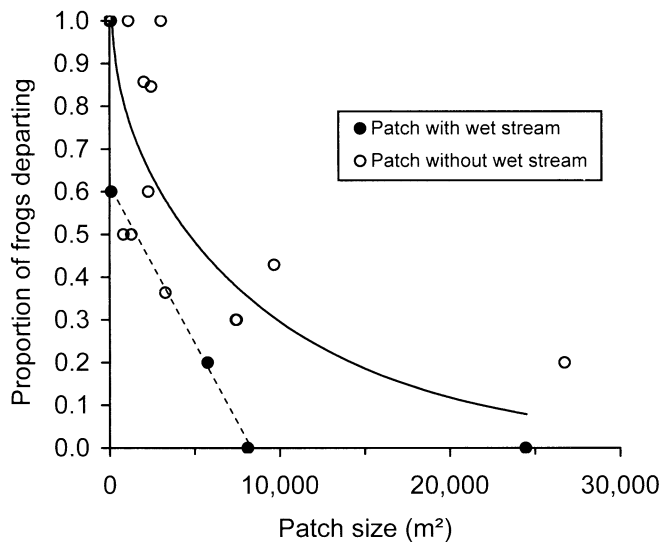


Figure 1. Relationship between the proportion of red-legged frogs departing from residual tree patches before the end of the trial and the size of the tree patch, for a) patches containing running streams (-----) and b) patches that either do not have streams or have dry stream beds only (——) near Campbell River, British Columbia, Canada, 2000–2001.

Effects of Tree Patch Size and Retention Level on Interpatch Distance

Mean distance between patches increased with patch size and decreased with retention level (Fig. 4). The shortest mean distance between patches was 11.2 m and the longest mean distance between patches was 167.3 m. When patch size was 0.1 ha, mean interpatch distance was consistently <50 m, regardless of retention level. When patch size was 1 ha, mean interpatch distance was <50 m at only 2 retention levels (30% and 40%), and when patch size was 2 ha, mean

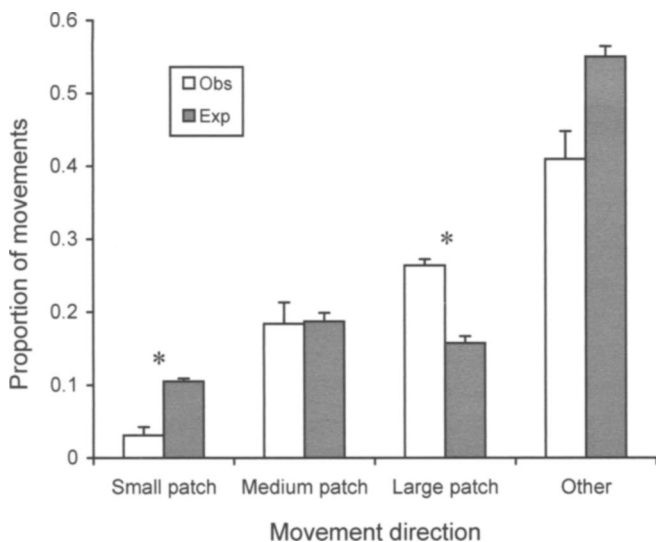


Figure 2. Observed and expected (based on random probabilities) proportions of red-legged frogs moving to 3 surrounding residual tree patches of various sizes (3,539 m², 5,888 m², and 8,173 m²) located equidistant from the release point, near Campbell River, British Columbia, Canada, 2000. Bars indicate \pm standard error from the mean. Asterisks indicate significant ($P < 0.05$) differences between observed and expected values.

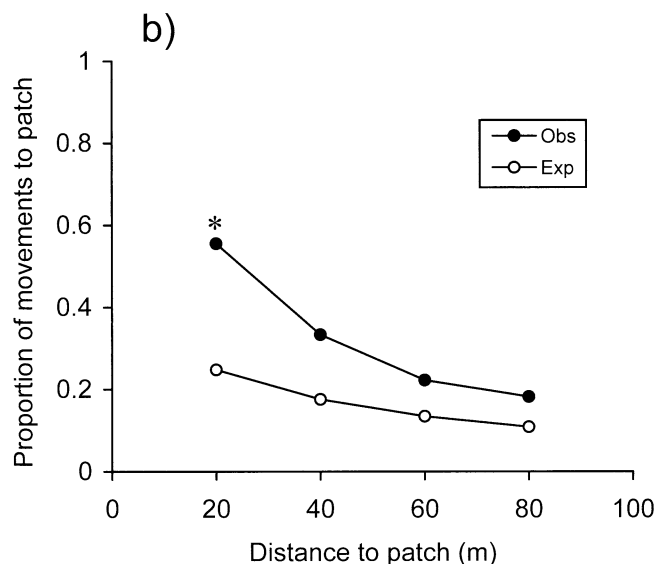
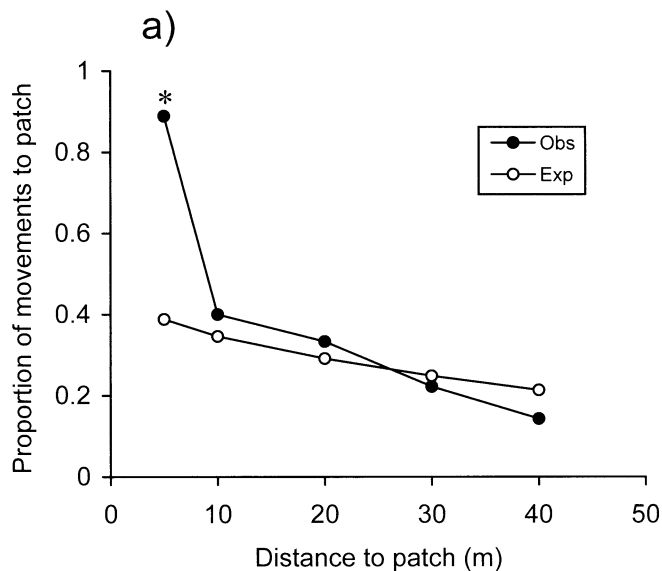


Figure 3. Observed and expected (based on random movement hypothesis) proportions of red-legged frogs moving to residual tree patch with increasing distance from 2 patches near Campbell River, British Columbia, Canada, 2000. Asterisks indicate significant ($P < 0.05$) differences between observed and expected values.

interpatch distance was <50 m at only the 40% retention level. Mean interpatch distance was <20 m only when patch size was 0.1 ha and retention level was $\geq 30\%$.

The effects of retention level were similar in magnitude to the effects of patch size. Doubling retention level from 10% to 20% decreased mean interpatch distance by approximately 44% and doubling patch size from 0.5 ha to 1 ha increased mean interpatch distance by approximately 36%. Quadrupling retention level from 10% to 40% decreased mean interpatch distance by 74% and quadrupling patch size from 0.5 ha to 2 ha increased mean interpatch distance by 84%.

Patch shape had relatively little effect on mean interpatch

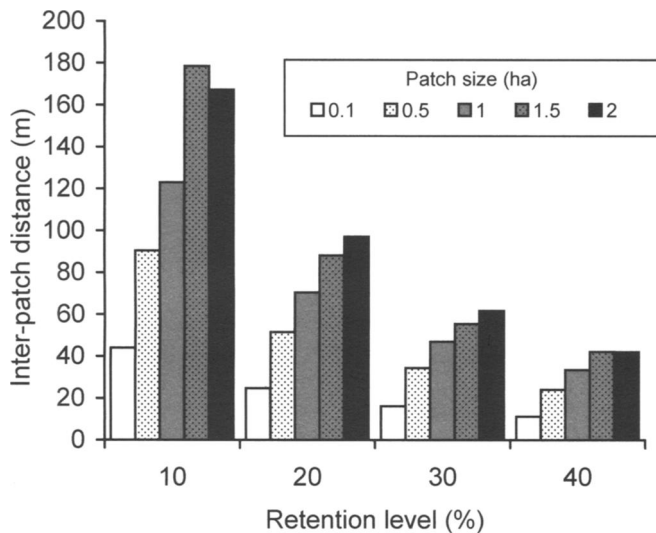


Figure 4. Simulated mean distance between residual tree patches that have been randomly located in a hypothetical, 40-ha square cut block, for 4 retention levels and 5 patch sizes.

distance, especially in the case of large patches. Circular tree patches resulted in 7–10% higher mean interpatch distances than rectangular tree patches, for patch sizes between 0.1 ha and 0.5 ha. The difference in mean interpatch distance between circular and rectangular tree patches had declined to approximately 4% for tree patches that were 1 ha in size, and to only 2% for tree patches that were 2 ha in size.

DISCUSSION

Residual tree patches can be important short-term refuges for migrating or dispersing amphibians, but their value is size-dependent. Virtually all frogs released at the base of individual trees or inside small tree clusters left before the end of the 72-hour trial period but the proportion that left decreased curvilinearly with increasing patch size. The midpoint occurred at 0.5 ha when approximately half the frogs stayed. Environmental conditions in larger tree patches were apparently favorable enough to induce the amphibians to stay rather than venture into the clear-cut, with its high temperature extremes, low soil and littoral moisture, high ultraviolet radiation, and stronger winds (Chen et al. 1992, Chen et al. 1995, Zheng et al. 2000). Amphibians were also likely protected from the typically elevated mortality rates in the matrix (Zug and Zug 1979, Rothermel and Semlitsch 2002). However, frogs left even the largest tree patch (2.76 ha), perhaps because edge effects can penetrate >100 m into the forest (Chen et al. 1992) and a 2.76-ha circular tree patch has only a 94-m radius. Tree patches of the size range examined in this study (0.07–2.76 ha) and that are typical of variable-retention operations may not harbor interior forest conditions, especially if they are long and narrow with a high perimeter to area ratio. On the other hand, the depth of edge effects can be extremely variable depending on aspect, climatic conditions (Chen et al. 1995), stand characteristics, and the type of forest and ecotone (Chen et al. 1992). Moreover, the strongest effects may be confined to the first 20–50 m (Young and Mitchell

1994, Mesquita et al. 1999). If the most important edge effects extended 30 m, a 0.5-ha circular patch would have an interior core measuring 20 m in diameter, whereas a 1-ha patch would have an interior core measuring 113 m in diameter.

Stream occurrence also contributed to the value of residual tree patches as temporary refugia for frogs. These results concur with the cooling and moistening power of small streams reported by Brosfoske et al. (1997), who found that 2-m- to 4-m-wide streams in Douglas-fir and western hemlock forests affected the microclimate for 31–62 m on either side. The persistence of frogs in patches with streams underscores the importance of wetlands and riparian areas in dictating the occurrence and diversity of amphibians (Findlay and Houlihan 1997, Kolozsvary and Swihart 1999). The similar positive response of birds and mammals (Doyle 1990) to riparian areas increases the justification for creating residual tree patches around streams, as the benefits are not limited to amphibians and extend to a broad range of other taxa.

The harvest strategy for increasing the permeability of cut blocks to amphibians must balance the trade-off between patch size and distance between patches. Numerous small tree patches reduce the interpatch distance but are less likely than bigger patches to attract amphibians or be used as a stopover as frogs move through the harvested matrix. Larger tree patches at the same retention level are more effective in attracting close-by amphibians and in providing temporary habitat, but they may be spaced too far apart to be systematically intercepted by amphibians moving through the matrix.

An interpatch distance that is short enough to consistently draw amphibians to the patch is not attainable, however, because selective movement towards the averaged-sized patch in the study did not occur >20 m away from the patch. This interstitial distance is not only operationally untenable, but it can only be achieved for the 0.1-ha patch size at retention levels $\leq 40\%$. Conversely, tree patches ≥ 0.8 ha will attract frogs from 50 m away, are operationally tenable, and can be attained for the 0.5-ha, 1-ha, and 1.5-ha patch sizes at ≥ 2 retention levels $\leq 40\%$.

The optimal patch size is, therefore, between 0.8 ha and 1.5 ha. Within this range, a balance is struck between the probability of intercepting the patch and the value of the patch as a temporary refuge. The optimal patch size will vary, however, with the presence of a stream, which increases the effective patch size. The optimal patch size will also depend on economic and operational considerations, with harvesting costs being higher for numerous small patches than for a few large ones with the same total area. Finally, the optimal patch size will depend on the climate. The ability of amphibians to negotiate cut-over areas is highly weather dependent, with the permeability of the cut matrix declining from 71.7% at 8° C to 0% at 40° C (Chan-McLeod 2003). In contrast, rain increases the odds of amphibians moving into harvested cut blocks by 1.2 for each mm increase in daily rainfall (Chan-McLeod 2003).

Thus, management prescriptions for hot and dry regions should emphasize a reduction in interpatch distance, whereas those for cooler and wetter regions should emphasize a bigger patch sizes.

This study provides evidence that red-legged frogs can benefit from residual trees and corroborates previous results that show a positive amphibian response to partial harvesting in stream buffers (Perkins and Hunter 2006). However, our conclusions contradict those of Knapp et al. (2003), who found that 4 partial canopy removal treatments resulted in salamander abundances that were comparable to those in clear cuts and lower than those in old growth. The contradictory results suggest that amphibians may accept residual tree patches as habitat, but the overall population declines, either because amphibians stay only briefly, or numbers decline in correlation with the harvested area (Lehmkuhl et al. 1999). Alternatively, the contradictory results may be scale-related, as the 2-ha treatment units in Knapp et al. (2003) were smaller than some of the individual tree patches in this study. Given that fewer than half the amphibians are expected to stay in tree patches <0.5 ha in size, it is unlikely that the 2-ha treatment units accommodated undisturbed areas that were big enough to be attractive to amphibians. The decline in salamander abundance reported by Harpole and Haas (1999) following leave-tree harvesting can similarly be attributed in part to the dispersed retention of single trees, which did not provide acceptable habitat for amphibians.

The benefits of residual tree patches for amphibians augment the benefits previously documented for birds (Merrill et al. 1998, Beese and Bryant 1999, Schieck et al. 2000, Tittler et al. 2001) and mammals (Moses and Boutin 2001, Sullivan and Sullivan 2001, Hogberg et al. 2002). Cross-taxa management is facilitated by the parallel response in herptile, avian, and small mammal species, with all 3 taxa favoring an aggregated dispersion pattern for leave trees (Merrill et al. 1998, Chambers et al. 1999, Schieck et al. 2000, Sullivan and Sullivan 2001, Tittler et al. 2001). The positive relationship between patch size and proportion of frogs staying in the patch corresponded to the positive benefit of increasing patch size for birds (Schieck et al. 2000). Merrill's (1994) recommended minimum patch size of 0.8 ha for birds agreed closely with our recommended patch size of 0.8–1.5 ha for amphibians. Schieck et al. (1995) concurred that there were no incremental benefits to patches >4 ha.

Residual tree patches likely improved landscape connectivity for amphibians even though they were encountered on a primarily accidental basis. The maintenance of a terrestrial habitat network is vital to the conservation of aquatic-breeding amphibians (Pope et al. 2000, Marsh and Trenham 2001, Wilson and Dorcas 2003) and the importance of landscape composition and configuration for amphibian distribution and species richness have been convincingly documented for a growing assemblage of species and regions (e.g., Findlay and Houlihan 1997, Kolozsvary and Swihart 1999, Joly et al. 2001, Guerry and Hunter 2002).

Conservation strategies that focus exclusively on buffer zones around breeding ponds or riparian areas will likely fail unless coupled with serious consideration of the terrestrial habitat (Dodd and Cade 1998, Wilson and Dorcas 2003). Residual tree patches located on high-order streams or creeks augment the tree buffers that are mandated for much larger riparian areas. Both wet and dry patches provide terrestrial linkages over a bigger area and in more directions than solid corridors with the same area. This is beneficial because movement orientations of dispersing amphibians can be multi-directional and vary with species and year (Dodd and Cade 1998).

A limitation of this study is that longer term use of residual tree patches was not investigated. Currently, there is only limited, circumstantial evidence to support the long-term and over-winter use of residual tree patches by anurans (Chan-McLeod and Wheeldon 2004). Future research should address the long-term use of such patches by amphibians and the comparative value of such patches to undisturbed forest of the same area.

MANAGEMENT IMPLICATIONS

Variable-retention harvesting can benefit amphibians by providing temporary refugia for moving animals. Our results indicate that residual trees should be retained in groups and not as individual, scattered trees. Residual tree patches should be between 0.8 ha and 1.5 ha and retention levels should be $\geq 25\%$ to create acceptable distances between patches. Residual tree patches should be located in areas with wet streams or at least where the neighboring stream density is high. Because there is an excellent potential for cross-taxa management, harvesting strategies should consider integrating multi-taxa objectives from the onset.

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