

# Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity

Brian D. Todd<sup>1\*</sup>†, Thomas M. Luhring,<sup>1</sup> Betsie B. Rothermel<sup>1,2</sup> and J. Whitfield Gibbons<sup>1</sup>

<sup>1</sup>Savannah River Ecology Laboratory, Drawer E, University of Georgia, Aiken, SC 29802, USA; and

<sup>2</sup>Archbold Biological Station, PO Box 2057, Lake Placid, FL 33862, USA

## Summary

1. Habitat loss is a leading cause of global amphibian declines. Forest removal is a particularly significant threat because an estimated 82% of amphibians rely on forests for part of their lives.
2. Biphase amphibians rely on suitable terrestrial habitat to support their post-metamorphic growth and survival and also to maintain appropriate habitat and landscape connectivity.
3. We created 4 replicate, 16-ha experimental arrays in the southeastern USA to examine the effects of forest removal on migratory movements of adult biphase amphibians. Each array contained four forest-harvesting treatments that included an unharvested control, a partially harvested stand, a clearcut with coarse woody debris retained, and a clearcut with coarse woody debris removed.
4. Some amphibian species emigrated from wetlands in significantly greater numbers through forest controls compared with harvested treatments. Also, salamanders were generally more sensitive to forest removal than were frogs, with a significantly greater proportion of salamanders migrating through forested habitat compared to frogs.
5. For several species, individuals were significantly more likely to avoid clearcuts when emigrating compared to immigrating. Individuals that emigrated into clearcut treatments were more likely to reverse direction and return to wetlands in some species.
6. *Synthesis and applications.* Our study identifies one mechanism by which forest removal shapes the abundance and distribution of amphibians in terrestrial habitat. To promote the persistence of amphibian populations, conservation efforts should focus on preserving forest habitat adjacent to reproduction sites. Such measures are especially important where forest habitat connects local populations or where it links reproduction sites to other habitat features necessary for amphibian growth, survival, or overwintering.

**Key words:** *Ambystoma*, *Bufo*, clearcutting, forestry, habitat loss, metapopulation, *Rana*, timber harvesting

## Introduction

Widespread species declines highlight the ongoing loss of global biodiversity and warn of a nearing-extinction crisis (Lawton & May 1995; Vitousek *et al.* 1997). Indeed, current global extinction rates are estimated to be many times greater than background rates revealed from the fossil record (Wilson 1999; McCallum 2007). Amphibians epitomize these rapid declines with as many as 33% of extant species currently

threatened, more than any other class of terrestrial vertebrate (Stuart *et al.* 2004). Although habitat loss and fragmentation are recognized as the greatest cause of amphibian imperilment, the destruction of habitat continues largely unabated (Alford & Richards 1999; Stuart *et al.* 2004). For amphibians with biphase life histories, loss of either aquatic or terrestrial habitat can diminish population persistence (Semlitsch 1998; Semlitsch & Bodie 2003).

Persistence of amphibian populations depends largely on processes that occur on at least two spatial scales: local and landscape. Post-metamorphic amphibians live, forage, and overwinter in terrestrial uplands near aquatic reproduction sites (Semlitsch 2008). Consequently, amphibians require suitable terrestrial habitat for growth and survival during non-breeding portions of the year (Semlitsch 1998; Semlitsch

\*Correspondence author. E-mail: btodd@vt.edu

†Present address: Department of Fisheries and Wildlife, Virginia Polytechnic Institute and State University, 100 Cheatham Hall, Blacksburg, VA 24060, USA

& Bodie 2003). Pond-breeding amphibians also require appropriate contiguous habitat that links their terrestrial activity centres to aquatic reproduction sites in order to successfully move between them. Loss of local connectivity between terrestrial and aquatic environments can negatively affect amphibians and has been shown to lead to population declines in biphasic amphibians (Becker *et al.* 2007; Harper *et al.* 2008).

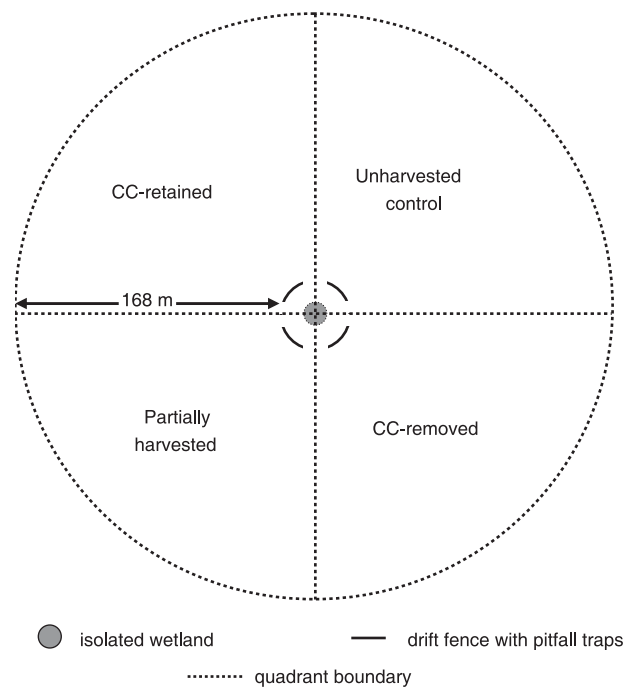
At the landscape level, patches of amphibian populations can experience reproductive failures due to pond drying, predator establishment (e.g. odonate larvae, fish), or other factors (Semlitsch *et al.* 1996). Persistent recruitment failures may cause local extinctions which require recolonization from other patches. Thus, the persistence of amphibian populations at the landscape level may depend partly on maintaining connectivity among population patches. Consequently, habitat composition at the landscape level has been shown to shape amphibian community composition (Werner *et al.* 2007a) and influences gene flow, species abundance, and population persistence at the landscape scale (e.g. Hitchings & Beebe 1997; Gibbs 1998; Gamble *et al.* 2007).

As many as 82% of amphibian species are forest-dependent (Stuart *et al.* 2004). Therefore, activities such as forest clearcutting and land conversion have great potential to affect amphibian populations. Indeed, past studies have shown that clearcutting can reduce amphibian richness and abundance by reducing survival and/or promoting evacuation of harvested habitats (deMaynadier & Hunter 1995; Todd & Rothermel 2006; Semlitsch *et al.* 2008). Our goal in this study was to test the effects of forest removal on amphibian movements to better understand the implications of forest loss for both local and landscape connectivity. We hypothesized that the migration of amphibians through forest clearcuts would be reduced compared with unharvested forests. We further expected that effects would be greater for forest-dependent species compared with more generalist species. We also hypothesized that frogs would be less affected by canopy removal than would salamanders because frogs are generally more vagile and have relatively lower rates of water loss for their mass (Spight 1968; Graeter *et al.* 2008). Frogs are also more likely to breed in open-canopy wetlands compared to salamanders, which typically breed in forested wetlands (Werner *et al.* 2007b). Finally, we hypothesized that amphibians exiting wetlands through clearcuts would be more likely to reverse course (i.e. immediately retreat) than those exiting through forests.

## Materials and methods

### STUDY SITE AND EXPERIMENTAL ARRAYS

We selected four forested sites on the Savannah River Site for study (see also Rothermel & Luhring 2005; Todd & Rothermel 2006). These sites were second-growth, managed-pine forests of loblolly pine *Pinus taeda* with a few interspersed hardwoods [oaks (*Quercus* spp.), red maple *Acer rubrum*, hickories (*Carya* spp.), dogwood *Cornus florida*, and sweetgum *Liquidambar styraciflua*]. Where present, understorey consisted of young sweetgum *L. styraciflua*, wax myrtle



**Fig. 1.** Diagram showing the arrangement of harvesting treatments and drift fences at each replicate experimental array. Note that the figure is not necessarily to scale.

*Morella cerifera*, and holly *Ilex opaca*, with ground cover dominated by Carolina jessamine *Gelsemium sempervirens*, grasses, and leaf litter.

We centred each of the four circular experimental sites on isolated, seasonal wetlands that hold water during winter and early spring. The circular sites extended outward from the wetland boundaries for 168 m. Each site was separated from roadways, open areas, and other wetlands by at least 250 m. We divided each circular site into four, 4-ha quadrants delineated by two perpendicular transects that intersected at the centre of the wetland (Fig. 1). Each quadrant was assigned randomly to one of four treatments: (i) unharvested control (> 25 years old); (ii) partially harvested stand in which the canopy was thinned to approximately 85% of that in the control; (iii) clearcut with coarse woody debris retained (CC-retained); and (iv) clearcut with coarse woody debris removed (CC-removed). The two forested plots were always opposite each other (Fig. 1). The isolated wetlands in the interior of the experimental arrays were not harvested. Logging occurred from February to April 2004. We performed no additional site preparation and allowed treatments to undergo natural vegetative succession.

### DATA COLLECTION

We installed a 45-m section of drift fence along the wetland edge bordering each treatment. Drift fences were centred in each treatment and stopped approximately 10 m from edges between treatments (Fig. 1). We constructed drift fences of aluminium flashing buried 15 cm into the ground and standing 45 cm tall. We placed six evenly-spaced pairs of 19-L pitfall traps (28 cm in diameter and 35 cm high) on opposite sides of each section of 45-m drift fence. Pitfall traps contained 1–3 cm of standing water and floating sponges. We monitored the traps for 10–11 months of each year (September or October to July), checking them daily from 1 February 2004 to 29

July 2005 and every 1–2 days from 6 October 2005 to 31 July 2007. We recorded all amphibian captures and marked adults upon their first capture emigrating from the wetlands. The marking scheme required clipping one front toe and one hind toe to indicate the year of first capture and the treatment into which the animal was emigrating. We did not clip inside front toes or the longest hind toe of frogs because they are used during reproduction (i.e. amplexus) and locomotion, respectively. We released all animals on the opposite side of the drift fence where they were captured so they could continue migrating. We did not enclose treatments or arrays with border-fences. Because past studies have shown that adult amphibians generally migrate linearly between their terrestrial homes and reproductive wetlands, follow routes perpendicular to the wetland shore, and are generally philopatric in their routes (Semlitsch 1981, 2008), we expected our captures to reflect migratory pathways and habitat choice of the animals.

Although we observed > 25 species of amphibians during the 4 years of our study, we limited our analyses to the following species with the greatest number of captures (migration periods are noted parenthetically): marbled salamanders *Ambystoma opacum* (Gravenhorst) (September to May), mole salamanders *A. talpoideum* (Holbrook) (November to June), southern toads *Bufo terrestris* (Bonnaterre) (February to July), ornate chorus frogs *Pseudacris ornata* (Holbrook) (November to April), American bullfrogs *Rana catesbeiana* Shaw (February to July), green frogs *R. clamitans* Latreille in Sonnini de Manoncourt and Latreille (February to July), southern leopard frogs *R. sphenoccephala* Cope (February to July), and eastern spadefoot toads *Scaphiopus holbrookii* (Harlan) (February to July). We pooled captures of ranids for analysis because there were too few captures to analyse each ranid species separately. Because logging did not commence until February 2004, we have three complete years of migration data for the autumn- and winter-breeding species (*A. opacum*, *A. talpoideum*, and *P. ornata*). The remaining five species were sampled during four complete migration seasons.

#### STATISTICAL ANALYSES

We analysed our data to answer the following four questions. (i) Did treatment affect the number of individuals entering and exiting the wetlands for each species? (ii) Did the proportion of amphibians moving through forested habitat differ between frogs and salamanders? (iii) Were individuals more likely to avoid clearcuts during emigration versus immigration for each species? (iv) Were individuals that emigrated into clearcuts more likely to retreat than individuals that emigrated into forested habitat? We define retreat here as recapture at the wetland of an individual that had been marked emigrating and released into one of the treatments earlier in the same season.

We used repeated measures multivariate analyses of variance, MANOVA (specifically profile analysis; Von Ende 2001) to test for treatment effects on migrations. We used the number of individuals captured in each treatment as our dependent variable repeated for each year, treatment as our main effect, and experimental array as a blocking factor. We performed separate MANOVA for each species and each migration direction (immigration or emigration). We only analysed data for adults and we used total counts from each year irrespective of sex. We also grouped species by taxon (salamanders vs. frogs) and performed additional MANOVA tests to investigate treatment effects on the number of animals of each group captured at drift fences.

We used MANOVA to test whether the proportion of amphibians migrating through the forested treatments (control and partially

harvested treatments combined) was greater in salamanders than in frogs. We performed a separate MANOVA for each migration direction and used taxonomic group as the main effect. Our dependent variable was the number of individuals captured at drift fences in the forested treatments repeated in years 2004–2006. We again used experimental array as a blocking factor.

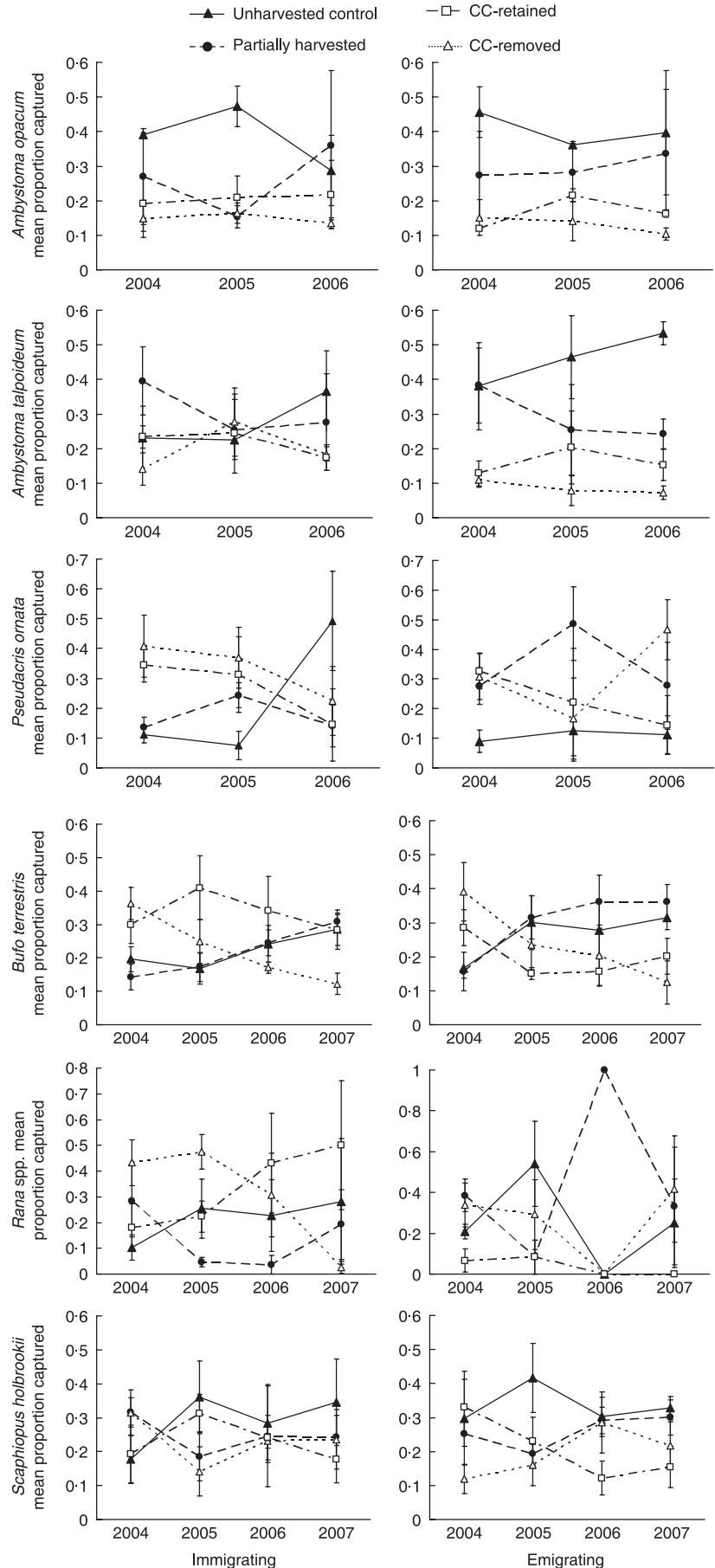
We used MANOVA to test whether the proportion of amphibians moving through forested treatments (i.e. avoiding the two clearcut treatments) was greater during emigrations than immigrations. Ranids were not analysed because of too few captures at one experimental array in 1 year. We used migration direction as the main effect, the numbers captured each year as our repeated measures, and experimental array as a blocking factor.

Using data from marked animals, we calculated the proportion of amphibians that retreated from each quadrant to determine whether they were more likely to reverse course after entering clearcut treatments compared to forested treatments (control and partially harvested). We calculated proportions for each species except ranids, for all frogs, and for all salamanders, and we performed analyses of variance (ANOVA) with experimental array as a blocking factor. We pooled data for each species separately across seasons. For all analyses, we square root-transformed count data and arcsine-square root-transformed proportions to normalize data. We defined significance at the  $\alpha = 0.1$  level, but we report unaltered *P*-values from all statistical tests.

#### Results

The number of captures and recaptures of migrating amphibians varied among species and years and at least a few species were not present at all sites (Table 1). We found no significant effects of treatment on the number of immigrating amphibians captured for any individual species or taxonomic group (Fig. 2; Table 2). However, we did find significant treatment-by-time interactions for *B. terrestris* and *Rana* spp. *Bufo terrestris* and *Rana* spp. tended to avoid immigrating through CC-removed habitats toward the end of the study and *B. terrestris* showed an increasing preference for the control and partially harvested treatments over time. Emigrating salamanders had the greatest affinity for forested habitats of all amphibians; treatment had a significant effect in salamanders combined and in *A. talpoideum* separately, with fewer individuals emigrating through clearcut treatments compared with the control and partially harvested treatments. In fact, both species of salamander displayed intensity-dependent reductions in mean numbers of emigrating animals consistent with the increasing disturbance of the four study habitats (Fig. 2). In contrast, significantly fewer *P. ornata* emigrated through forest controls compared with the other treatments (Fig. 2; Table 2). There were significant treatment-by-time interactions in both *B. terrestris* and all frogs combined (Fig. 2; Table 2). Overall, the CC-removed treatments had the fewest amphibians migrating through them (Fig. 2).

The proportion of salamanders immigrating to wetlands through forested habitats was greater than that of frogs ( $F_{1,3} = 10.45$ ,  $P = 0.05$ ; Fig. 3). Likewise, the proportion emigrating through forested habitats was also significantly greater in salamanders than in frogs ( $F_{1,3} = 56.8$ ,  $P < 0.001$ ; Fig. 3). Treatment-by-time interactions were also significant



**Fig. 2.** Mean (SE) proportion of amphibians captured migrating in and out of four harvesting treatments during breeding seasons each year. Note that the scale of the y-axis differs for some figures.

**Table 1.** Total number of captures and recaptures of adult amphibians at experimental sites. Recaptures include individuals marked in any previous year. The number of sites at which each species occurred is also listed

| Species                      | No. of captures |                |            |                |            |                 |                 | No. of sites |  |
|------------------------------|-----------------|----------------|------------|----------------|------------|-----------------|-----------------|--------------|--|
|                              | 2004            |                | 2005       |                | 2006       |                 | 2007            |              |  |
|                              | Total captures  | Total captures | Recaptures | Total captures | Recaptures | Total captures  | Recaptures      |              |  |
| <i>Ambystoma opacum</i>      | 921             | 448            | 37         | 320            | 1          | NA <sup>†</sup> | NA <sup>†</sup> | 2            |  |
| <i>Ambystoma talpoideum</i>  | 382             | 368            | 7          | 371            | 8          | NA <sup>†</sup> | NA <sup>†</sup> | 4            |  |
| <i>Pseudacris ornata</i>     | 198             | 120            | 7          | 54             | 0          | NA <sup>†</sup> | NA <sup>†</sup> | 3            |  |
| <i>Bufo terrestris</i>       | 1153            | 942            | 35         | 358            | 8          | 587             | 8               | 4            |  |
| <i>Rana</i> spp.             | 76              | 94             | 0          | 19             | 0          | 27              | 0               | 4            |  |
| <i>Scaphiopus holbrookii</i> | 77              | 4235           | 48         | 430            | 1          | 946             | 23              | 4            |  |

<sup>†</sup>The period of migrations for *A. opacum*, *A. talpoideum*, and *P. ornata* extended beyond the study, and incomplete data from 2007 were omitted from analyses for those species as reflected in the table.

**Table 2.** Results of repeated measures MANOVA testing for treatment effects on the number of individuals migrating through upland habitat. Individual yearly component ANOVAs for each test are omitted. 'n,d' represents the numerator and denominator degrees of freedom, respectively. Bold emphasis denotes significance at the  $\alpha = 0.1$  level

| Group or species             | Immigrating |             |                  | Emigrating |             |                 |
|------------------------------|-------------|-------------|------------------|------------|-------------|-----------------|
|                              | n,d         | F           | P                | n,d        | F           | P               |
| Salamanders as group         |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 0.92        | 0.47             | 3,9        | <b>7.89</b> | <b>&lt;0.01</b> |
| Time $\times$ habitat        | 6,18        | 0.81        | 0.58             | 6,18       | 1.21        | 0.34            |
| <i>Ambystoma opacum</i>      |             |             |                  |            |             |                 |
| Habitat                      | 3,3         | 1.4         | 0.39             | 3,3        | 2.31        | 0.25            |
| Time $\times$ habitat        | 6,6         | 1.07        | 0.47             | 6,6        | 1.5         | 0.31            |
| <i>Ambystoma talpoideum</i>  |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 0.51        | 0.69             | 3,9        | <b>7.68</b> | <b>&lt;0.01</b> |
| Time $\times$ habitat        | 6,18        | 0.88        | 0.53             | 6,18       | 0.75        | 0.62            |
| Frogs as group               |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 0.41        | 0.75             | 3,9        | 0.71        | 0.57            |
| Time $\times$ habitat        | 9,27        | 1.13        | 0.37             | 9,27       | <b>2.37</b> | <b>0.04</b>     |
| <i>Bufo terrestris</i>       |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 1.94        | 0.19             | 3,9        | 0.14        | 0.93            |
| Time $\times$ habitat        | 9,27        | <b>4.59</b> | <b>&lt;0.001</b> | 9,27       | <b>2.6</b>  | <b>0.03</b>     |
| <i>Pseudacris ornata</i>     |             |             |                  |            |             |                 |
| Habitat                      | 3,6         | 2.43        | 0.16             | 3,6        | <b>4.04</b> | <b>0.07</b>     |
| Time $\times$ habitat        | 6,12        | 1.88        | 0.17             | 6,12       | 0.34        | 0.91            |
| <i>Rana</i> spp.             |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 0.71        | 0.57             | 3,9        | 1.94        | 0.19            |
| Time $\times$ habitat        | 9,27        | <b>2.66</b> | <b>0.02</b>      | 9,27       | 0.39        | 0.93            |
| <i>Scaphiopus holbrookii</i> |             |             |                  |            |             |                 |
| Habitat                      | 3,9         | 0.25        | 0.86             | 3,9        | 1.3         | 0.33            |
| Time $\times$ habitat        | 9,27        | 0.89        | 0.55             | 9,27       | 1.53        | 0.19            |

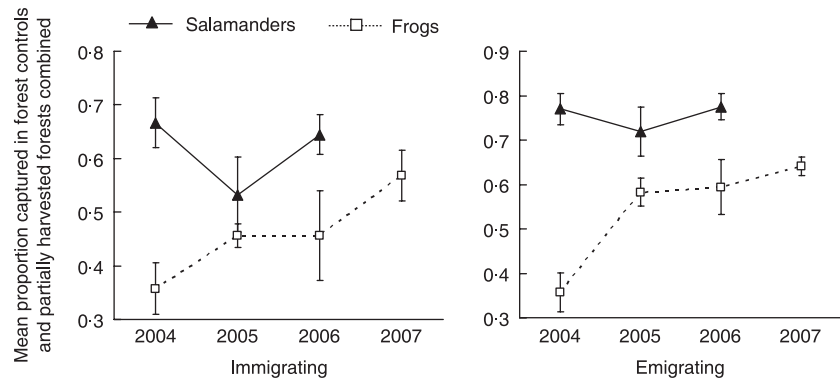
for comparisons between salamanders and frogs (immigrating:  $F_{2,6} = 4.46$ ,  $P = 0.07$ ; emigrating:  $F_{2,6} = 6.86$ ,  $P = 0.03$ ), as the proportion of frogs migrating through forested treatments increased from the first to the second year, whereas the proportion of salamanders migrating through forested treatments decreased slightly between the first and the second year (Fig. 3).

**Table 3.** Results of repeated measures MANOVA testing whether a greater proportion of individuals used forested habitat (i.e. avoided the two clearcuts) when emigrating than when immigrating. Individual yearly component ANOVAs for each test are omitted. 'n,d' represents the numerator and denominator degrees of freedom, respectively. Bold emphasis denotes significance at the  $\alpha = 0.1$  level

| Group or Species             | n,d | F            | P               |
|------------------------------|-----|--------------|-----------------|
| Salamanders as group         |     |              |                 |
| Direction                    | 1,3 | <b>13.63</b> | <b>0.03</b>     |
| Time $\times$ direction      | 2,6 | 0.78         | 0.50            |
| <i>Ambystoma opacum</i>      |     |              |                 |
| Direction                    | 1,1 | 0.66         | 0.57            |
| Time $\times$ direction      | 2,2 | 0.54         | 0.65            |
| <i>Ambystoma talpoideum</i>  |     |              |                 |
| Direction                    | 1,3 | <b>52.4</b>  | <b>&lt;0.01</b> |
| Time $\times$ direction      | 2,6 | 1.13         | 0.38            |
| Frogs as group               |     |              |                 |
| Direction                    | 1,3 | <b>23.05</b> | <b>0.02</b>     |
| Time $\times$ direction      | 3,9 | <b>3.31</b>  | <b>0.07</b>     |
| <i>Bufo terrestris</i>       |     |              |                 |
| Direction                    | 1,3 | <b>62.29</b> | <b>&lt;0.01</b> |
| Time $\times$ direction      | 3,9 | <b>5.33</b>  | <b>0.02</b>     |
| <i>Pseudacris ornata</i>     |     |              |                 |
| Direction                    | 1,2 | 0.02         | 0.91            |
| Time $\times$ direction      | 2,4 | 1.08         | 0.42            |
| <i>Scaphiopus holbrookii</i> |     |              |                 |
| Direction                    | 1,3 | 3.56         | 0.16            |
| Time $\times$ direction      | 3,9 | 0.7          | 0.58            |

For several species and groups, the proportion of individuals emigrating through forested treatments significantly exceeded the proportion immigrating through them in any given year. *Ambystoma talpoideum* and salamanders combined, and *B. terrestris* and frogs combined, all avoided clearcuts to a greater extent when leaving the wetlands than when entering (Table 3). There were significant treatment-by-time interactions for *B. terrestris* and frogs combined.

Significantly, more salamanders ( $F_{1,3} = 5.6$ ,  $P = 0.09$ ), frogs ( $F_{1,3} = 8.9$ ,  $P = 0.06$ ), and *B. terrestris* ( $F_{1,3} = 6.4$ ,  $P = 0.09$ ) retreated from clearcuts than from forested habitats.



**Fig. 3.** Mean (SE) proportion of salamanders or frogs captured migrating through forested habitat (control and partially harvested) during breeding seasons each year. Note that the scale of the y-axis differs for some figures.

## Discussion

Differences among species in their responses to forest removal reflect underlying biological differences and identify expected sensitivities to habitat alteration. For example, salamanders typically have lower tolerances to water loss and greater surface area-to-volume ratios than frogs (Thorson & Svihla 1943), making them more susceptible to body water loss. Frogs are also more vagile and make lengthier overnight movements than salamanders (Rittenhouse & Semlitsch 2007; Graeter *et al.* 2008), which may allow frogs to more easily flee or traverse inhospitable habitat. Consequently, these factors may promote avoidance of cleared habitat by salamanders, as has been shown in the spotted salamander *A. maculatum* (Rittenhouse & Semlitsch 2006), but not by frogs. Landscape-level studies have also found that salamander presence and abundance are highly correlated with forest cover, often more so than for frogs (deMaynadier & Hunter 1995; Hermann *et al.* 2005). Such disparity between the two groups is further evidenced by our finding that greater proportions of salamanders avoided clearcuts during migratory movements than did frogs.

Our finding that the numbers of amphibians immigrating to wetlands did not vary significantly among treatments suggests that small clearcuts (< 4 ha) do not act as barriers to reproductive immigrations *per se*. This was true even for forest-associated species such as ambystomatid salamanders, although this does not entirely eliminate all potential negative consequences from immigrating through open habitats. For example, a previous study found signs of elevated physiological stress in spotted salamanders immigrating to wetlands through open parking lots compared to unharvested forests (Homan *et al.* 2003), a finding that may signify lower survival for those individuals at the wetland (Romero & Wikelski 2001).

In our study, the greatest relative effect in which individuals preferred forest controls during immigration occurred for marbled salamanders *A. opacum*, the species expected to be the most forest-dependent of all our study animals. In contrast, movements in frogs were often more ambiguous. For example, *S. holbrookii* is a frog species that remains buried most of the year and breeds for only a few days during torrential rains (Lannoo 2005), a period during which environmental differences between treatments and subsequent physiological risks of moving through clearcuts are likely to be minimal.

Indeed, nearly equivalent proportions of *S. holbrookii* were captured moving through the four treatments each year. Ranid movements have also been shown to be highly dependent on rainfall (Todd & Winne 2006), and ranids exhibited no clear, consistent movement preferences over the course of the study. Instead, significant treatment-by-time interactions for ranids seemed driven by yearly variation in the relatively few captures of these species (Table 1). In contrast, *B. terrestris*, the only other species with a significant treatment-by-time interaction, demonstrated a clear change in habitat preference over the course of the study. *Bufo terrestris* is a habitat generalist that typically breeds in open-canopy wetlands (Lannoo 2005). Consequently, we expected that this species might prefer clearcuts. However, because we allowed our clearcuts to undergo natural vegetative succession after harvesting, the clearcuts rapidly filled with dense emerging vegetation, especially toward the end of the study, causing a concomitant decline in the number of toads moving through them. One possible cause for the change in preference of *B. terrestris* over time may be that these habitats grew difficult for *B. terrestris* to navigate because of this succession. In other words, it may have been easier for this species to orient and move through habitat when not obstructed by dense vegetation. Alternatively, high levels of transpiration from emerging vegetation, and loss of moisture-retaining ground cover from the timber harvesting (Todd & Andrews 2008), may have made clearcuts increasingly inhospitable to amphibians, driving even generalist *B. terrestris* to avoid clearcuts later in the study.

The direction of a migration reflects different life-history needs, with amphibians immigrating to breed at wetlands and emigrating to find suitable habitat in which to feed and survive to future breeding events. Our results demonstrate that amphibians will cross cleared habitat to reach reproductive ponds during the breeding season but that some species prefer forested habitat when emigrating from wetlands. There are several possible reasons for such a difference in observed migratory behaviour. First, during breeding seasons, the need to reach wetlands and reproduce may outweigh possible long-term fitness costs derived from time spent navigating and traversing inhospitable habitat. In other words, when the compulsion to breed is great, there may be some trade-off regarding longer-term survival (Stearns 1989). After breeding, however, more amphibians may emigrate to forested habitat because they recognize it as habitat more suitable for growth

and survival (deMaynadier & Hunter 1995; Todd & Rothermel 2006). Secondly, breeding immigrations take place in winter and spring when environmental conditions are mild and discrepancies between the treatments are minimal. In contrast, emigrations take place during late spring and summer, when environmental differences between treatments are great (as described in Todd & Andrews 2008). Accordingly, amphibians probably face greater pressure to select suitable migration routes when leaving wetlands than they do when entering. A third possibility is that post-reproductive amphibians are in poorer body condition, leading to greater costs of moving through cleared habitat when leaving the wetlands. A final possibility is that survival of clearcut-immigrating amphibians at breeding ponds is lower than that of forest-immigrating amphibians. This would lead to a greater proportion of amphibians surviving to retrace their migratory routes out through forests than through clearcuts. Additional studies of uniquely marked animals are necessary to distinguish among these competing explanations.

The effect of forest removal on amphibian movements described in this study suggests that habitat connectivity deteriorates when upland forest is removed, and indicates that terrestrial land-use can shape the distribution and passage of amphibians in uplands. Vos *et al.* (2007) found similar results in European common frogs *R. temporaria* in which the animals preferred to move through hedgerows or meadows compared to cleared arable lands. In laboratory studies, Rittenhouse *et al.* (2004) found that spotted salamanders preferred forest soil to that of old agricultural fields. Therefore, to the extent that forest loss can fracture habitat connectivity and affect local population persistence, our results indicate that habitat choice by emigrating amphibians will probably play a larger role than disruption of reproductive immigrations for forest-dependent species.

The observed reduction in the number of salamanders emigrating into clearcuts represents one mechanism leading to the eventual impoverishment of amphibian species richness and abundance following forest canopy removal (e.g. Gibbs 1998). Ultimately, such effects on habitat choice may act in concert with other processes, such as habitat evacuation or reduced survival, to cause amphibian declines (Todd & Rothermel 2006; Semlitsch *et al.* 2008). Despite salamanders generally being more sensitive to forest loss than many frogs (deMaynadier & Hunter 1995), we found that frogs as a group, and *B. terrestris* singly, moved through forested habitat to a greater degree when emigrating than when immigrating. Similarly, salamanders, frogs, and *B. terrestris* were more likely to retreat from clearcuts than forests, possibly as a consequence of clearcuts being unfavourable for movement and survival due to higher temperatures and fewer refugia (Todd & Andrews 2008), factors important to desiccation-prone animals that dwell on the forest floor.

#### MANAGEMENT IMPLICATIONS

Previous studies have shown that biphasic amphibians suffer declines in abundance and richness when upland forests are

cleared (Gibbs 1998; Herrmann *et al.* 2005; Becker *et al.* 2007). Our primary goal in this study was to determine the extent to which forest removal affects amphibian movements that can lead to such declines. Our results show that for some species, fewer post-reproductive amphibians will migrate through clearcuts compared with unharvested forests, identifying one mechanism affecting the abundance and distribution of terrestrial populations. Moreover, because our results demonstrate that salamanders are more sensitive to forest removal than frogs, they provide improved guidance for prescriptive land-use practices. In regions and habitats where amphibian communities include salamander species of conservation interest, our results indicate that managers should preserve adjacent forest habitat for both its role in sustaining populations as well as its role in connecting reproduction sites to other landscape features (e.g. overwintering sites) or to larger forest tracts in general.

One particular area where the preservation of forested corridors or the retention of continuous forestland is expected to be extremely critical is in regions with multi-pond complexes that support amphibian communities. The demonstration of metapopulation dynamics is beyond the scope of our current study. In fact, we intentionally chose isolated wetlands in our study to minimize possible effects of nearby wetlands on movement patterns of species at our sites. However, other studies increasingly demonstrate the role of landscape connectivity in amphibian population dynamics and persistence (Gamble *et al.* 2007; Stevens & Bagnette 2008). Based on the movement responses we observed in our study, upland forest removal affects overland passage of amphibians, particularly salamanders. Ultimately, such effects may lead to reproductive isolation in populations disconnected from others by clearcuts and forest loss. Where metapopulation dynamics are suspected, or in areas where mitigation wetlands are being created or restored, reforestation of the surrounding landscape should be particularly beneficial to the population genetics and dynamics of amphibian communities in the landscape.

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