REPRODUCTION OF COMMON FROGS, RANA TEMPORARIA, IN A MANAGED CONIFER FOREST AND BOG LANDSCAPE IN WESTERN **IRELAND**

REILLY R. DIBNER^{1, 2}, COLIN LAWTON¹, AND FERDIA MARNELL³

¹School of Natural Sciences, Martin Ryan Institute, National University of Ireland, Galway, University Road, Galway, Ireland ²Program in Ecology and Department of Zoology and Physiology, University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82071, USA, e-mail: rdibner@uwyo.edu

³National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, 7 Ely Place, Dublin 2,

Ireland

Abstract.-Landscape management schemes can have unanticipated effects on native species. While we tend to label habitat alterations as distinctly good or bad for specific species, it is not always clear what constitutes good habitat and what is low quality habitat. In many managed landscapes, there is a cyclical nature to these alterations, with some stages in the management cycle increasing suitability and others degrading it. In Ireland, afforested blanket bogs are managed to create a cycle of mature conifer forest alternating with a clear-felled landscape. These plantation forests have the potential to fragment naturally occurring amphibian habitat and reduce access to suitable breeding sites, though it is not clear how each management stage actually affects amphibian populations. We studied one of Ireland's three amphibians, the European Common Frog (Rana temporaria), to identify if parts of these plantations contained good breeding habitat. We conducted our study in the west of Ireland, comparing breeding habitat availability and use among pools in mature plantation forests, clear-felled areas, unplanted blanket bogs, and roadside drainage ditches. Frog breeding use and reproductive output was highest in drainage ditches and clear-felled sites. Mature plantations had lower pool densities and spawn clump densities than either drainage ditches or clear-felled sites, and no larval development. Pools with high pH, large surface area, and high temperatures had the highest probability of spawn presence. Plantation forestry can be detrimental to Common Frogs, but applying sequential harvest strategies may allow this species to persist within plantations as habitat availability shifts over time.

Key Words.-amphibians; conifer plantations; Common Frog; Ireland; Rana temporaria

INTRODUCTION

European landscapes have been altered for millennia for subsistence and commercial profit. Landscapes managed for agricultural and timber production are often defined by a patchwork of land cover types, ranging from entirely unsuitable for most species, to suitable areas.

This static view of fragmented landscapes does not, however, fully capture the seasonal and inter-annual dynamics of managed lands, where stages of vegetative growth often rotate regularly through a "mosaic cycle" (Kleyer et al. 2007). These stages are likely to vary in habitat quality for native species and, over time, may oscillate in value from optimal to marginal to entirely unsuitable (Bibby et al. 1989; Virkkala 2004; Wilson et al. 2009). This cyclic change in the ecological value of production landscapes makes it overly simplistic to classify specific land uses as strictly beneficial or detrimental for native species in a given time. In addition, native species will exhibit differing abilities to adapt to changing environments (Agrawal 2001; Donohue et al. 2001). The interaction between this plasticity, habitat quality, and the timing of management county, the conservation status of the species is not well

operations will determine if forestry and agricultural lands can support at-risk populations.

While amphibians currently face a variety of threats, including disease, exploitation, habitat loss, and climate change (Jennings and Hayes 1985; Beebee 1996; Dodd and Smith 2003; Pounds et al. 2006; Vredenburg et al. 2010), habitat loss is one of the most obvious and to a certain extent, most reversible, threats for temperate amphibians (Beebee and Griffiths 2005). Good habitats are often distributed discontinuously, and even common species are susceptible to population loss due to changes in habitat quality (Sinsch 1990; Stebbins and Cohen 1995). Amphibian habitat conservation relies on the protection of suitable wetlands as well as the surrounding terrestrial landscape (Dodd and Cade 1998), as habitat fragmentation can isolate small, localized populations (Marnell 1999).

The Common Frog, Rana temporaria, is found in a variety of ecosystems across Europe and is protected under the European Union Habitats Directive (Council of the European Union 1992). Even though the species is widespread throughout Ireland (Foss and O'Connell 1997; King et al. 2011), with populations in every

understood. "Vhe "Irish "National "Parks "and "Y kf nkhg Service ""(NPWS) "found "that "various "pressures constrain Common Frog range and future prospects, and specifically identified plantation forestry as an important threat (NPWS 2007). It is possible, however, that certain stages of the conifer plantation management cycle may provide suitable amphibian breeding habitat that could mitigate some of these threats. Marnell (1998) characterized habitat correlates for breeding Common Frogs and found that proximity to terrestrial habitat was a particularly important determinant of pond or pool use. In contrast to other amphibians, this species prefers shallow pools to large ponds for breeding (Vági et al. 2013). Adult Common Frogs are highly terrestrial, dispersing into grasslands and bogs following the spawning period (Blackith and Speight 1974).

The main objective of our research was to assess how the Common Frog responded to landscape-level (habitat cover) factors and local (small pools) variables. In particular, we investigated potential differences in breeding site use of Common Frogs in mature plantation forests, clear-felled areas, unplanted bogs, and roadside drainages in the west of Ireland. We hypothesized that habitat availability would be higher in unplanted bog and clear-felled areas than in mature conifer stands and that Common Frogs would select pools with higher pH and higher temperature for breeding sites. We used our results to identify which cover types were most likely to provide Common Frogs with suitable breeding habitat, thereby providing some mitigation of the effects of this particular land conversion.

MATERIALS AND METHODS

Study sites.—We conducted surveys for potential breeding habitat and breeding activity of Common Frogs in western Ireland in 2009 and 2010. The 2009 field sites were in the Nephin Beg Mountains north of Newport, County Mayo, Ireland (Fig. 1A and B), and the 2010 field sites were northeast of Recess in Connemara, County Galway, Ireland (Fig. 1C). All study areas were between 180 m and 700 m asl and had similar slope gradients, between 0–6%. The bedrock geology was predominantly schist, gneiss, and quartzite, and the soils were deep peat.

In our study areas, conifer plantations were intermixed with natural peat bogs and accessible in many places by logging roads with wide drainage ditches. Plantation areas alternate through time between open, early-successional stages created by clear-felling, and closed, dense, mature forests near the end of the rotation period. All forest sites were composed of mixed non-native conifers dominated by 30–40 year-old Lodgepole Pine (*Pinus contorta*) and Sitka Spruce (*Picea sitchensis*). The ground vegetation in both forests, where present beneath twigs and leaf litter, was almost exclusively

Sphagnum sp. moss. Clear-felled areas included in the study were harvested between 2005 and 2007 (Declan Whelan, pers. comm.) and, at the time of sampling, had undergone at least two years of regeneration. These sites were replanted following harvest and were dominated by mosses, particularly Sphagnum and Polytrichum spp.; heathers (Calluna vulgaris and Erica tetralix); Purple Moor Grass (Molinea caerulea); Soft Rush (Juncus effusus); as well as conifer seedlings that measured less than one meter in height. The vegetation of the unplanted blanked bog in Connemara was dominated by Purple Moor Grass, Black Bog Rush (Schoenus nigricans), and Cottongrass (Eriophorum angustifolium), with a persistent layer of Sphagnum spp., a mix of heathers, and occasional occurrences of Bog Asphodel (Narthecium ossifragum) and sundews (Drosera spp.).

We surveyed mature plantation forest and clear-felled areas, as well as the connecting roadside drainage ditches and unplanted blanket bog, common natural habitats of the Common Frog (Blackith and Speight 1974). We used a stratified random sampling approach to select a total of 45 1-ha plots, each of which was relatively homogeneous. Between the two years and two sites there were 25 plots in plantation forest, 15 in clearfelled forest, and 5 in unplanted blanket bog (Table 1; Plots were a minimum of 300 m apart Fig. 1). (Appendix) and we used Moran's I test (Fortin and Dale 2005) to identify spatial autocorrelation in abiotic Second, we surveyed roadside drainages variables. adjacent to the Nephin and Glennamong Forest plots; these roads were with little or no regular vehicle traffic.

Data collection in survey plots.—We recorded presence/absence of spawn, number of spawn clumps, pool surface area, temperature, and pH at each potential breeding pool within each plot. For the purposes of this study, we defined potential breeding habitat as any water body $\geq 0.25 \text{ m}^2$ in area and $\geq 5 \text{ cm}$ deep during the breeding season (Cooke 1975). We calculated spawn density at two different scales: spawn clumps per (1 ha) plot to compare differences among cover types, and spawn clumps per square meter of pool to compare frog use among pools.

Spawn counts.—We began spawn surveys in the third week of January of both 2009 and 2010 to ensure that we would not miss the onset of the breeding period. We visited all pools in all plots on a 10- to 14-day rotation from before spawning commenced and until we saw no fresh spawn clumps. Spawn numbers were recorded by clump, and the 10- to 14-day sampling frequency made it possible to distinguish individual clumps from one another based on the similarity in shape and size of individual eggs. In May 2009 we resurveyed pools in clear-felled and mature forest plots that had contained spawn to check for larval presence.



FIGURE 1. Locations of study sites. A) Nephin Forest, B) Glennamong Forest, and C) Illion Forest. Common Frogs (*Rana temporaria*) occur throughout all counties on the island of Ireland. The symbols mark the northwestern corner of each sampling plot and the northwestern starting point of each drainage ditch transect.

Pool characteristics.—We used a WTW pH 3210 precision pH meter with a SenTix RJS electrode to measure pool pН and temperature (WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany), and a 50-m tape to measure pool dimensions. We took temperature and pH measurements at each visit and reversed the visitation order each round so that we would have an even spread of sampling times for each pool. We took measurements 10 cm from the northern edge of the pool between 0800 and 1400 each sampling day. For our analyses we used the mean

temperature and pH values from all six visits.

Data collection in roadside ditches.—We surveyed five 100-m lengths of drainage ditches within the Nephin Forest and a 1500-m drainage ditch in Glennamong Forest for spawn, following the same sampling procedure as for plot surveys and applying the same autocorrelation test. Most spawn clumps were confined to wider pool areas within the stream channel, so we recorded dimensions for these areas to calculate spawn density within pools. For the few clumps deposited

TABLE 1. Summary of plot numbers and survey areas for the Common Frog, Rana temporaria, in Ireland among cover types and between years.

Cover Type	Nephin 2009	Glennamong 2009	Illion 2010
Mature forest	10 plots (1 ha each)	10 plots (1 ha each)	5 plots (1 ha each)
Clear-fell	10 plots (1 ha each)	-	5 plots (1 ha each)
Blanket bog	_	-	5 plots (1 ha each)
Roadside ditch	5 × 100 m	1 × 1500 m	

within the flowing channel, we used the distance between the farthest neighbor clumps and the channel width to calculate density per m^2 . We sampled the drainages three times during the 2009 breeding season, beginning in February with sampling visits each separated by 10–14 days.

Analysis.--We conducted two sets of analyses: the first was measuring the effects of cover type on pool variables and frog use to address our first hypothesis, and the second was measuring the effects that each pool variable had on spawn presence and spawn density within pools to address our second hypothesis. For the first set of analyses we summarized plot-wide characteristics by taking the average pool density per hectare, spawn density per hectare, temperature, area, and pH for all pools within each 1-ha plot (Table 2). We ran one-way ANOVAs to measure the effect of cover type on each of the mean plot values, as well as on spawn presence. Due to the multiple differences in sampling regions in the two years, we analyzed the 2009 and 2010 data separately, and also separated analyses for the roadside drainage ditch data. We used the Lilliefors

(1967) adaptation of the Kolmogorov-Smirnov test for normality to identify whether or not plot means departed from a normal distribution. To normalize variables that were significantly non-normal, we applied a 0.1 power transformation. We were cautious about making inferences from the results due to the relatively low sample size of different cover types in 2010.

Next, we examined the combined effects of abiotic factors and cover type on spawn presence and spawn density per m² at the level of individual pools, including data from all plots and both years. Because many poollevel explanatory variables co-vary (e.g., cover type and water chemistry), simple one-way tests for each variable are not meaningful tests for the best explanatory factors for frog use. Following the suggestions of many authors in the ecological literature (e.g., Burnham and Anderson 2002; Johnson and Omland 2004), we used information theory approaches to find the best-supported model for each dependent variable and present these best models. We fit logistic models (general linear models, or GLMs, with a logistic link function) to the spawn presence/absence data and used GLMs with a negative binomial link function to analyze the spawn clumps per

TABLE 2. Summary of average values for the Common Frog, *Rana temporaria*, in Ireland for pool characteristics and frog use among the three cover types. ANOVA results comparing differences among these values are presented for each variable among cover types and between years. The elements in each cover type cell are: average value \pm one standard error; in parentheses, the range of measured values (min value – max value); and the sample size, *n*.

Dependent	Plantatio	n Forest	Clea	r-fell	Bog		2009			2010	
variable	2009	2010	2009	2010	2010	Adj R ²	F	Р	Adj R ²	F	р
Pool density (pools/ha)	2.2 ± 0.1 (0-18) n = 20	2.6 ± 2.4 (0-12) n = 5	8.3 ± 1.9 (1-22) n = 10	45.4 ± 5.9 (31-61) n = 5	3.4 ± 3.4 (0-17) n = 5	0.264	10.0 5	0.004	0.828	34.73	<0.001
Spawn density (clumps/ha)	1.1 ± 0.7 (0-14) n = 20	$0 \\ N/A \\ n = 5$	32.5 ± 13.5 (0-139) n = 10	58.8 ± 40.2 (1-217) n = 5	9.6 ± 9.6 (0-48) n = 5	0.258	11.0 9	0.002	0.096	1.745	0.216
Surface area (m ²)	2.3 ± 0.4 (0.25- 12) n = 43	2.9 ± 1.1 (0.5-12) n = 13	2.1 ± 0.2 (0.25-10) n = 83	1.7 ± 0.1 (0.25- 13.5) n = 280	2.7 ± 0.5 (0.25-8) n = 17	-0.042	0.32 1	0.579	-0.228	0.350	0.721
рН	4.4 ± 0.1 (3.52- 6.2) n = 43	4.0 ± 0.1 (3.84– 4.96) n = 13	4.6 ± 0.1 (3.5-6.14) n = 83	4.3 ± 0.1 (3.7–7.52) n = 280	4.7 ± 0.1 (4.44– 5.06) n = 17	-0.062	0.01 1	0.916	-0.369	0.057	0.945
Temperature (°C)	7.8 ± 0.1 (7.1-88) n = 43	5.3 ± 0.1 (4.4-5.9) n = 13	10.2 ± 0.2 (6.5–16.3) n = 83	10.9 ± 0.2 (1.8–17.1) n = 280	12.7 ± 0.4 (10.2– 15.3) n = 17	0.570	21.1 0	<0.001	0.763	12.26	0.012
% Pools with spawn	2.6 ± 1.4 (0-22) n = 43	$0 \\ N/A \\ n = 13$	34.1 ± 9.9 (0-85) n = 83	17.3 ± 9.8 (2.2-55.9) n = 280	3.5 ± 3.5 (0-17.6) n = 17	0.407	19.2 1	<0.001	0.160	2.335	0.139
# Spawn per pool	0.5 ± 0.3 (0-7) n = 43	$0 \\ N/A \\ n = 13$	3.9 ± 0.9 (0-50) n = 83	0.8 ± 0.3 (0-50) n = 280	2.8 ± 2.1 (0-35) n = 17	0.242	6.149	0.022	-0.162	0.512	0.628

 m^2 data. For the GLMs we included combinations of the two non-area pool characteristics (pH and temperature) and the two categorical variables (cover type and year-region).

We ranked each set of models using Akaike's Information Criterion correction for small samples sizes (AICc; Burnham and Anderson 2002). The best model had the smallest AICc value. Next we calculated AICc weights (w) to estimate the probability that a model was the best one for the observed data, given the candidate set of models, and summed AICc weights across models for each predictor variable.

We ran the same models and tests described above on the roadside drainage surveys to identify which set of predictor variables were most indicative of spawn presence and density within pools. This set of models did not include year-region or cover type since we only sampled roadside habitat in 2009 and all transects were within plantation forest. We performed all analyses in the statistics program R (R Development Core Team 2010).

RESULTS

Between the two years we located and sampled 436 potential breeding pools. Pool density varied from 0 to 61 pools per hectare and spawn density ranged from 0 to 59 spawn clumps per hectare (Table 2). In 2009 frogs spawned from the middle of February through the middle of March, while in 2010 there was spawning activity from early March to early April; we conducted six sampling rounds in each year.



FIGURE 2. Pool characteristics for the Common Frog, *Rana temporaria*, in Ireland. Pool characteristics varied among habitat cover types. A) Pool density was significantly higher in clear-felled plots than in mature forest and unplanted bog plots. There was no significant difference between pool density in mature forest and unplanted bog. B) Temperature was higher in bog pools than in clear-felled pools, and clear-felled pools were warmer than forested pools. The bottom and top of the outer box represent the upper limits of the first and third quartiles (the middle 50%) and the horizontal line inside the box marks the median. The vertical whiskers indicate the range of values.

Effects of cover type at plot level.—Cover type had a strong consistent effect on the density of potential breeding sites (ANOVA: 2009 F = 10.05, df_{between groups} (bg), within groups (wg) = 1, 28, P = 0.0037; 2010 F = 34.73, df_{bg,wg} = 2, 12, P < 0.001; Fig. 2A) and pool temperature (ANOVA: 2009 F = 21.2, df _{bg,wg} = 1, 16, P < 0.001; 2010 F = 12.26, df _{bg,wg} = 2, 5, P = 0.012; Fig. 2B) though the other differences among cover type were inconsistent between sites and year (Table 2). We applied post-hoc tests using Tukey's honest significant difference to our 2010 data, which indicated that breeding pool density per ha was higher in clear-felled areas (45.4 ± 5.9 SE pools) than in either mature forest $(2.6 \pm 2.4 \text{ pools})$ or unplanted bog $(3.4 \pm 3.4 \text{ pools})$, while there was no significant difference between mature forest and bog. The mean temperature was lowest in forested plots in both years (2009: $7.8 \pm 0.1^{\circ}$ C, 2010: $5.3 \pm 0.1^{\circ}$ C), and the post-hoc tests showed that temperatures in clear-felled plots ($10.9 \pm 0.2^{\circ}$ C) and bog plots $(12.7 \pm 0.4^{\circ} \text{ C})$ were significantly higher than temperatures in mature forest (5.3 ±0.1° C). Mean pH and temperature followed this same pattern, but the relationship between pH and cover type was not significant in either year.

In 2009 frogs used clear-felled sites more than mature plantation sites. A significantly higher percentage of pools in clear-felled sites had spawn ($34.1 \pm 9.9\%$, ANOVA: 2009 F = 19.2, df_{bg,wg} = 1, 16, P < 0.001) compared to mature plantation forest sites ($2.6 \pm 1.4\%$). Spawn density per hectare was also significantly higher in clear-felled areas (32.5 ± 13.5 , ANOVA: 2009 F = 11.09, df _{bg,wg} = 1, 28, P = 0.002) than in mature forest sites (1.1 ± 0.7). The same trends applied in 2010 but were not significant, perhaps due to low rainfall in the region followed by a heat wave in April that dried out most pools. In 2009 we found larvae in 23% of pools in clear-felled plots that had contained spawn and none in the mature forest pools that had contained spawn.

Effects of pool characteristics on use.—The best model for frog spawn presence included all measured variables: cover type, pH, pool area, year-region, and temperature (Nagelkerke's R^2 : 0.406; Fig. 3). Summed AICc weights (total weights of all models including a given factor) showed very high support for the predictive power of pool area, pH, and temperature, each with a summed AICc weight of 0.99. In general, the pools with high pH, large surface area, and high temperatures had the highest probability of spawn presence.

In contrast with these strong effects on spawn presence, we found much weaker effects of pool characteristics on spawn density. The best model for spawn density within pools had low predictive power, with an R^2 value of only 0.028 (Table 3).

Herpetological Conservation and Biology

TABLE 3. Best model fits for the Common Frog, *Rana temporaria*, in Ireland for spawn presence (logistic regression) and spawn density (negative binomial distribution) in plots and roadside ditch surveys. Results shown are: the sample size corrected AIC (AICc); the AIC weight of this model (a measure of the probability that it was the best model of all the alternatives tested); the adjusted R^2 value; and, for the linear Gaussian models, *F* and *p* for overall model fit.

Dependent Variable	Best Model	AICc	wAICc	Adj R ²	F	Р
Spawn Presence	Cover Type + pH + Surface Area + Year + Temp	245.213	0.988	0.406	NA	NA
Spawn Density	pH	-100.028	0.314	0.028	2.575	0.102
Spawn Presence (Ditch)	pH	49.214	0.298	0.147	NA	NA
Spawn Density (Ditch)	Temp	-21.374	0.378	0.033	1.823	0.190

Roadside drainage ditches.—The best predictor for spawn presence in roadside ditches was pH (Nagelkerke's R^2 : 0.147; Fig. 4), with a summed AICc weight of 0.75. Spawn were more likely to be in less acidic pools. Spawn clump densities were higher in roadside drainages than in either mature conifer plantations or clear-felled areas. In the five 100-m lengths of drainage ditches that we sampled adjacent to dirt and gravel roads in Nephin Forest, there were 387 spawn clumps in 42 pools. In Glennamong Forest we found 35 pools that contained spawn in the 1.5 km of drainage along the forest road. For comparison, out of the 10 hectares of adjacent forest that we surveyed in Glennamong, there were only six pools that met the minimum standard for frog breeding sites and none contained spawn. As with the 1-ha plots, we found low predictive power of pool characteristics on spawn density (Table 3).

DISCUSSION

Aquatic habitat availability and quality varied significantly among plantation management phases, in turn influencing Common Frog breeding site use and reproductive success. Clear-felled sites appeared to



FIGURE 4. The effect of pH for the Common Frog, *Rana temporaria*, in Ireland. In drainage ditches, pH had the strongest effect among the variables on spawn presence. The predicted relationship between pH and spawn presence is from the best fit GLM for spawn presence (fit using a negative binomial link function). This model includes only pH (Table 3). There was a higher probability of finding spawn in pools with high pH than in low pH pools.

provide frogs with better breeding habitats than other landcover types, as pool density and spawn density were both highest there. We found partial support for our first hypothesis, as temperatures were higher in both clearfelled and unplanted bog plots than in mature plantation



FIGURE 3. Predicted relationships for the Common Frog, *Rana temporaria*, in Ireland between spawn presence and several habitat variables. Spawn presence as a function of A) Pool surface area, B) pH, and C) temperature. Pool area, pH, and temperature required for spawn presence were much higher in mature plantation forest. All predicted relationships graphed indicate the best fit model. Each line shows predicted relationships based on the best fit GLM with a logistic link function for spawn presence (see Table 3) and holding all non-plotted factors included in this model at their mean values.

plots, but the difference in pH among the three cover types was not significant. On the other hand, while pool density was significantly higher in clear-felled sites than in the other cover types, there was no difference between pool density in mature plantation forest and unplanted bog plots. Our second hypothesis was clearly supported, with frog presence more likely in pools with higher The pool area, pH, and temperatures and pH. temperature required for spawn presence were much higher in mature plantation forest, suggesting that the combined effects of cover type with pool characteristics are important in predicting spawn presence. While our two hypotheses were at least partially supported, neither pH nor temperature were significant predictors of spawn density.

Frogs used roadside drainage ditches over other pools in the same area. The extreme case was in Glennamong Forest where all spawn deposition was along the road corridor; all 10 forest plots were devoid of spawn. On a cautionary note, DiMauro and Hunter (2002) found that roadside ditches could function as ecological traps if the hydroperiod was not long enough to support frogs through metamorphosis. Roadside drainage ditches used for spawning can become population sinks when the adjacent road is used regularly by motor vehicles (Ercelawn, A. 1999. End of the road: the adverse ecological impacts of roads and logging: a compilation of independently reviewed research. Available from http://www.nrdc.org/land/forests/roads/eotrinx.asp

[Accessed 13 September 2011]) but the roads in this study had low traffic volume and thus are more likely to be useful habitat for frogs. These roads were heavily used during planting and harvest, but most received very little traffic outside of those times. Small, low-use roads may provide connectivity between other areas of good habitat, or may function as breeding habitat on their own.

While clear-felled areas may be suitable for frogs in the short term, these areas are regularly replanted and quickly develop dense vegetation. This vegetation succession shortens the hydroperiod of the small pools (e.g., by evapotranspiration) and may also change the thermal condition in the ponds. The quality of the habitat declines as the conifer seedlings become established and the canopy closes, both reducing available ground moisture and sunlight at the ground layer. For frogs that are adapted to abundant natural light exposure, the reduction of light at a breeding site could be sufficient to render that habitat unsuitable (Skelly et al. 1999, 2002).

Bogs are good foraging habitat for Common Frogs (Blackith and Speight 1974), but their importance as reproductive sites is unclear. While there was a low number of pools in the bog plots, a high percentage of those pools contained spawn. The small sample size makes it difficult to extrapolate the landscape-level value

of this habitat. For a suitably long hydroperiod, blanket bogs may provide habitat for Common Frogs at several life stages, not just for foraging.

We did not find suitable breeding habitat for frogs in mature conifer plantations. Low ground moisture content may have made these mature plantations inhospitable to Common Frogs and could have impeded movement to the few pools that did meet the minimum standards of suitable habitat. Mazerolle and Desrochers (2005) postulated that dehydration was one reason that Green Frogs (Rana clamitans) were less likely to move across disturbed surfaces in a bog. Considering the relatively low incidence of pools and wet areas in the mature conifer plantations, it is reasonable to speculate that dehydration was an important avoidance factor in the frog's landscape cover preference. In mature plantation forest sites that do have pools with suitably long hydroperiods, other effects of canopy cover may restrict both breeding use and larval development. Forest canopy cover can reduce larval growth rates and food resource availability for frogs due to lower dissolved oxygen content and colder temperatures (Skelly et al. 1999; Werner and Glennemeier 1999).

The disparity between the probabilities for spawn presence based on pH in clear-felled, bog, mature plantation areas, and roadside ditches (Fig. 3B) suggests that additional factors influence what constitutes acceptable pool characteristics. The probability of spawn presence increased in both bogs and clear-felled areas in much more acidic conditions than in mature plantation forest. The high predictive power of area and temperature for the probability of spawn presence indicates that these pool variables significantly interact with pH to reduce the suitability of mature plantation forest pools for breeding frogs. Further, spawn presence does not necessarily translate linearly into successful reproductive offspring; spawn must survive to become larvae and larvae must survive to reproduce as young adults in order for a successful reproductive cycle to be complete. The failure of any spawn to develop into larvae within the 2009 mature forest sites suggests that mature plantation forests could be population sinks. This result highlights the idea that cover type is important for development and provides a starting point for further research.

Planning conservation strategies.—Clear-felled areas were good for both pool formation and temporary breeding sites; mature plantations were less suitable, and roadside drainage ditches were the most used breeding sites. Roadside ditches are relatively consistent potential breeding habitat within the rotating "mosaic cycle" of habitat that varies in quality. This constancy could be vital for Common Frogs to persist in the longterm. Key management actions to improve frog habitat in plantation forests include using sequential clear-felling of adjacent plots to maximize the easy availability of accessible breeding habitat, and maintaining the structure of roadside ditches wherever possible. Translating current forestry management practices into practical conservation strategies is a critical transition for preserving threatened species and, in the case of the Common Frog, small changes could have large implications for local persistence.

Acknowledgments.—The Irish National Parks and Wildlife Service funded this research in full and provided access to expertise. Coillte Teoranta supported this research by granting access to conifer plantations and sharing maps of harvest sites. Eoin McLoughlin, Niamh Quinn, Caroline Sullivan, and John Cuniffe provided vital assistance with fieldwork. Daniel Doak, Diane Renshaw, and Jon Loman shared valuable editorial comments on the paper throughout the course of its preparation. Many thanks to Kerry Cutler for generous assistance with programming in R.

LITERATURE CITED

- Agrawal, A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294:321–326.
- Beebee, T.J.C. 1996. Ecology and Conservation of Amphibians. Chapman and Hall, London, England.
- Beebee, T.J.C., and R. Griffiths. 2005. The amphibian decline crisis: A watershed for conservation biology? Biological Conservation 125:271–285.
- Bibby, C.J., N. Aston, and P.E. Bellamy. 1989. Effects of broadleaved trees on birds of upland conifer plantations in North Wales. Biological Conservation 49:17–29.
- Blackith, R.W., and M.C.D. Speight. 1974. Food and feeding habits of the frog *Rana temporaria* in bogland habitats in west of Ireland. Journal of Zoology 172:67–79.
- Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Cooke, A.S. 1975. Spawn site selection and colony size of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). Journal of Zoology, London 75:29–38.
- Council of the European Union. 1992. Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Union 35:7–50.
- DiMauro, D., and M.L. Hunter, Jr. 2002. Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests. Forest Science 48:397–406.
- Dodd, C.K., Jr., and B.S. Cade. 1998. Movement patterns and the conservation of amphibians in small,

temporary wetlands. Conservation Biology 12:331-339.

- Dodd, C.K., Jr., and L.L. Smith. 2003. Habitat destruction and alteration: historical trends and future prospects for amphibians. Pp. 94–112 *In* Amphibian Conservation. Semlitsch, R.D. (Ed.). Smithsonian Institution, Washington, DC, USA.
- Donohue, K., E. Hammond-Pyle, D. Messiqua, S.M. Heschel, and J. Schmitt. 2001. Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. Evolution 55:692–702.
- Fortin, M.-J., and M. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, New York, New York, USA.
- Foss, P., and C. O'Connell. 1997. Hop to it Irish frog survey: A baseline ecological survey conducted by the Irish Peatland Conservation Council on the distribution, habitat preference, breeding date and success of *Rana temporaria* in Ireland. Irish Peatland Conservation Council, Dublin, Ireland. 40 p.
- Jennings, M.R., and M.P. Hayes. 1985. Pre-1900 overharvest of California Red-legged Frogs (*Rana aurora draytonii*): The inducement for Bullfrog (*Rana catesbeiana*) introduction. Herpetologica 41:94–103.
- Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.
- King, J.L., F. Marnell, N. Kingston, R. Rosell, P. Boylan, J.M. Caffrey, Ú. FitzPatrick, P.G. Gargan, F.L. Kelly, M.F. O'Grady, et al. 2011. Ireland Red List No. 5: Amphibians, Reptiles and Freshwater Fish. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, Ireland. 77 p.
- Kleyer, M., R. Biedermann, K. Henle, E. Obermaier, H.-J. Poethke, P. Poschlod, B. Schröder, J. Settele, and D. Vetterlein. 2007. Mosaic cycles in agricultural landscapes of northwest Europe. Basic and Applied Ecology 8:295–309.
- Lilliefors, H.W. 1967. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association 62:399–402.
- Marnell, F. 1998. Discriminant analysis of the terrestrial and aquatic habitat determinants of the Smooth Newt (*Triturus vulgaris*) and the Common Frog (*Rana temporaria*) in Ireland. Journal of Zoology, London 244:1–6.
- Marnell, F. 1999. The distribution of the Common Frog *Rana temporaria* L. in Ireland. Bulletin of the Irish Biogeographical Society 23:60–70.
- Mazerolle, M.J., and A. Desrochers. 2005. Landscape resistance to frog movements. Canadian Journal of Zoology 83:455–464.
- National Parks and Wildlife Service. 2007. Rana temporaria (1213) Conservation Status Assessment

Ireland. 5 p.

- Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E.L. Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161-167.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/ [Accessed 14 April 2013].
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology, Ecology & Evolution 2:65-79.
- Skelly, D.K., L.K. Freidenburg, and J.M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology 83:983-992.
- Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326-2337.
- Stebbins, R.C., and N.W. Cohen. 1995. A natural history of amphibians. Princeton University Press, Princeton, New Jersey, USA.

- Report, National Parks and Wildlife Services, Dublin, Vági, B., T. Kovács, R. Băncilă, T. Hartel, and B.P. Anthony. 2013. A landscape-level study on the breeding site characteristics of ten amphibian species in central Europe. Amphibia-Reptilia 34:63-73.
 - Virkkala, R. 2004. Bird species dynamics in a managed southern boreal forest in Finland. Forest Ecology and Management 195:151-163.
 - Vredenburg, V.V., R.A. Knapp, T.S. Tunstall, and C.J. Briggs. 2010. Dynamics of an emerging disease drive population amphibian large-scale extinctions. Proceedings of the National Academy of Sciences of the United States of America 107:9689-9694.
 - Werner, E.E., and K.S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999:1-12.
 - Wilson, M.W., S. Irwin, D.W. Norriss, S.F. Newton, K. Collins, T.C. Kelly, and J. O'Halloran. 2009. The importance of pre-thicket conifer plantations for nesting Hen Harriers Circus cyaneus in Ireland. Ibis 151:332-343.



REILLY DIBNER received her B.A. from Yale University and M.E.Sc. from the School of Forestry Yale and Environmental Studies. She began studying frogs in Ireland on a Fulbright grant and continued related research funded by the Irish National Parks and Wildlife Service. She is currently studying horned lizards as a Ph.D. candidate in the Program in Ecology at the University of (Photographed by John Wyoming. Cunniffe).



DR. COLIN LAWTON is a lecturer in terrestrial ecology in the School of Natural Sciences of National University of Ireland, Galway. His research interests include conservation ecology, management of invasive species, and parasitology. He carried out his Ph.D. at Trinity College, Dublin on the impact of the invasive Grey Squirrel in Ireland and has continued to work on Irish squirrels as well as population studies on other native Irish mammals. (Photographed by Anne Marie Power).



DR. FERDIA MARNELL is Head of Animal Ecology in the Irish National Parks and Wildlife Service. This post involves the coordination of national surveys and monitoring program of protected vertebrates throughout Ireland. Recently completed projects include the first nationwide survey of the Common Frog (Rana temporaria) in Ireland and a breeding study of the endangered Natterjack Toad (Epidalea calamita). He has published on a wide range of species including bats, lampreys, otter, mountain hare, water beetles, and newts. (Photographed by Rob Ovington).

APPENDIX.	UTM coordinates for	or the northwest of	corner of all plo	ots and north	ern or wester	n starting poi	nt of each
drainage dit	ch section for the Co	ommon Frog, Ran	<i>a temporaria</i> , i	n Ireland. A	ll UTM coord	linates are Zo	ne 29N in
the WGS84	datum.						

Site	Plot	Cover	Size	UTM E	UTM N	Elev (m)
Glennamong	G1_09	Forest	1 ha	457829.91	5981303.30	668
Glennamong	G2_09	Forest	1 ha	457802.07	5981013.17	612
Glennamong	G3_09	Forest	1 ha	458086.91	5980891.57	560
Glennamong	G4_09	Forest	1 ha	458084.88	5980169.61	628
Glennamong	G5_09	Forest	1 ha	458401.79	5980537.94	526
Glennamong	G6 ⁻ 09	Forest	1 ha	458700.64	5980170.17	514
Glennamong	G7 ⁻ 09	Forest	1 ha	458899.07	5980616.73	432
Glennamong	G8 ⁻ 10	Forest	1 ha	459224.99	5980373.39	363
Glennamong	G9_09	Forest	1 ha	459510.10	5979947.62	354
Glennamong	G10 09	Forest	1 ha	459859.25	5980310.22	221
Altahonev	A1_09	Clear	1 ha	460460 70	5988173 48	671
Altahoney	A2_09	Clear	1 ha	460759.15	5987035 15	419
Altahoney	A3_09	Clear	l ha	460766 38	5986809 11	609
Altahoney	A4_09	Clear	1 ha	461005.06	5986280 32	415
Altahoney	A5_00	Clear	1 ha	461566.62	5085440.30	340
Altahoney	A5_09	Clear	1 ha	460317.88	508//68 32	503
Altahonov	A0_09	Clear	1 ha	460001 61	5084200.00	420
Altahoney	A/_09	Clear	1 ha	460991.01	5082501 50	439
Altanoney	A8_10	Clear	1 114	400993.41	5985591.50	308
Altanoney	A9_09	Clear	l na	462087.38	5982/28.64	235
Altahoney	A10_09	Clear	l ha	461958.12	5983910.00	3/6
Altahoney	AIF_09	Forest	l ha	461125.62	598/8/3.51	4/9
Altahoney	A2F_09	Forest	l ha	460896.12	5987229.66	414
Altahoney	A3F_09	Forest	l ha	461175.75	5986965.93	400
Altahoney	A4F_09	Forest	1 ha	461286.37	5986249.95	397
Altahoney	A5F_09	Forest	1 ha	461393.40	5985196.12	379
Altahoney	A6F_09	Forest	1 ha	459901.92	5984030.86	516
Altahoney	A7F_09	Forest	1 ha	460902.54	5984701.35	451
Altahoney	A8F_10	Forest	1 ha	460715.45	5984005.38	432
Altahoney	A9F_09	Forest	1 ha	461753.16	5982613.04	268
Altahoney	A10F_09	Forest	1 ha	462208.54	5983647.68	266
Illion	I1F 10	Forest	1 ha	455003.78	5925622.22	237
Illion	I5F 10	Forest	1 ha	455451.33	5925597.25	273
Illion	I9F_10	Forest	1 ha	455075.74	5925337.85	235
Illion	I10F 10	Forest	1 ha	455372.89	5925288.06	241
Illion	I14F ¹⁰	Forest	1 ha	455267.50	5924990.69	222
Illion	I3 10	Clear	1 ha	455559.43	5925717.49	294
Illion	18 10	Clear	1 ha	455917.48	5925761.90	321
Illion	111 10	Clear	1 ha	456085.09	5925496 74	303
Illion	113_10	Clear	l ha	455886.28	5925177.83	231
Illion	115_10	Clear	1 ha	456179.37	5925309.07	328
Illion	115_10 12B_10	Bog	1 ha	455170.36	5925966.40	225
Illion	$12D_{10}$ 17B_10	Bog	1 ha	454802.64	5925884 73	200
Illion	17D_10 10B_10	Bog	1 ha	454408 48	5025833 12	167
Illion	17D_10 111B_10	Bog	1 ha	151155 11	5925655.42	197
Illion	1110_10 1150_10	Dog	1 11a 1 ho	454453.44	5025240.14	105
Altaborar	AD1 00	Dug	1 11a	434324.08	50880249.03	193
Altanoney	AD1_09	Ditch	100m	401027.40	5988050.92	402
Altanoney	AD2_09	Ditch	100m	460839.58	5986546.75	440
Altahoney	AD3_09	Ditch	100m	460568.16	5984/0/.16	513
Altahoney	AD4_09	Ditch	100m	460851.91	5983886.25	391
Altahoney	AD5_09	Ditch	100m	462053.06	5983836.84	322
Glennamong	GD 09	Ditch	1500m	457780.71	5981383.58	696