Movement behaviour of adult western toads in a fragmented, forest landscape

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Abstract

Habitat loss and fragmentation are among the best documented explanations for the dramatic declines amphibians are experiencing globally. The western toad (*Bufo boreas*) is an IUCN red-listed species whose distribution range has been significantly affected by habitat modification. Our objective was to determine how forest fragmentation affects western toad movement behaviour. We used radio-telemetry to follow daily movement patterns of 23 adult male toads in a fragmented landscape near Vancouver, Canada, composed of forest patches and small, recent clear-cuts. Movement parameters were analysed using a Geographic Information System and mixed effects models. Results showed that toads in forests were able to perceive clear-cut edges from as far as 150 m. Greater than 60% of toads released in forest patches chose to enter the clear-cuts from adjacent forests, indicating high boundary permeability. In addition, toad movement parameters were not significantly reduced in these disturbed environments, suggesting that clear-cuts do not restrict movement. Although toads appeared to favour these disturbed environments, further research is required in larger, more industrial-size clear-cuts. The results of this research suggest that the western toad may not be negatively affected by small-scale forest harvesting at our latitude.

Keywords

Fragmented landscapes, *Bufo boreas*, perception ability, boundary permeability, landscape connectivity, patch resistance.

Introduction

As the human footprint continues to expand around the world, habitat loss and fragmentation continue to increase (Vitousek et al. 1997; Sanderson et al. 2002). The resulting landscape is patchy, with areas of suitable habitat isolated by areas of less suitable habitat, known as the 'matrix'. In order to persist, species must disperse between suitable areas and recolonise patches following local extinctions (Fahrig and Merriam 1994). The connectivity between suitable patches has major implications for population viability, since the probability of local extinction commonly increases with the extent of fragmentation, degree of isolation, and limitations on dispersal (Fahrig 2002; Stevens et al. 2004). Alterations to landscapes that modify or restrict organism movement may have negative consequences on population persistence (Fahrig and Merriam 1994; Fahrig 2003).

Metapopulation theory is commonly applied to model populations in altered and fragmented landscapes (Hanski and Gilpin 1997). A key to this metapopulation framework is an organism's ability to move through the matrix, which will be a result of the interaction between the landscape structure and the organism's movement behaviour (Goodwin and Fahrig 2002). Three major components will determine if an organism can successfully persist in these disturbed landscapes and thus how severely they will be affected by habitat fragmentation. First, an individual's capability of perceiving suitable habitat patches (Zollner and Lima 1997). Second, the individual must be able to cross the boundary between two landscape types, known as boundary permeability (Stamps et al. 1987; Stevens et al. 2006). Thirdly, the matrix habitat can facilitate or impede an individual’s movement, referred to as landscape connectivity or patch resistance (Taylor et al. 1993; Stevens et al. 2006). However, all habitats are not equivalent and the influence of the matrix will often be species-specific (Ricketts 2001; Stevens et al. 2004). Understanding how specific organisms move through fragmented landscapes is crucial for both species conservation and theory development (Berggren et al. 2002; Stevens et al. 2004).

Maintaining connectivity between remnant habitat patches is especially vital for amphibians, since many amphibian species exist in metapopulations which rely on successful dispersal for persistence (Gill 1978; Marsh and Trenham 2001). At a landscape scale, individual amphibians can move between ponds, whereas at the local scale, dispersal between critical habitat elements (aquatic and forest) plays a crucial role in amphibian life histories (Rothermel 2004). Restriction of these movements would have dire consequences for both local amphibian subpopulations and the overall maintenance of regional populations (Hecnar and M’Closkey 1996; Cushman 2006). The effects of landscape connectivity and matrix permeability has been studied in insects (e.g. Goodwin and Fahrig 2002; Haynes and Cronin 2006), birds (e.g. Bélisle and St. Clair 2002; Castellón and Sieving 2006) and small mammals (e.g. Bowman and Fahrig 2002; Selonen and Hanski 2003). However, studies involving amphibians are scarce (e.g., Stevens et al. 2004; Stevens et al. 2006; Rittenhouse and Semlitsch 2006).

In the Pacific Northwest of North America, a significant portion of habitat fragmentation occurs through forest harvesting, including clear-cut logging and associated forest practices (such as road creation). Clear-cut logging results in major modifications to habitat, yet little is known of how clear-cuts impact movement patterns on a landscape scale (Pawson et al. 2006). Changes in both the abiotic environment and biotic communities can be dramatic following clear-cutting. Clear-cuts are often hostile environments for amphibians and many species are negatively impacted by this land-use practice (Knapp et al. 2003). Despite this, little research has focused on the consequences of fragmentation caused by forest harvesting on amphibians.

In this study we investigated the impacts of forest fragmentation on movement patterns in a generalist amphibian, the western toad, *Bufo boreas*. We used translocation and radio-telemetry to examine individual movement behaviour within patches of forested habitat and recent clear-cuts (or matrix - terms used interchangeably). We tested three main hypotheses. (1) Given that toads have the ability to orient themselves towards vital habitats, such as natal breeding ponds, we hypothesised that toads will be able to perceive suitable patches from within non-suitable patches. To test this, we looked at initial movement directions for evidence of strong affinities towards specific habitat types. (2) Habitat boundaries are permeable, and as an indicator of forest/clear-cut boundary permeability, we examined the ability of toads to cross this habitat edge. (3) Given the complexity and potential inhospitability of recent clear-cuts, we hypothesised that this matrix habitat would restrict toad movement through the landscape and we expected toads to avoid these environments. This study compared movement patterns between habitat types and patch exit time as indicators of landscape resistance.

Methods

Study Species

The western toad is distributed throughout western North America ranging from Baja California to southeastern Alaska (Stebbins 1985). *Bufo boreas* is a generalist species, common in a variety of habitats including forests, wetlands, open meadows and occasionally in disturbed areas such as clear-cuts, ditches and gravel pits (Wind and Dupuis 2002; Bartelt et al. 2004). Breeding occurs in the spring when toads congregate along the shallow margins of small water bodies. Western toads are highly philopatric and considered explosive breeders, with females laying an average of 12,000 eggs in less than a week (Olson et al. 1986). Toads are known to travel long distances, primarily by climbing and crawling - dispersal distances of up to 7.2 km from the breeding site have been recorded and home ranges vary between 0.1 ha and 4 ha, depending on habitat condition (Davis 2000; Muths 2003; Bartelt et al. 2004). Bartelt et al. (2004) and Muths (2003) found that female toads moved up to 2.6 times further than males (May to October), with greatest distances for males around 0.94 km and females 2.44 km from the breeding pond.

Recently, western toads have declined dramatically throughout much of their range in the United States and although they appear to be faring well in Canada, they have been listed as Near Threatened on the IUCN red-list of threatened species (Carey 1993; Fisher and Shaffer 1996; Hammerson et al. 2004; Muths and Nanjappa 2005). Declines have been primarily associated with disease (largely chytridiomycosis), UV radiation and habitat loss (e.g. Carey 1993; Muths et al. 2003; Hammerson et al. 2004). However, evidence for the impacts of fragmentation on movement dynamics in this species remains scarce and studies looking at the effects of forestry practices are nonexistent.

Study Sites

This study was conducted from May to June 2006 in the University of British Columbia’s Malcolm Knapp Research Forest (49° 16’ N, 122° 34’ W), approximately 60 km east of Vancouver, British Columbia, within the Coastal Western Hemlock biogeoclimatic zone. The research forest is highly fragmented and contains patches of various habitats, including second growth forest and recent clear-cuts. Four study patches were selected as release sites for this translocation experiment (Figure 1), two forested patches (Maple Ridge Forest (2.87 ha) and Wood Lot Forest (4.91 ha)) and two recently harvested patches (CC03 (3.06 ha) and CC05 (3.23 ha)). The two forest patches were second growth forest (>70 years) composed primarily of Western hemlock (*Tsuga heterophylla*), along with Douglas-fir (*Pseudotsuga menziesii*) and Western red cedar (*Thuja plicata*), with an understory of Salmonberry (*Rubus spectabilis*) and ferns (primarily Sword fern, *Polystichum munitum*). The two clear-cut patches were less than 3 years old and vegetation consisted primarily of young Red alder (*Alnus rubra*) and invasive Himalayan blackberry (*Rubus discolor*). Slash from both sites had been piled along the western and southern edges of the patches. The four patches were surrounded by continuous forest, except to the north of patch CC05. This area was fragmented by a hydroline right-of-way and other clear-cut patches. In addition, there were numerous forest roads in the area and the forest gradually increased in elevation to the north.

Radio-telemetry

Thirty-two male toads were captured from Edith Lake near Squamish, British Columbia (49° 46’ N, 123° 06 W) and transported in individual containers to the MKRF. Toads were kept in large plastic containers containing moss, natural cover objects and water bowls, and fed crickets. All toads were measured with calipers (snout-to-vent length) and weighed using a field scale, then fitted with radio-transmitters (BD-2G, Holohil Inc, Carp, ON) attached with polyethylene belts. The harnesses were constructed and attached using a method devised by Bartelt and Peterson (2000), who found little impact on toad behaviour. A Telonics TR-4 receiver and Yagi directional antenna were used to locate toads every 1-3 days. A Garmin GPSMap60CSx was used to obtain toad locations to within 3 m accuracy in the clear-cuts and with < 5 m error in the forests. At each location, 100 measurements were taken and the average was used to obtain a position in lat/long WGS 84.

All toads were tested for the chytrid fungus, *Batrachochytrium dendrobatidis*, before their introduction into the MKRF and only toads that did not test positive were used in this study (23 of 32 toads) (Deguise and Richardson in press). The twenty-three toads were randomly assigned to sites (n = 6 for the Wood Lot, CC03 and CC05 sites and n = 5 for the Maple Ridge site) and released one meter from each other along a north-south transect. Individual toads were placed in a bucket that was then flipped carefully up side down at the release site. Toads were given 2 minutes to adjust and then the bucket was removed using a long string from at least 2 m away to minimise disturbance to the toads. Initial headings were recorded for each individual, along with GPS coordinates and habitat descriptions. All toads were given one full day to acclimatise to their new environments before radio-tracking began. The position of every toad was determined every 1 to 3 days for a total of three weeks (trial 1). At the end of three weeks, all toads were captured and returned to the same enclosures. This time frame was decided upon after some of the toads started to travel long distances into difficult terrain or through areas with active logging. Toads were kept in captivity for two nights, after which they were randomly assigned to one of the two sites of the opposite treatment and released using the same procedures as described above. Once again, toads were given one day to acclimatise and then their positions were determined every 1 to 3 days for another three weeks (trial 2). At the end of the study, all remaining toads were collected from the research forest and returned to their breeding site. Conducting two experimental trials increased our overall sample size and determined whether movement patterns were related to initial starting habitat. During this study, five toads were lost but all of their radio-transmitters were recovered and three of those had evidence of chewing, presumably from predators. Data points for these individuals were truncated to the last confirmed sighting of the toads.

GIS Analysis of Movement Paths

All GPS data were imported into ArcMap (Environmental Systems Research Institute [ESRI] 2005) and projected into UTM Zone 10N. The straight-line distance between each toad location was deemed a step length and the joining of each step length formed the movement path. Using Hawth's Analysis Tools for ArcGIS (Beyer 2004), I extracted step lengths, total distances, turning angles and net displacements from each toad movement path. Only turning angles associated with step lengths greater than 5 m were used in the analyses. Step lengths smaller than 5 m have high errors associated with their turning angles and cannot be accurately associated with movement events due to limitations of GPS accuracy (Jerde and Visscher 2005). Since the number of days between toad relocations differed, measurements of total distance were divided by the number of days a toad was tracked, which provided an estimate of movement rate in meters per day.

Given that the majority of toads left their initial release patches and moved in different habitat types, movement paths had to be divided by their occurrence in three habitat classes (forest, matrix and road) before we could analyse the effects of habitat type on movement patterns (Turchin 1998; Goodwin and Fahrig 2002). Forest habitat was classified as areas with a closed canopy and trees greater than 15 m in height (see previous forest site descriptions for more detail). Roads in the Malcolm Knapp Research Forest are all gravel and single lane with ditches on either side. Matrix habitat was defined as any area that had experienced a recent disturbance and had vegetation no higher than 5 m. The majority of this habitat consisted of clear-cut patches, including the two clear-cut sites used as release patches in this study. An additional 7.8% of toad movement locations occurred in areas that could not clearly be classified as forest, clear-cut or road. All of these ambiguous observations occurred in a hydroline right-of-way, which was last cleared in 2003 and contained primarily shrubs and young willow trees. Due to the small number of locations in this area, we grouped them with locations in clear-cuts (matrix habitats) to minimise the division of movement paths. For each movement path in each of the three habitat types, we measured movement rate (calculated as meters moved per day), maximum single movement (the largest movement made over a single two day period) and net displacement (straight-line distance between the release point and final recapture point). When possible, we also extracted the mean vector length, r, a measure of the straightness of the movement path, where an r value of 1 indicates a completely straight line.

Weather Data

Data for daily precipitation and air temperatures were taken from a meteorological station located at the entrance of the Malcolm Knapp Research Forest, approximately 1 km NW from the study site.

Statistical Analysis

Movement Patterns

Circular statistics were used to calculate mean angles for each toad movement path and overall directionality. Rayleigh's test was used to determine if toad movement directions were statistically different from random (Batschelet 1981). A modified version of Rayleigh's test, the V-test, was used to test whether initial movement angles of toads released in forest patches were oriented towards the clear-cuts. This test provides increased power by specifying a hypothetical direction and determining if observed angles are statistically clustered around this hypothesised angle (Batschelet 1981; Zollner 2000). In our case, this presumed direction was the mean angle towards the clear-cuts from the forest patches (Maple Ridge = 0º, Wood Lot = 90º, Figure 1). Watson's U^2 test was used to compare directions between toads in the two trials.

We analysed the differences in movement patterns of toads in the three habitat types (forest, matrix and road) as separate, mixed-effects models for each of the three dependent variables: movement rate, maximum single movement and net displacement (all log transformed to meet assumptions of normality). Using mixed effects models allowed us to analyse the two trials together since these models accommodate correlated error structures associated with non-independence of data points that exist not only between repeated measurements of movement for individual toads but also between the two trials (Buckley et al. 2003). Habitat type was included as a fixed effect in the model, while trial was included as a random effect. The effect of individual toads was incorporated in the error term. To account for the repeated measures used in this experiment and the unequal time spacing, we specified a SP(POW) spatial power covariance matrix structure (SAS ver. 9.0, SAS Institute Inc., Cary, NC). However, certain assumptions had to be made given that every toad was not in the experiment for the same duration, nor did every toad participate in a second trial. Likelihood ratio tests were used to test the significance of the random factor (differences between the two experimental trials). Bonferroni corrections were made to adjust for multiple comparison tests. We ensured that the assumptions of normality and equal variance were met by examining fixed-effect residuals from each model using normal probability plots and residual versus predicted plots.

Simple linear regression was used to test whether toad movement behaviour was related to the change in mass of an individual toad within each trial (mass at completion of trial – mass upon release into trial) and multiple regression was used to compare daily average distances to mean air temperature and precipitation in the preceding 48 hours. Distance data for the multiple regression were cube-root transformed to meet assumptions of normality and equal variance of residuals. Paired t-tests were used to compare the proportion of time (arcsine, square root-transformed) spent in forest and matrix habitats. Only toads that completed the trials were included in these analyses.

Days to Exit Release Patches

Translocating toads into forest and clear-cut patches was performed to assess the ability of toads to move through these habitats. Comparing the number of days it took for a toad to exit these patches gives an indication of an individual’s ability to move and in turn, provides information on the potential resistance of the landscape to movement (Castellón and Sieving 2006). To test the hypothesis that the number of days to exit a release patch differed between the treatments, we also used mixed models. We looked for significant differences in the days to exit release patches between the two trials and between the two treatments within trials. The same models were used as described in the previous section with days to exit the habitat as the response variable.

Cox's regression was used to compare exit times from release patches between the two treatments. This type of regression is appropriate for any "time to event" analysis, in our case, days before exiting the release patch (Castellón and Sieving 2006). Habitat type was used as an independent class variable, along with three other landscape variables that were predicted to influence exit times: patch size, distance to the nearest edge and percent forest cover in a 100 m radius around the release site. The two experimental trials were analysed separately to maintain the assumption of independence between data points. Before conducting the analyses, Spearman rank correlations were calculated to verify that none of the predictor variables were strongly correlated ($r > 0.7$).

All circular statistics were performed using R v 2.2.1 (CircStats package, copyright 2005, The R Foundation for Statistical Computing). Mixed effect models (PROC MIXED) and Cox's regression (PROC TPHREG) were conducted in SAS v 9.0 (SAS Institute, Cary, USA) and all other analyses were done in S-PLUS (Insightful Corp., Seattle, USA).

Results

Twenty-three toads were initially translocated to the Malcolm Knapp Research Forest where a total of 474 locations were recorded. Toads were radio-tracked for an average of 21.26 ± 0.1 (SE) days in trial 1 and for 17.61 ± 1.3 days in trial 2. Toads ranged in size from 72.1 to 95.9 mm (mean ± SE = 83.83 mm ± 1.2) and body mass ranged from 40.62 to 103.3 g. The mean body mass of the toads upon release into their respective treatments was 65.31 g ± 2.97 for trial 1 and 60.11 g ± 3.46 for trial 2. Upon capture and removal from the experiment, the average mass was 60.98 g ± 3.34 for trial 1 and 65.74 g ± 3.98 for trial 2.

Movement Patterns

Toads spent proportionately more time in matrix habitat (mean ± SE = 0.64 ± 0.05 days) than in forested habitat (0.36 ± 0.05 days). The same pattern emerged when the two trials were analysed separately, yet these differences were not significant in trial 1 (paired t = -1.414, df = 18, p = 0.174, Figure 2) but were in trial 2 (paired t = -2.4, df = 17, p = 0.028, Figure 2).

Toad movement directions over the entire course of this study were not statistically random ($r = 0.529$, n = 42, $p < 0.001$) and were oriented around a mean angle of 44.84° (circular variance = 0.471). Comparing the two trials, the mean directions were still oriented to the northeast (trial 1: mean = 54.92°, r = 0.487, n = 19, p = 0.007; trial 2: mean = 36.01°, r = 0.653, n = 18, $p < 0.001$; Figure 3) and these directions were not statistically different ($U^2 = 0.089$, n = 42, $p > 0.05$).

Initial post-release movement directions (first 5 days) for toads released in the forest sites were statistically oriented towards the clear-cuts (Maple Ridge site: mean direction = 44.25°, r = 0.412, n = 9, p = 0.04; Wood Lot site: mean = 76.77°, r = 0.548, n = 10, p = 0.006; Figure 4). Within clear-cut sites, Rayleigh’s test showed that initial movements were not statistically different from random (CC03: mean = 26.04°, r =

0.246, n = 9, p = 0.593; CC05: mean = 23.62°, r = 0.316, n =10, p = 0.379; Figure 4). For these initial directions, movement was more linear in forest sites (mean vector length *r* = 0.512, n = 19) than in the clear-cut sites (*r* = 0.282, n = 19).

Irrespective of habitat type and trial, the greatest movement rate by an individual was 121 m/day and the lowest was 3 m/day (during one trial). For all toads, most bouts of movement were between 0 and 40 m/day (Figure 5). One individual moved a total of 1999 m over 19 days whereas another only moved 65 m in 21 days. The highest single movement event in a period of approximately 24 hours was 982 m. The largest net displacement by a single toad was 1482 m and the smallest was 17 m.

Averages of movement rate, maximum single movement and net displacement were all higher in forest habitat (33.72 m ± 12.11, 150.34 m ± 28.95, 209.23 m ± 39.41, respectively) than in matrix habitat (20.19 m ± 4.1 and 134.57 m ± 27.13, 187.03 m ± 39.74, respectively, Figure 6). These differences were not significantly different for maximum single movement ($F_{1,15}$ = 2.91, p = 0.109) and for net displacement ($F_{1,15}$ = 2.76, p = 0.118), but they were for movement rate ($F_{1,15}$ = 5.46, p = 0.034). However, for 9 of 43 (21%) toad movement paths, a portion of the path occurred on forest roads. The average movement rate (126.8 m ± 48.58), average maximum single movement (375.73 m ± 98.31) and average net displacement (431.94 m ± 106.51) on roads were all higher than those in forest and matrix habitat (Figure 6). Movement rate and maximum single movement differed significantly between matrix and roads but not for net displacement (Table 1). Differences between forest and road were not statistically different for maximum single movement and net displacement, but there was a difference in movement rate (Table 1). In all cases, there was no significant difference between the two trials (movement rate: $F_{1,37} = 3.40$, $p = 0.073$; max single move: $F_{1,37} = 1.08$, $p = 0.306$; net displacement: $F_{1,37} = 0.83$, $p = 0.368$).

Toad movement patterns were not associated with body size or climate. There was no relationship between daily movement rates and the change in body mass of individual toads (trial 1: $R^2 = 0.078$, $F_{1,17} = 1.453$, $p = 0.245$; trial 2: $R^2 = 0.165$, $F_{1,16} = 3.154$, $p = 0.095$). Daily movement was also unrelated to both temperature and precipitation in the preceding 48 hours ($R^2 = 0.035$, $F_{2,35} = 0.628$, $p = 0.539$).

Days to Exit Release Patches

Of the 23 toads initially released, 20 were followed for the duration of the first trial, of which 15 (75%) left their release patches and dispersed into the surrounding landscape. In trial 2, 18 toads completed the experiment, of which 17 (94.4%) dispersed from their initial patches. Over both trials, mean (± SE) time to exit the release patch was longer in the clear-cut treatment (11.38 days ± 1.92) than in the forest treatment (5.53 days ± 1.2) and this difference was statistically significant ($F_{1,15} = 18.34$, df = 15, $p < 0.001$, Figure 7). These patterns were consistent in both trial 1 (clear-cut = 17.11 days ± 1.68, forest = 7.5 days ± 2.03) and trial 2 (clear-cut = 5.4 days ± 2.05, forest = 3.33 days ± 0.75). Within trial 1, there was a significant difference in times to exit between the two treatments ($F_{1,17} = 12.93$, $p = 0.002$, Figure 7) but not in the second trial ($F_{1,16} = 0.94$, $p = 0.347$, Figure 7).

Spearman rank correlations found a significant negative association between habitat type and the percent forest cover in a 100 m radius of area around each site ($r = -0.89$, $p < 0.001$), so the forest cover variable was dropped from the models. All other correlations were not strongly associated with habitat type ($r < 0.7$). Cox's regression showed that the habitat type of the release patch (forest or clear-cut) was a significant predictor of time to exit the patch in trial 1 (Wald $X^2 = 8.92$, $p = 0.003$) but not in trial 2 (Wald $X^2 = 0.719$ $p = 0.396$). Patch area was also significant in predicting time to exit in trial 1 ($X^2 = 7.19$ $p = 0.007$) but the nearest edge was not ($X^2 = 2.15$ $p = 0.142$). In trial 2, none of the predictor variables were significant in predicting time to exit.

Discussion

Overall, these results indicate that small, recent clear-cuts did not act as movement barriers for adult western toads. Results showed that a toad's perceptual range may reach at least 150 m and that the boundary permeability between forests and clear-cuts was quite high. Movements were not significantly restricted in this matrix habitat and therefore landscape connectivity for the western toad may not be seriously affected by forest harvesting.

Contrary to expectation, adult toads seemed to show an attraction for clear-cuts and actively chose to enter these habitats from neighbouring forested environments. The affinity for clear-cuts was evident by the initial post-release movements of toads in forested sites, in which the majority of toads directed themselves towards the forest/clear-cut edge. Even though the clear-cut sites had slash piles along the forest/clear-cut edges, greater than 60% of toads released in the forest sites did eventually enter the matrix habitat, although this was disproportionate to habitat availability. Thus, we conclude that the permeability of the forest/clear-cut edge was high, despite the possible obstruction by the slash piles. To our knowledge, this is the first study to show that western toads chose to enter and stay in recent clear-cuts (< 5 years), apparently favouring this habitat over adjacent second-growth forests.

Adult toads released in forest sites did not orient themselves at random and we conclude that they could perceive the clear-cut edge from up to 150 m away. However, toads released in clear-cut sites did not orient themselves in a specific direction. Amphibians can orient themselves toward their native ponds (Sinsch 1990; Mazerolle and Desrochers 2005) and towards forested habitat during migratory movements (Rittenhouse and Semlitsch 2006). However, Rothermel (2004) demonstrated that juvenile salamanders did not exhibit target-oriented behaviour, even as close as 5 m to a forest edge. Even though toads in our experiment did show significant orientation towards specific habitat types, we cannot dismiss the possibility of random walk events given the small size of habitat patches.

In terms of landscape resistance, the majority of movement patterns were not significantly reduced in the matrix habitat. Although all movement rates were lower in the matrix than in forested habitat, toads moved through this environment, indicating that the permeability of clear-cuts was relatively high for western toads. If clear-cuts significantly restricted movement rates, we would have expected toads to take much longer to leave these release patches (Castellón and Sieving 2006). Although toads took longer to exit, this was likely due to the toad’s preference for this environment and not an inability to move through the matrix. For both movement rates and the number of days to exit release patches, there were cases where specific toads moved through the matrix at rates equal or faster than those recorded in forested habitats and on roads, providing evidence that lower movement rates and longer exit times in the matrix was not necessarily due to reduced permeability.

Many recent studies have tested movement behaviour in various matrix habitats, with some showing decreased movement ability and others showing no difference, supporting the claim that matrix permeability is species specific (Ricketts 2001). Although few studies have looked at matrix permeability in amphibians, this claim appears to hold true. Similar to our results, Patrick et al. (2006) found that clear-cuts did not present greater resistance and were not significant barriers to juvenile wood frogs (*Rana sylvatica*). Stevens et al. (2004) found that the movement ability of juvenile natterjack toads (*Bufo calamita*) was best on surfaces mimicking sandy soils and roads, whereas performance was poorest in forest environments. On the contrary, Chan-McLeod (2003) found that clear-cuts acted as barriers to movement for adult red-legged frogs (*Rana aurora*). Furthermore, Mazerolle and Desrochers (2005) concluded that anthropogenically-disturbed areas, especially those devoid of cover, increased landscape resistance for adult northern green frogs (*Rana clamitans melanota*) and northern leopard frogs (*Rana pipiens*). However, in our study, toad movement was not significantly inhibited in the matrix habitat and we thus conclude that small, recent clear-cuts provide little resistance to movement and that sandy and gravelled roads facilitated movement.

Forest fragmentation also occurs through road construction and a major by-product of forest harvesting practices is the creation of logging roads to access clear-cuts. Through both direct effects, such as road kill, and indirect effects, like the facilitation of predator movement and ingress of invasive species and diseases, roads are rarely shown to have a positive effect (Forman and Alexander 1998). For amphibians, diversity and abundance is known to decline in relation to proximity to roads (Fahrig et al. 1995; Marsh et al. 2005), even on low traffic and abandoned logging roads (Semlitsch et al.

2007). However, logging roads may serve as movement corridors for toads and assist movement through the landscape. All movement parameters measured in this study were higher on logging roads, suggesting that they were facilitating movement ability, possibly encouraging dispersal and helping maintain connectivity in the landscape. Every toad that encountered a road stayed on or near the road, where they would either bask along its edges and burrow in the ditches, or use the roads to move long distances. The longest movement bouts recorded during this study occurred on roads, including one individual that moved 982 m in approximately 24 hours. Other studies have found that amphibians use ditches for movement and prefer cement substrates when given a choice (Mazerolle 2004; Stevens et al. 2006). In this study, toads were observed using the roadside culverts or verges for movement and not the actual road surface. Since road mortality in toads and other amphibians is generally high (Hels and Buchwald 2001), it is uncertain whether the risk of mortality would outweigh the benefits of increased movement through landscapes and better connectivity between populations.

Although the western toad is often thought of as a forest-associated species, it has been found in a variety of habitats (Bartelt 2000; Davis 2000). Most toad species are known to bask and burrow in sandy soils. Recent clear-cuts may potentially present a very suitable environment for this species, with ample sunlight, sandy soils, many potential refugia, and a high abundance of invertebrates (Niemela et al. 1993; Pawson et al. 2006). Davis (2000) found that adult toads seemed to prefer young regenerating forests created by logging (~10-15 years) to closed canopy forests and Bartelt et al. (2000) found that both males and females selected sites in clear-cuts 10-15 years old. Tocher et al. (1997) found four frog species migrating into and colonising matrix habitats following logging in an Amazonian forest. Other studies have found that certain amphibians do not avoid heavily disturbed areas, such as the California red-legged frog, *Rana draytonii* (Bulger et al. 2003), and American bullfrogs, *Rana catesbeiana* (Patrick et al. 2006). Although toads are less sensitive to desiccation than other amphibians and can tolerate the higher temperatures and lower moisture in clear-cuts (Stebbins and Cohen 1995), we believe clear-cuts may be favourable during the early summer months only. Later in the season, this habitat could potentially be very inhospitable when temperatures are extremely high and there is very little precipitation, resulting in a significant risk of desiccation for toads. A temperature logger placed in a clear-cut site under shade (CC05) for the duration of the study recorded temperatures above 35°C for four consecutive days in July 2006 and study sites received only 44 mm of rain during July and August combined. Davis (2000) did find western toads to be relatively inactive in the dry, late summer, remaining in moist terrestrial microhabitats or in water. Since this study did not follow toads for the duration of the summer and we did not consider physiological states (e.g. dehydration) of toads during their time spent in the clear-cuts, further research is needed before any definitive conclusions can be made in terms of the long-term suitability of clear-cuts for western toads.

Precipitation and temperature are often strong determinants of anuran movement in disturbed landscapes (Mazerolle 2001; Johnston and Frid 2002). However, Rothermel (2004) found that juvenile American toad (*Bufo americanus*) movements were not constrained by rainfall, and we found no relation between adult western toad movements and precipitation or temperature. Several studies have shown that bufonids are more resistant to desiccation, and may therefore have a greater tolerance to the climatic conditions found in recent clear-cuts (Todd and Rothermel 2006).

The majority of studies on the ecological impacts of clear-cut harvesting occur at spatial scales of less than 10 ha (Pawson et al. 2006) and this experiment was no exception. In British Columbia, clear-cuts are on average about 23 ha (BC Market Outreach Network 2004), whereas the clear-cuts used in this study were all less than 5 ha. Toads were able to move 500 m in a couple of days and readily crossed the small clear-cuts used in this study. However, larger clear-cuts typically found in British Columbia may pose a much greater obstacle for toads and would require extended periods of time in this matrix habitat. There is the possibility of a clear-cut threshold size, under which the ecological impacts of clear-cuts are limited (Pawson et al. 2006), yet this has not been investigated. Overall, results at small spatial scales are frequently not applicable at larger scales.

This study suggested that clear-cuts may not be movement barriers to adult western toads and may actually provide suitable habitat for this species. We showed that edge and clear-cut permeability was high and as such, forest fragmentation may not interfere with landscape connectivity. Data on movement abilities in these different habitats can be used to parameterise spatially explicit movement models and metapopulation models. Increased understanding of how disturbed habitats influence movement behaviour, will ultimately lead to better management of the impacts of habitat fragmentation on population persistence.

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Table 1. Summary of the differences in movement behaviours based on least squares means analyses for the three habitat types (forest, matrix, road). Applying a Bonferroni correction for multiple comparisons (3), the significance level is 0.017, shown in bold font.

Response Variable	**Comparison**	**DF**	**t-value**	**p-value**
Movement rate	Forest vs. Matrix	21	2.65	**0.015**
	Forest vs. Road	21	-2.70	**0.014**
	Matrix vs. Road	21	-4.82	**< 0.001**
Maximum single movement	Forest vs. Matrix	21	2.09	0.049
	Forest vs. Road	21	-1.35	0.193
	Matrix vs. Road	21	-2.98	**0.007**
Net displacement	Forest vs. Matrix	21	1.93	0.068
	Forest vs. Road	21	-0.97	0.345
	Matrix vs. Road	21	-2.47	0.022

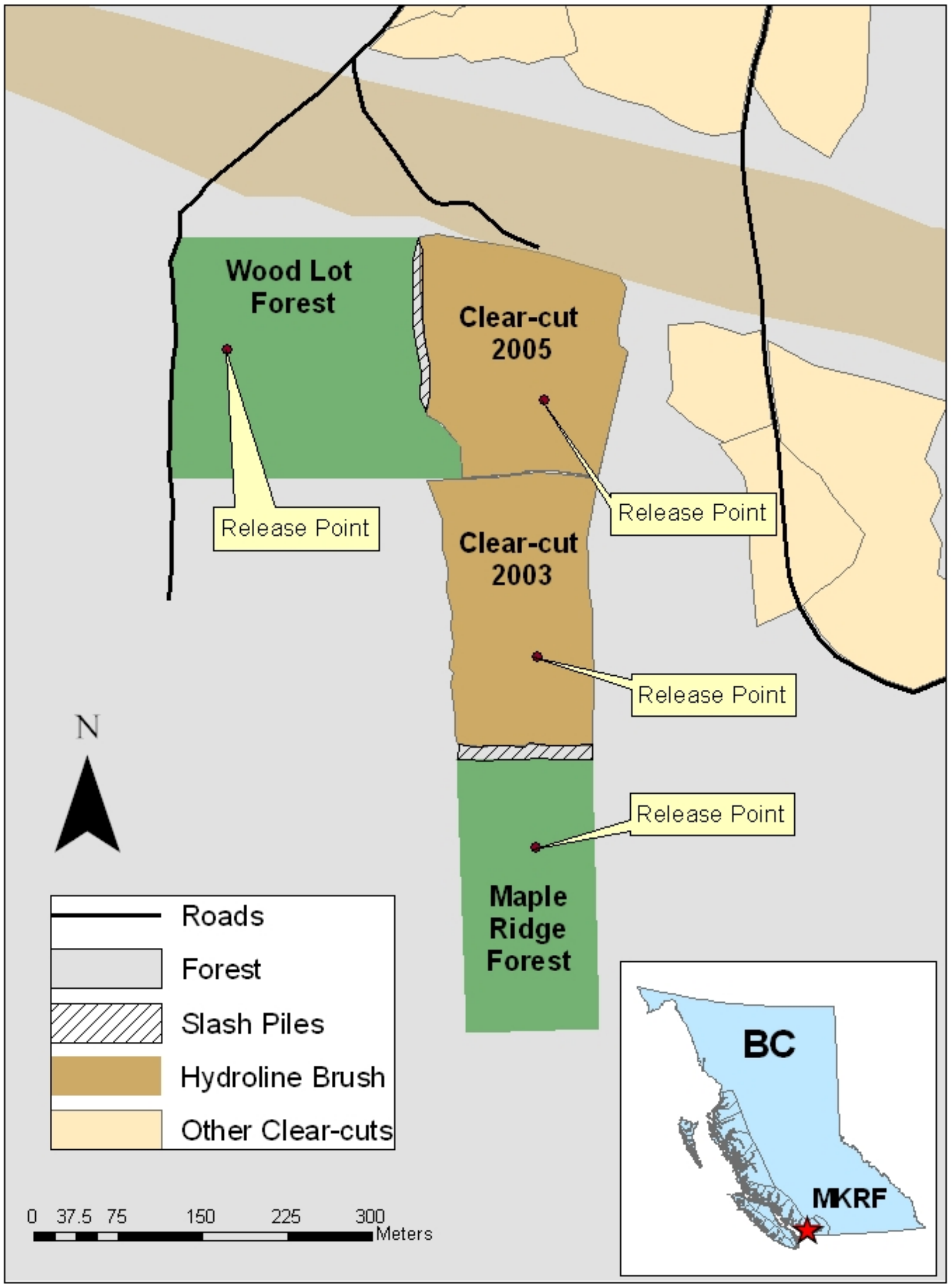

Figure 1. Map of the Malcolm Knapp Research Forest in southwest British Columbia, Canada, showing the location of the four experimental patches and release sites for toads.

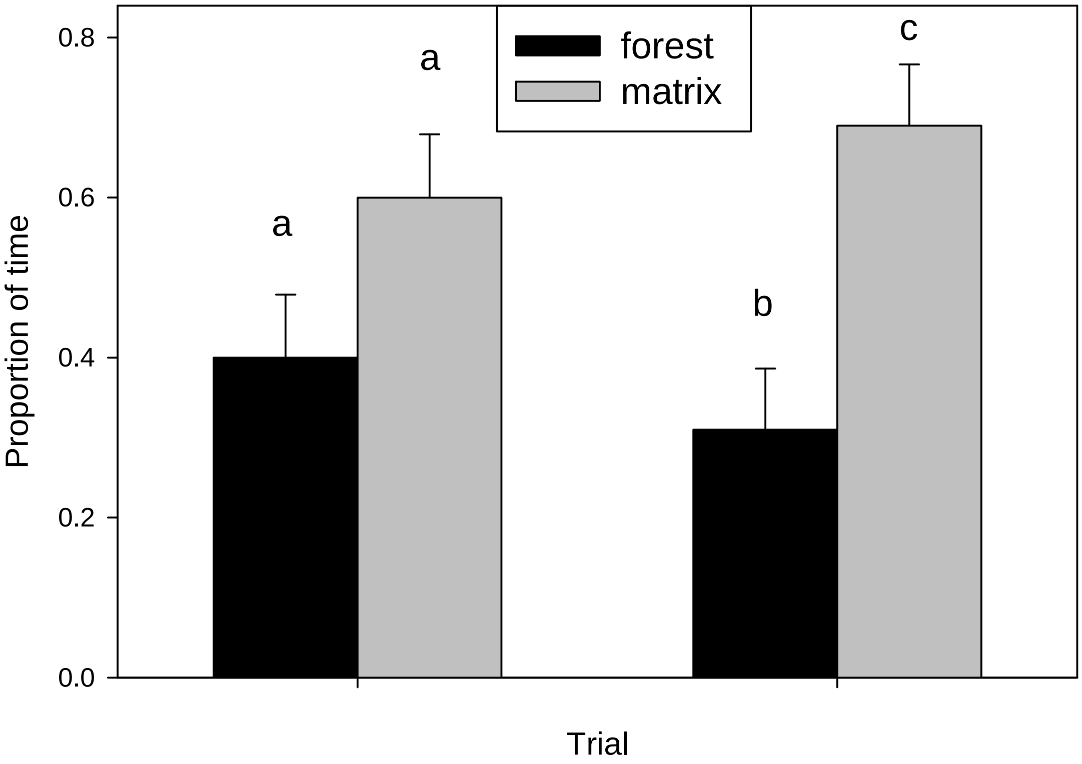

Figure 2. Proportion of time spent by radio-marked toads in the two habitat types in trial 1 (n = 19) and trial 2 (n = 18).

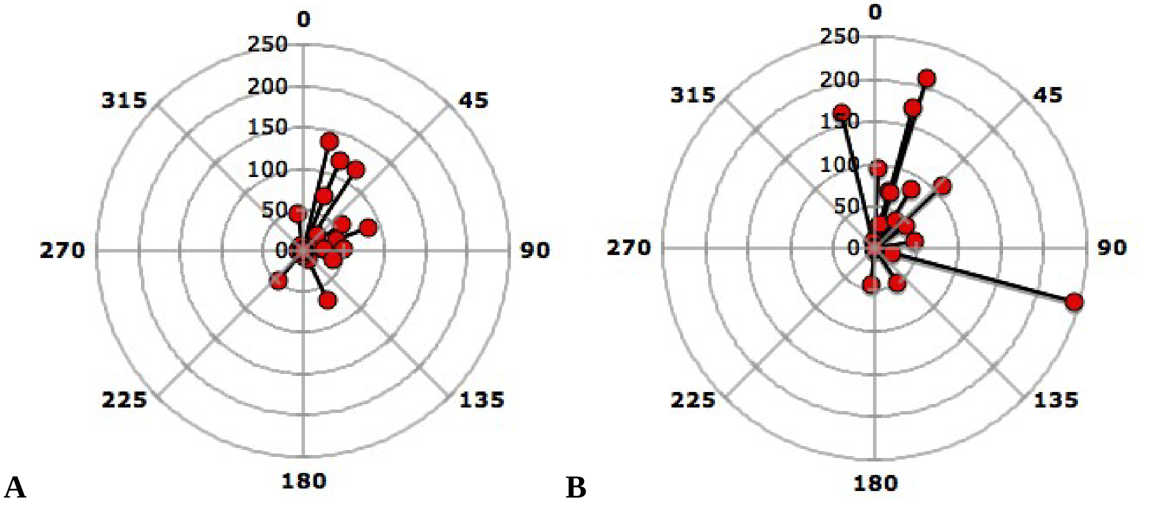

Figure 3. Average daily distances and directions (degrees from North) for toads released in either forests or clear-cuts in trial 1 (A, n = 19) and trial 2 (B, n = 18). Each dot represents an individual toad and lines are the average distance moved from its release point regardless of habitat type.

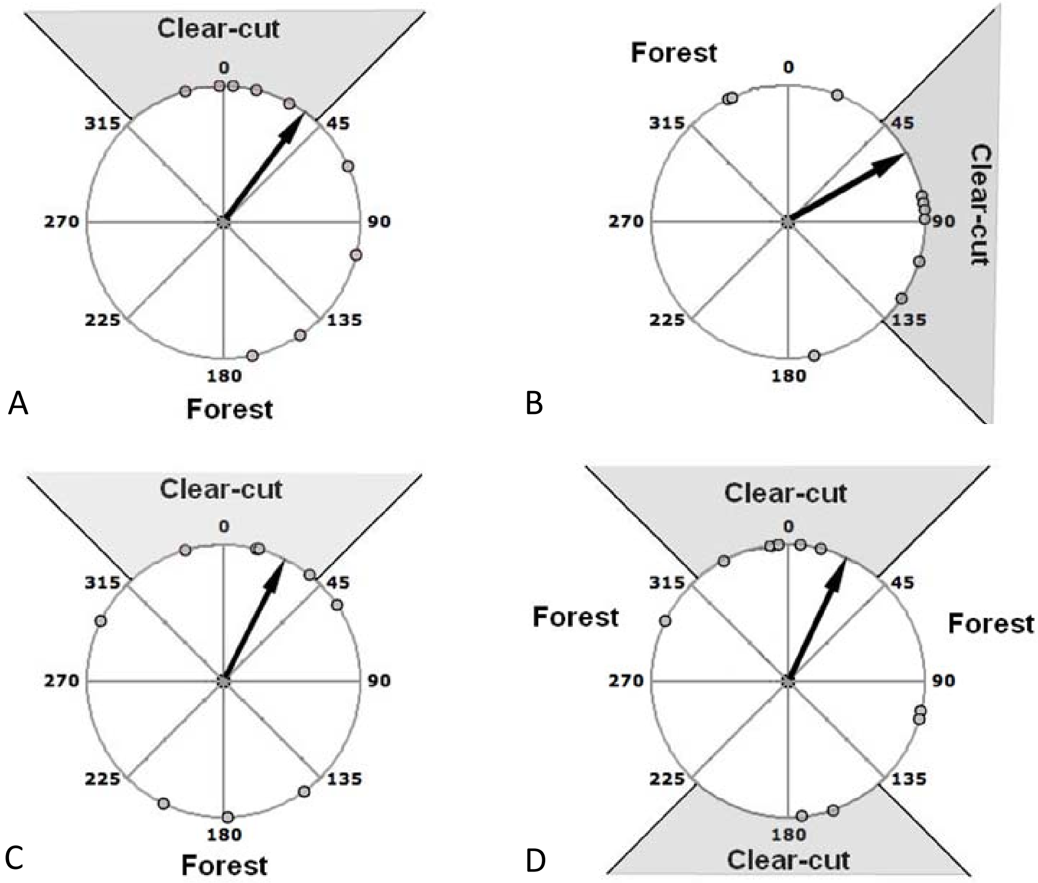

Figure 4. A and B. Initial directions (first 5 days) of toads released in forest sites: A) Maple Ridge (n = 9), B) Wood Lot (n = 10). The centre point represents the release point for individual toads (A = 90 m from edge, B = 150 m from edge) and the arrow represents the mean angles of movement (Maple Ridge = 44.25°, Wood Lot = 76.77°). **C and D.** Initial directions (first 5 days) of toads released in clear-cut sites: C) CC03 (n = 9), D) CC05 (n = 10). The centre point represents the release point for individual toads (C = 60 m from nearest edge, D = 60 m from nearest edge) and the arrow represents the mean angles of movement (CC03 = 26.04°, CC05 = 23.62°).

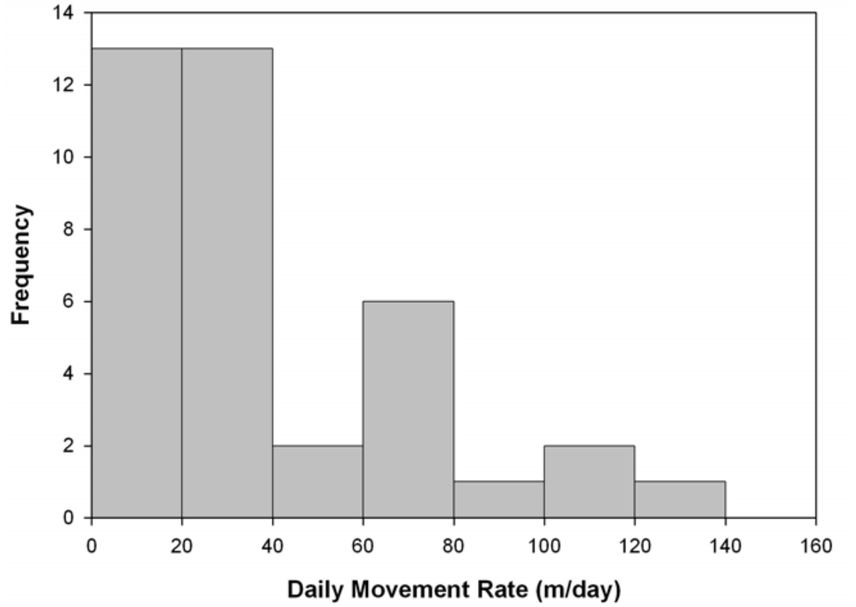

Figure 5. Distribution of average daily movement rates for all toads in the entire experiment (n = 38).

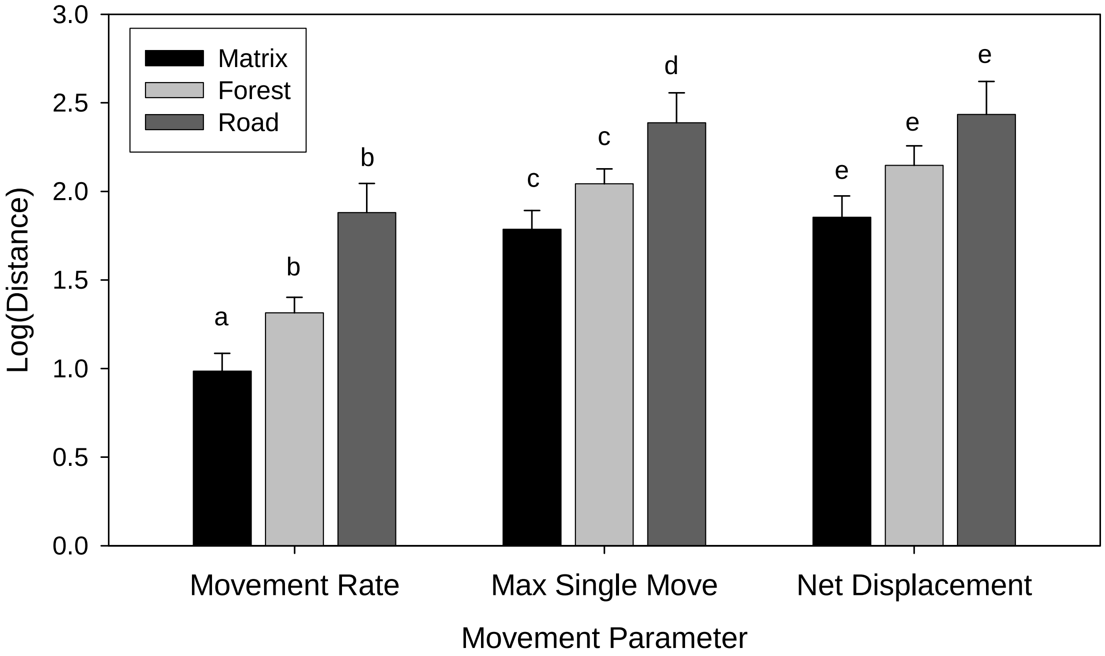

Figure 6. Average movement rate, maximum single movement and net displacement (+ 1 SE) for the three habitat types, matrix (n = 32), forest (n = 20) and road (n = 9). The two experimental trials were combined and data were log transformed. Each movement parameter was analysed separately from the others, so letters represent significant differences within parameters only.

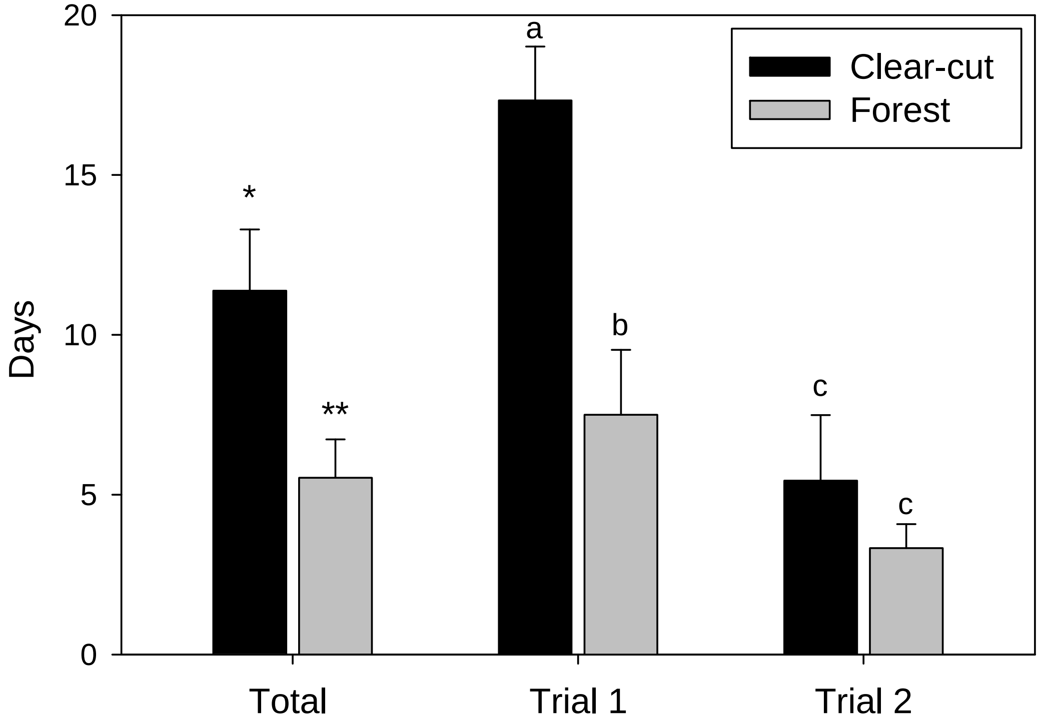

Figure 7. Number of days toads spent in their release patches (trial 1: n = 19, trial 2: n = 18) before dispersing into surrounding landscape (means + 1SE). Data for the two trials were combined (Total) and then analysed separately by trials. Asterisks and letters represent significant differences within each separate analysis.