

Colonization and Extinction Patterns of a Metapopulation of Gold-spotted Pond Frogs, *Rana plancyi chosonica*

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ABSTRACT: We investigated colonization and extinction patterns in a metapopulation of the gold-spotted pond frog (*Rana plancyi chosonica*) near the Korea National University of Education, Chungbuk, Korea, by surveying the frogs in the nine occupied habitat patches in the study area four times per breeding season for three years (2006–2008) and recording whether the patches were occupied by frogs as well as how many frogs were calling in the patches. We then developed five a priori year-specific models using the Akaike Information Criterion (AIC). The models predicted that: 1) probabilities of colonization and local extinction of the frogs were better explained by year-dependent models than by constant models, 2) there are high local extinction and low colonization probabilities, 3) approximately 31% number of patches will be occupied at equilibrium, and 4) that considerable variation in occupation rate should occur over a 30-year period, due to demographic stochasticity (in our model, the occupation rate ranged from 0.222 to 0.889). Our results suggest that colonization is important in this metapopulation system, which is governed by mainly stochastic components, and that more constructive conservation effects are needed to increase local colonization rates.

Key words: Akaike Information Criterion, Demographic stochasticity, Metapopulation, *Rana plancyi chosonica*

INTRODUCTION

The ability to predict the persistence of a metapopulation (a group of spatially separated populations of the same species that interact at some level; Levins 1970) of an endangered amphibian species in fragmented habitat is crucial for species conservation and management plans because habitat fragmentation may be one of the major causes for global declines of amphibian populations (Alford and Richards 1999, Lopez and Pfister 2001, Dodd and Smith 2003, Vuilleumier et al. 2007). Habitat fragmentation can lead to isolation of local populations and reduce the possibilities for dispersal among populations. When habitats are isolated, making recolonization unlikely, local populations are placed at risk of extinction despite the ability of the isolated habitats to support the species for period of time (Gilpin and Hanski 1991, Pope et al. 2000, Fryxell 2001, Smith and Green 2005). Thus, conservation strategies for amphibians that consider metapopulation dynamics, including colonization and extinction processes, may increase the probability of long-term persistence of endangered species (Goodman 1987, Harrison et al. 1988, Hanski et al. 1995, Gotelli 1998).

Metapopulation concepts have been applied to amphibians, especially pond-breeding species that are characterized as having spatially isolated habitats, site fidelity, and limited dispersal ability

(Sjögren 1991, Skelly and Meir 1997, Skelly et al. 1999, Smith and Green 2005). The approach of “ponds as patches” (considering each pond as a usable habitat patch for a species) allows metapopulations to be easily identified and characterized, and permits the development of dynamic models to evaluate population persistence. Metapopulation models can also be constructed to estimate the parameters of species persistence based on patch-occupancy data (presence or absence of a population) rather than on population abundance within a patch (Gotelli 1998, Lopez and Pfister 2001, Gu and Swihart 2003, MacKenzie et al. 2003).

Call surveys of amphibian species have been extensively used to characterize the population status on local and regional levels due to their low money and time costs (McDiarmid and Donnelly 1994, Clinchy et al. 2001, Gu and Swihart 2003, MacKenzie 2005, Pellet and Schmidt 2005). However, call surveys may result in biased estimates of patch occupancy for a species if the detection probability is <1 (i.e., if there are false absences) (MacKenzie et al. 2002, 2003). MacKenzie et al. (2002, 2003) suggested that the bias can be prevented by performing multi-visit call surveys of the same patches over a long sampling period (e.g., several years).

Local populations of the gold-spotted pond frog, *Rana plancyi chosonica*, are declining in South Korea due to fragmentation and modification of their breeding patches caused by construction of buildings and roads, cutting of hillsides, and use of wetlands as

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agricultural fields. The frogs live in wetlands in both the breeding and non-breeding periods, and are relatively sedentary, with small individual home ranges averaging $\sim 713.8 \text{ m}^2$ (Ra et al. 2008). Thus, the metapopulation approach is appropriate for the evaluation of the effects of isolation and the extinction risk for gold-spotted pond frog populations (Smith and Green 2005).

We examined the distribution of gold-spotted pond frog populations near the Korea National University of Education (KNUE) for three years. Then, we investigated the metapopulation processes of extinction and colonization to provide basic information to guide conservation and management plans for this endangered species and explored long-term trends for the metapopulation through model simulations. We developed simple occupancy models to estimate the patch occupancy, colonization, and local extinction probabilities of local populations of gold-spotted pond frogs assuming that detection probability is less than one. Our models were based on three assumptions: first, that patches are closed to changes in occupancy within years, but open between years to allow migration across breeding patches; second, that false detection does not occur when the species is absent and that detection events are independent among the patches; and third, that detection probabilities were constant across multiple surveys within years.

MATERIALS AND METHOD

We conducted call surveys in rice fields and natural wetlands near the KNUE, Darak ri and Tapyeon ri, Chungwon gun, Chungbuk, Korea over three breeding seasons (2006–2008, Fig. 1). The study areas mainly consisted of rice fields with homogeneous habitat characteristics and a similar vegetation type. The patches were well divided by the banks and road around the rice fields. We identified nine breeding patches (seven rice fields and two fallow wetlands) of gold-spotted pond frogs with an average size of $3,308.4 \pm 1,152.3 \text{ m}^2$ (range, 1,169–5,131 m^2) and an average inter-patch distance of $170.6 \pm 160.9 \text{ m}$ (range, 38–513 m). All other potential patches (mainly rice fields) in the study area were also surveyed, but frog populations were not found in these patches.

Each patch was surveyed four times per breeding season for three years (resulting in a total of 108 patch visits) to examine whether the patch was occupied by the gold-spotted pond frogs and if so, how many frogs were calling. The calling activity of the gold-spotted pond frogs was relatively high between 21:00 and 02:00 (Sung et al. 2007) and playbacks of frog calls evoked high rates of calling activity from silent resident males, even in the daytime (H. C. Sung, unpublished data). Two observers conducted call surveys from 30 minutes after sunset until midnight by walking slowly along the edge of wet rice fields or ditches at a speed of

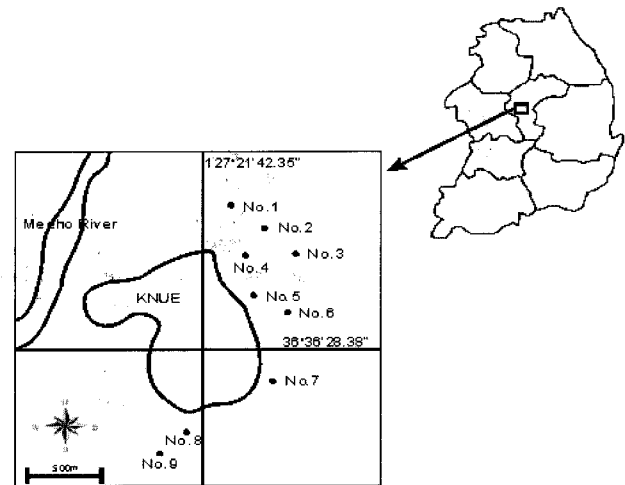


Fig. 1. Study area for call surveys of gold-spotted pond frog (*Rana plancyi chosonica*) populations near the Korea National University of Education (KNUE). Nine patches (patches 1–9) were occupied at least once during the three study years (2006–2008).

100 m per 5 minutes. After that, we played back mating calls to elicit responses so that we could further confirm the existence of the frogs and count the number of calling frogs (Sung et al. 2005). We visited the patches in a random order to avoid using the same surveying time for each patch across censuses.

Five metapopulation models (Table 1) were built with the program PRESENCE (available from <http://www.proteus.co.nz>) following the methods of MacKenzie et al. (2003). The program uses AIC (Akaike's Information Criterion; Burnham and Anderson 1998, Burnham and Anderson 2002) to select the best model that fit our survey data. The models in a candidate set were ranked by AIC values and ΔAIC (the difference between the model with the lowest AIC and the given model). The best model was the model with the lowest AIC value and the model weights (w ; relative likelihood of each model) indicated the degree of relative support of a model. We obtained model average estimates of detection probability (\hat{p}), patch occupancy rate ($\hat{\Psi}$), local extinction probability ($\hat{\epsilon}$), and colonization probability ($\hat{\gamma}$) based on the model weights, from which we inferred regional extinction and persistence probabilities. Dots (e.g. $\Psi(\cdot)$) indicate constants, and yr (e.g. $\Psi(\text{yr})$) indicates a year-dependent parameter. In addition, we estimated the equilibrium number of patches occupied (the fraction of patches remains constant over time) as:

$$\Psi = \frac{\gamma}{\gamma + \epsilon}$$

The equilibrium number of patches represents the minimum number of occupied patches that would allow a metapopulation to

Table 1. Summary of model selection procedure and parameter estimates for the gold-spotted pond frog (*Rana plancyi chosonica*). ΔAIC is the difference between the model with the lowest AIC and the given model; w is the Akaike weight; $\widehat{\Psi}$ is the estimated proportion of patches occupied; \widehat{p} is the estimated detection probability; $\widehat{\gamma}$ and $\widehat{\varepsilon}$ represent the estimated colonization and local extinction probabilities, respectively.

Model	ΔAIC	w	K	$\widehat{\Psi}$	\widehat{p}	$\widehat{\gamma}_{2007}$	$\widehat{\gamma}_{2008}$	$\widehat{\varepsilon}_{2007}$	$\widehat{\varepsilon}_{2008}$
$\Psi(\cdot), \gamma(\text{yr}), \varepsilon(\text{yr}), p(\text{yr})$	0	0.7604	8	0.890	0.777	0.38	0.195	0.620	0.805
$\Psi(\cdot), \gamma(\text{yr}), \varepsilon(\cdot), p(\cdot)$	3.62	0.1244	7	0.891	0.774	0.591	0.194	0.409	0.806
$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{yr})$	4.2	0.0931	6	0.896	0.774	0.325	0.325	0.410	0.410
$\Psi(\text{yr}), \gamma(\cdot), p(\text{yr})$	7.71	0.0161	7	0.569	0.677	0.408	0.408	0.592	0.408
$\Psi(\text{yr}), \gamma(\text{yr}), p(\text{yr})$	9.7	0.0060	8	0.567	0.668	0.521	0.371	0.479	0.629
Model average				0.884	0.774	0.402	0.211	0.573	0.761

persist in the study area, which consists of multiple patches (Gotelli 1998).

To reveal the turnover rate of occupied patches (τ_t), we used the following equation, which was originally developed by MacKenzie et al. (2006):

$$\tau_t = \frac{(1 - \Psi_t) \gamma_t}{\Psi_{t+1}}$$

where τ_t is the probability that occupied patch at t (year) + 1 is a newly occupied patch. Finally, simulations of metapopulation dynamics were performed with estimated parameters from this study to predict the fate of the breeding patches over 30 years. We used the Spearman's rank test (Zar 1999) to examine the relationship between the size of each occupied patch and the maximum number of frogs living in the patch. Numerical data in the text were presented as mean \pm SD.

RESULTS

Gold-spotted pond frogs were found in eight of nine surveyed patches in 2006, four in 2007, and five in 2008. During the study, only one patch was newly occupied by the frogs in the second year and only one patch occupied in the second year was re-occupied in the third year. The highest number of frogs counted by call surveys during the study period was 45 in patch No. 1 and the lowest was one in patches No. 5 and 6. No significant correlation appeared between the sizes of the occupied patch and the number of frogs therein determined by call surveys ($r_s = 0.42, n = 9, p = 0.26$).

Of the five metapopulation dynamics models, the most parsimonious model $\Psi(\cdot), \gamma(\text{yr}), \varepsilon(\text{yr}), p(\text{yr})$ was constructed from the AIC analysis with an Akaike weight of 0.7604, or 76% likelihood of being the best model (Table 1). The most parsimonious model suggested that colonization, local extinction, and detection proba-

bilities are year-specific, but that the overall level of occupancy is constantly maintained. The next two competing models $\Psi(\cdot), \gamma(\text{yr}), \varepsilon(\cdot), p(\cdot)$ and $\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{yr})$ also had some support, with AIC weights of 0.09 and 0.124, respectively. In those models, year-specific colonization and detection probabilities was also included. Model averaging, used to address model selection uncertainty (Burnham and Anderson 2002), indicated that the overall estimated patch occupancy rate was 0.884, with a detection probability of 0.774, and that the colonization probability appeared to be lower in 2008 (0.21) than in 2007 (0.40) while local extinction probability was much higher in 2008 (0.76) than in 2007 (0.57) (Table 1).

From the means of the yearly local extinction probabilities, the regional extinction probability was predicted to be 2.61%, the regional persistence probability was 97.4%, and the probability of continued local persistence for each patch for 10 years was 0.00167%. In addition, the predicted proportion of occupied patches at equilibrium was 0.315. The probability that a patch was newly occupied at time $t+1$ was 5.3% in 2007 and 3% in 2008. We predicted the metapopulation dynamics over the next 30 years with the estimated parameters (initial patch occupancy = 0.889, mean local extinction probability = 0.667 and colonization probability = 0.306). The average fraction of occupied patches over the next 30 years was estimated as 0.448 (± 0.161 ; range, 0.222–0.889).

DISCUSSION

Our results allow us to draw the following inferences about the metapopulation dynamics of the gold-spotted pond frog population in the vicinity of the KNUE over a three-year period: 1) probabilities of colonization and local extinction were better explained by year-dependent models than by constant models of any parameter,

2) metapopulation models predicted high local extinction and low colonization probabilities, 3) our models predicted that almost 31% of all patches would be occupied in the equilibrium condition of the metapopulation, and 4) simulations using the estimated parameters predicted considerable variation over the next 30 years (range, 0.222~0.889) due to demographic stochasticity. In addition, this study area showed quite high patch occupancy rates compared with occupancy rates of 0.170 in the city of Chungju and Chungwon gun (Sung et al. 2007). However, as our surveys were based on pre-existing patches, rather than newly found patches, the observed difference in occupancy rates is probably biologically meaningless.

High extinction probabilities in metapopulation dynamics are related to fragmentation and isolation of habitat patches, which are important factors influencing population persistence (Moilanen 1999, Hanski and Gaggiotti 2004, Smith and Green 2005). The total patch area is assumed to be correlated with patch density (i.e., the number of individual patches of a particular type per unit area of landscape) if patch areas are homogeneous. So, either can be used to represent the carrying capacity, and both factors are likely to be correlated with the extinction probability. However, we found no correlation between the size of an occupied patch and the number of frogs in that patch. Similarly, in metapopulation systems of eight species of butterflies, amphibians, and birds, the correlations between patch size and the number of individuals were also weak (Pellet et al. 2007). In addition, the theory of island biogeography predicts that large patches should have higher colonization rates than small patches in a metapopulation because of a positive correlation between patch area and the immigration rate (Gilpin and Diamond 1976). Unfortunately, our data were insufficient to reveal the effect of patch area on metapopulation processes. In the future, more close investigations of this metapopulation using biologically realistic and patch-specific models are needed to address this issue.

Limited dispersal plays a role in structuring metapopulations, so the dispersal abilities of amphibians under metapopulation conditions should be tested prior to applying metapopulation theory (Smith and Green 2005). Gold-spotted pond frogs live a sedentary lifestyle close to water with daily movement averaging only 9.8 m during both the breeding and non-breeding seasons, and they hibernate at the edges of wetlands, an average of ~32 m from their breeding patches (Ra et al. 2008). For these reasons, breeding populations of gold-spotted pond frogs are highly disjunct, and migration between subpopulations for the frogs may be limited, which indicates that a metapopulation approach may be appropriate for predicting the fate of this species in the study area.

The results raise conservation concerns on the long-term persistence of the gold-spotted pond frog metapopulation in this study area, mainly because the local extinction probability exceeds the

colonization probability, which resulted in declines in the number of subpopulations in the metapopulation system during the study period. In particular, small populations in which the probability that new local subpopulations will be created by colonization events is low (3~5.3%) are likely to become extinct before the population size can increase. The relatively small size of the metapopulation could accelerate population extinction due to demographic stochasticity and environmental stochasticity in metapopulation dynamics (Gotelli 2001). To date, the data are insufficient to evaluate whether the unoccupied patches are suitable for breeding by the gold-spotted pond frog. However, in our study area, adjacent potential breeding habitats mainly consisted of homogeneous rice fields, so colonization of neighboring unoccupied patches might be possible. However, the shortest distance between neighboring metapopulations was 2.8 km. Considering the numerous obstacles (e.g. hills, villages) between metapopulations, it seems very unlikely that migration among them could occur. Thus, this study suggests that increasing the colonization rate for local subpopulations may be a key to improving the probability of long-term persistence of this metapopulation. Constructive conservation and management plans should be designed to increase local colonization rates and to protect existing subpopulations, resulting in enhancement of the probability of persistence of the whole metapopulation

ACKNOWLEDGMENTS

This subject was supported by Korea Ministry of Environment as "The Eco-technopia 21 project (#052-071-044)".

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(Received March 30, 2009; Accepted May 20, 2009)