Spatial Scale and Determination of Species Status of the Green Frog

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Abstract: Although the importance of spatial scale in determining species status (abundance and distribution) is widely recognized, most ecological investigations have been conducted at local scales. Our goal was to investigate the importance of spatial scale in assessing the status of the green frog (Rana clamitans melanota) in the center of its range in eastern North America. Using repeated surveys at 160 ponds from 1992 to 1994, we investigated patterns of occupancy, abundance, and turnover at local, sub-regional, regional, and geographic scales to determine the status of the green frog in southwestern Ontario, Canada. Patterns of pond occupancy were stable at the geographic scale. Occupancy was stable in two regions and decreased in one. At the sub-regional scale, occupancy was stable in six sub-regions, increased in one, and decreased in two. Patterns of adult abundance were stable at the geographic scale. At the regional scale trends in adult abundance were increasing, decreasing, or stable in each of three regions. At the sub-regional scale abundance was stable in three, increasing in one, decreasing in two, and no trend occurred in three sub-regions. At the local scale abundance was stable at 20% of ponds, increased at 17.8%, decreased at 14.4%, and no trend existed at 47.8%. Colonization and extinction rates ranged from 0 to 0.20 and 0 to 0.35 ponds/pond occupied/year, respectively, and differed among regions. Local extinctions took place at 25% of ponds during the study, but no sub-regional or regional scale extinctions occurred. Small populations (<10 adults/pond) were prone to local extinction. Determination of the status of the green frog is scale dependent. Although green frog populations are dynamic, it is common and stable at the geographic scale, but its status varies among regions or sub-regions. Although processes that negatively affect a species may operate at the local scale, a large-scale perspective is necessary to determine status.

Escala Espacial y Determinación del Estatus de la Especie de Rana Verde

Resumen: Aunque la importancia de la escala especial para la determinación del estatus de la especie (abundancia y distribución) es ampliamente reconocida, la mayoría de las investigaciones, ecológicas se han conducido en escalas locales. Nuestra meta fue investigar la importancia de la escala especial en la evaluación del estatus de la rana verde (Rana clamitans melanota) en el centro de su rango de distribución en el este de Norte América. Mediante muestreos repetidos en 160 estanques de 1992 a 1994 investigamos los patrones de ocupación, abundancia y reemplazo en escalas local, sub-regional, regional y geográfica para determinar el estatus de la rana verde en el suroeste de Ontario, Canadá. Los patrones de ocupación de estanques fueron estables en la escala geográfica. La ocupación fue estable en dos regiones y decreció en una. En la escala sub-regional la ocupación fue estable en seis sub-regiones, se incrementó en una y decreció en dos. En la escala regional la abundancia de adulto tendió a incrementar, decrecer o estabilizarse en cada uno de las tres regiones. En la escala sub-regional la abundancia fue estable en tres sub-regiones, incrementó en una, decreció en dos y no hubo tendencia en tres. En la escala local, la abundancia fue estable en 20% de los estanques, incrementó en 17.8%, decreció en 14.4% y no hubo tendencia en 47.8%. Las tasas de colonización y extinción variaron entre 0 a 0.20 y 0 a 0.35 estanques/estanque ocupado/año respectivamente, y fueron diferentes entre regiones. Durante el estudio ocurrieron extinciones locales en 25% de los estanques, pero no ocurrieron...
Introduction

Determining the status of species is of fundamental interest to both ecologists and conservation biologists. By status, we mean a species’ occupancy (incidence) and abundance, and whether its populations are stable, increasing or decreasing. Because of the increasing global loss of biological diversity, there is increased urgency to accurately determine the status of species. Although extinction of species is the most troublesome scenario in conservation, a species cannot go extinct until all of its populations are extinct (Ehrlich & Daily 1993). Population viability theory and the concept of minimum viable population size suggest that small and fluctuating populations are vulnerable to local extinctions resulting from catastrophes, environmental or demographic stochastic factors, or genetic factors (Shaffer 1987).

Determining the status of species is often difficult because of limited knowledge of population dynamics and distribution. Ecological studies have traditionally been conducted at local scales and over short time spans (Schluter & Ricklefs 1993). Extrapolating conclusions from studies conducted at limited scales to larger scales or different locations can be misleading (Schneider 1994). Different patterns can either emerge or be hidden depending on the scale of perception (Wiens et al. 1986; Schneider 1994). Interest in the issue of spatial and temporal scale has increased rapidly in both ecology (Schneider 1994) and conservation biology (Noss 1992). Although both temporal and spatial scale are recognized as important, more attention has concerned the lack of long-term studies than the lack of studies conducted at expanded spatial scales.

An expanded spatial scale recognizes the roles of regional (Ricklefs & Schluter 1993) and metapopulation (Hanski & Gilpin 1991) processes. In metapopulations local extinctions may occur frequently, but recolonization permits species persistence at the regional scale. Patterns of regional occupancy (fraction of patches occupied) are ultimately determined by the balance between local colonization and extinction. Some species may live in naturally isolated local populations or habitat fragmentation may impose metapopulation structure (Taylor 1991). Many amphibian species live in isolated habitats (Pechmann & Wilbur 1994; Blaustein et al. 1994a), and an increasing number of studies suggest the existence of metapopulation structure in amphibian species (Gill 1978; Sjögren 1991, 1994; Bradford et al. 1993; Berman & Sapozhnikov 1994).

Much attention has been devoted to the question of global amphibian declines (Blaustein & Wake 1990; Phillips 1990; Wake & Morowitz 1991; Pechmann & Wilbur 1994). Studies suggest declining populations of some species but not others, and some geographic areas are affected, whereas others are not. Much of the debate has centered on the issues of natural variation in amphibian population size and the best methods for investigating suspected declines. The general consensus is that long-term studies are urgently needed (Pechmann et al. 1991; Blaustein et al. 1994a). Although the importance of spatial issues to amphibian decline has been recognized (Blaustein & Wake 1990; Pechmann & Wilbur 1994), few studies have been conducted at expanded scales (but see Stumpel 1987; Sjögren 1991).

We employed a multi-scaled approach to examine the distribution, abundance, and dynamics of a common North American amphibian species, the green frog (Rana clamitans melanota). Using repeated surveys at 160 ponds we investigated patterns of occupancy, abundance, and turnover (colonization-extinction dynamics) at local, sub-regional, regional, and geographic scales to determine the status of the green frog in southwestern Ontario, Canada.

Study System and Methods

Green Frog

The green frog is a large (5.7–9.0 cm, mean snout-vent length) aquatic frog that occurs in the eastern United States and southeastern Canada (Conant & Collins 1991). The green frog and bronze frog (R. clamitans) are the only two subspecies of R. clamitans. The green frog occurs from northern Ontario and Quebec south into Alabama and Georgia, occupying most of the species range, whereas the bronze frog occurs on the southern fringe of the range. All citations we use refer to R.c. melanota. The green frog is a habitat generalist, occupying nearly every type of permanent water habitat and commonly occurring in semi-permanent or permanent ponds (Walker 1946; Minton 1972; Vogt 1981; Harding & Hol-
man 1992; Hecnar 1997). Throughout the activity season (= March to October) adults remain at or near the shoreline or in areas of shallow water with emergent vegetation (Breckenridge 1944; Walker 1946; Logier 1952; Minton 1972; Vogt 1981). Subadults may forage or disperse widely (Vogt 1981; Harding & Holman 1992; pers. obs.). Most subadults (97%) disperse from their natal pond and movements less than or equal to 4.8 km have been recorded (Schroeder 1976). Green frogs are prolonged breeders and have a resource defense polygynous mating system with larger males tending to have multiple mating opportunities (Wells 1977). Males defend small territories (Martof 1953a,b) and attract females by calling day and night (Wells 1978). Females lay one or two clutches per year (Wells 1976), and clutch size ranges from 1000–4000 eggs in a floating mat of eggs (Vogt 1981). Turnover of individuals in green frog populations is high. Of marked frogs about 45% of adults are recaptured, but only about 5% of metamorphs are recaptured (Martof 1956a). Green frogs reach maximum adult size at greater than or equal to 3 years and can live a decade; however, few individuals greater than 5 years old occur in nature (Martof 1956b). In the northeastern United States and southern Ontario, green frogs generally emerge from their aquatic hibernation sites in late March or early April and breeding occurs from May to early August (Logier 1952; personal observation).

**Study Area**

The study area in southwestern Ontario, Canada, has flat to rolling terrain in the Great Lakes basin (Hecnar 1997) and occupies a central position in the species’ range. Climate ranges from moderate to cool temperate (mean annual temperature 6.0–9.1°C). Flora of the area includes species of the deciduous forest region and the deciduous-boreal ecotone of the Great Lakes-St. Lawrence forest region (Rowe 1972).

The landscape has been highly modified by humans since the mid-1800s. Extensive forests and wetlands covered the area prior to European settlement, but by 1850 maximal forest clearance for agriculture had occurred (Moss & Davis 1989). Forest cover (by township) in southwestern Ontario presently ranges from about 2–80%. Large-scale wetland drainage began by the 1880s. Wetlands in pre-settlement times covered 68.9% of the southern portion of the study area and 23% of the northern portion (Snell 1987). Today, wetlands cover (by county) from 2.9% to 10.0% of the basin. Human population in the area is about 3 million and most of the landscape remains under intense agricultural use (Statistics Canada 1993). Much of the present wetland habitat consists of artificial ponds constructed for agricultural use.

For regional comparisons within the study area, we used wetland regions that were based on physiographic characteristics such as geology, drainage, and vegetation (Anonymous 1984). These study units represent a more natural partitioning of the landscape than political boundaries or a grid system. The three wetland regions we used were the Essex Plain (5341 km²), Stratford Plain (9469 km²), and the Grey-Bruce Uplands (7487 km²).

For sub-regional comparisons we used groups of ponds at the watershed scale. We determined sub-regions by examining locations of ponds and drainage patterns from maps and by considering the nature of the landscape. We chose nine sub-regions within the three wetland regions, four in Essex, three in Stratford, and two in Grey-Bruce. Mean (± 1 SE) area of the sub-regions was 27.9 ± 5.71 km², mean nearest neighbor distance between sampled ponds was 1.5 ± 0.61 km, and mean distance between closest ponds in adjacent sub-regions was 12.0 ± 1.72 km. Sub-regions are Harrow (43 km²), Ojibway (12 km²), Amherstburg (14 km²), and Albuna (15 km²) in Essex; Bayfield (26 km²), Parkhill (65 km²), and Hay Township (17 km²) in Stratford; and McGregor Point (29 km²), Allan Park (30 km²), and Grey-Bruce.

We used ponds as local study units rather than other types of wetlands because they are easily delimited spatially, may act as functional islands, are an important green frog habitat, and provide a study system capable of being analyzed on a geographic scale. We located ponds using topographic maps and by inquiring at conservation authorities and provincial and national parks. Some ponds were discovered by chance or by information provided by private landowners. After locating a pond we added it to our list if permission for access was obtained. To avoid biased selection all ponds accessed were included. Thus, the suite of ponds we used should represent a realistic subset of the spectrum of available ponds. Of the ponds we studied 87% were artificial, mean (± 1 SE) depth was 1.95 ± 0.096 m, area was 6867 ± 3362.7 m², and age was 29.3 ± 1.68 years.

We surveyed 120 ponds in 1992, added 36 more ponds in 1993, and 4 more in 1994 for a total of 160 ponds. For sub-regional analyses we used 125 of the 160 ponds. We did not use 35 of the ponds because they occurred in other sub-regions and were too few in number to use as additional groups for analysis.

**Survey Methods**

We conducted surveys from late March to late July in each of 3 years (1992–1994) and visited each pond on at least 3 days per year. The duration of our study period covered the peak of adult green frog activity. Searches involved three to seven people intensively searching the perimeter to approximately 10 m landward from the pond edge, and wading, canoeing, and dip-netting throughout the pond. The same core of per-
sonnel (senior students and biologists) were used in
each year and one of us (S.J.H.) was present on each sur-
vey. Considering survey intensity, green frog behavior,
and personnel used, we assume that interobserver differ-
ences were minimal. We recorded green frogs as present
if any age class (egg, tadpole, subadult, adult) was ob-
served or if calls were heard on any visit at a pond dur-
ing the year, or absent, if no age class was detected. Dur-
ing each visit we counted the number of adult green frogs
observed at each pond. We used the maximum number of
adults counted at a pond on a single survey for each
year as an estimate of population abundance. A rigorous
estimate of population size would require marking indi-
viduals or using removal sampling. Our method is ap-
propriate for adult green frogs because they do not wander
far from water, they are conspicuous, and they show site
fidelity. Although we recognize the role of juvenile dis-
persers in metapopulations, we did not include recent
metamorphs in the counts because in most cases they
were impossible to count and most disperse from their
natal ponds.

Turnover is the extinction of local populations and es-
-tablishment of new populations in empty habitat
patches by dispersers from existing local populations
(Hanski & Gilpin 1991). To study turnover at ponds we
estimated extinction and colonization rates based on
changes in presence or absence of green frogs between
years in each sub-region. To calculate extinction rate we
divided the number of ponds where local extinctions oc-
curred in a given year by the total number of ponds oc-
cupied in the previous year. To calculate colonization
rate we divided the number of newly occupied ponds in
a given year by the total number occupied in the previ-
ous year. In this way we were able to produce estimates
sub-region. Connell and Sousa (1983) recommended a
minimum time span of at least one complete turnover of
individuals to assess population persistence. The dura-
tion of our study (three seasons) would be close to a sin-
gle turnover because few green frogs are greater than 5
years old (Martof 1956b). We used annual surveys rather
than an extended interval because increasing census in-
terval time tends to underestimate turnover rates (Dia-
mond & May 1977; Connell & Sousa 1983; Clark &
Rosenzweig 1994). For example, if we waited 5 years
before resurveying a pond, as many as two extinctions
and two colonizations could have taken place without
being detected.

To investigate the relationship between population
size and risk of extinction, we compared adult abun-
dance at individual ponds in one year with presence or
absence in the following year. We used 76 populations
time intervals for a single analysis ($n = 182$). This al-
lowed us to make an empirical estimate of local extinc-
tion probability as a function of adult abundance.

Statistical Analyses

For all statistical analyses we used SYSTAT 5.01 (Wilkin-
son 1990). To investigate differences among regions or
sub-regions in occupancy or abundance, we used re-
peated measures analyses of variance (ANOVA) because
the same ponds were used in each year. In the repeated
measures ANOVAs, occupancy or abundance was the
dependent variable, region or sub-region was the group-
ing factor, and year was the repeated measure. For abun-
dance we conducted a nested repeated measures
ANOVA, with sub-regions nested within regions. Nested
analyses could not be conducted for occupancy, coloni-
-zation or extinction because these data are calculated
for the individual sub-regions whereas, abundance is
based on counts at the scale of local ponds. To deter-
mine if mean occupancy and abundance differed among
spatial scales and over time, we conducted repeated
measures ANOVAs with scale as the grouping factor.

To homogenize variances and normalize variables we
transformed data using arcsine for occupancy, square
root for population size, and log$_{10}$ for colonization and
extinction rate. In the colonization and extinction rate
analyses, variance remained heterogeneous after trans-
formation so we used the Kruskal-Wallis non-parametric
test in lieu of ANOVA. To examine the rates over the en-
tire study (1992–1994), we reanalyzed colonization and
extinction using the mean rates for the 3-year period.
When repeated measures ANOVAs were significant
($p < 0.05$) we used pairwise multiple comparisons us-
ing the Tukey-Kramer method for unequal sample sizes
(Day & Quinn 1989).

To investigate trends in occupancy and abundance
over 1992 to 1994, we classified patterns into four cate-
gories: increasing, decreasing, stable, or no trend. To be
classified as increasing or decreasing the sequential an-
ual data had to show a monotonic trend. We defined a
stable population as one where the number of adults did
not change by greater than one individual/year. Other
cases were classified as having no apparent trend. We
considered trends to be present between 1992 and
1994, if occupancy changed greater than 10% or where
abundance error bars did not overlap. To examine
trends at the local scale, we used ponds for which we had
3 consecutive years of survey data (90 ponds for
abundance, 105 ponds for occupancy). We classified
trends in local occupancy (absent = 0, present = 1) for
1992, 1993, and 1994 as follows: stable (1,1,1), increas-
ing (0,1 or 0,1,1), decreasing (1,0,0 or 1,1,0), or no
trend (0,1,0 or 1,0,1).

Differences in numbers of degrees of freedom between
descriptive statistics and the repeated measures ANOVAs
exist because the repeated measures analyses use only
the subset of ponds for which we have 3 consecutive
years of data. Degrees of freedom are fewer for abundance
than occupancy analyses because occupancy is based on
any life stage being present at a pond, whereas abundance
is based only on ponds where adults were present.

To examine the relationship between turnover rates
and occupancy, we used linear regression on appropri-
ately transformed variables. We report descriptive statis-
tics as means ± 1 standard error of the mean.

Results

Occupancy

At the geographic scale, the green frog was widely dis-
tributed among ponds and occupancy was stable from
1992 to 1994. Green frogs were present at 77.5% (93 of
120) of ponds in 1992, 80.1% (125 of 156) in 1993, and
73.8% (118 of 160) in 1994.

At the regional scale occupancy varied from 47.5% in
Essex in 1994, to 100% in Stratford in 1992 (Fig. 1). Re-
peated measures ANOVA (Table 1) indicated that occu-
pancy differed significantly among regions, but did not
differ over time, nor was there a significant year × region
interaction. Multiple comparisons indicated that occup-
ancy was significantly lower \( p < 0.01 \) in Essex than
in Stratford and Grey-Bruce in each year.

At the sub-regional scale occupancy ranged from
36.4% in Ojibway in 1994 to 100% in McGregor Point
and Bayfield in 1992 and remained at 100% in all years in
Hay Township and Parkhill. Occupancy appeared to be
stable in six sub-regions (Harrow, Ojibway, McGregor,
Bayfield, Hay Township, Parkhill), increasing in one (Al-
lan Park), and decreasing in two (Amherstburg, Albuna)
(Fig. 2). All four sub-regions in Essex showed a general

Repeated measures ANOVA, using scale as a factor, in-
dicated mean occupancy did not differ significantly be-
tween sub-regional and regional scales, among years, or
in the interaction between year and scale (Table 2). Never-
theless, variation in occupancy decreased with increas-
ing spatial and temporal scale (Fig. 3a,b).

Table 1. Univariate and multivariate repeated measures ANOVA of green frog occupancy among regions for 1992 to 1994.

<table>
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<th>Unitivariate Source</th>
<th>SS</th>
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<th>MS</th>
<th>F</th>
<th>p</th>
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<th>( \eta ) _HF (^b)</th>
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<tr>
<td>Year</td>
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<td>2</td>
<td>74</td>
<td>1.85</td>
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<td>0.219</td>
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<td>Error</td>
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<tr>
<td></td>
<td>Pillai trace = 0.548</td>
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<td>5</td>
<td>3.036</td>
<td>0.137</td>
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<td></td>
<td>H-L trace = 1.214</td>
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<td>5</td>
<td>3.036</td>
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</tr>
<tr>
<td>Year 3</td>
<td>Wilk's ( \lambda )= 0.326</td>
<td>4</td>
<td>10</td>
<td>1.879</td>
<td>0.191</td>
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<td></td>
<td>Pillai trace = 0.688</td>
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<td>4</td>
<td>8</td>
<td>2.024</td>
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\( \lambda = \theta \) = 0.667 \hspace{1cm} S = 2, \hspace{1cm} M = -0.5, \hspace{1cm} N = 1.5

\(^a\) Greenhouse-Geisser epsilon = 0.6116.
\(^b\) Huynh-Feldt epsilon = 0.9430.
At the regional scale mean adult abundance ranged from 3.4 ± 0.45 in Essex to 33.8 ± 20.49 in Grey-Bruce (Fig. 4). The general trend in adult abundance at the regional scale from 1992 to 1994 was increasing in Essex, stable in Stratford, and decreasing in Grey-Bruce (Fig. 4). Nested repeated measures ANOVA indicated that mean abundance differed significantly among regions and sub-regions (Table 3), abundance changed over time, and there were significant year × region and year × sub-region interactions. At the regional scale multiple comparisons revealed that abundance was significantly lower in Essex than in either Stratford or Grey-Bruce in 1992 and 1993 (p < 0.01). In 1994 abundance in Essex was significantly lower than in Stratford (p < 0.001), but not significantly different from Grey-Bruce (p = 0.325).

At the sub-regional scale, mean adult abundance varied from 2.2 ± 0.32 in Amherstburg to 54.0 ± 41.04 in Allan Park, both in 1992 (Fig. 5). At the sub-regional scale general trends in population size differed. Adult abundance appeared stable in three sub-regions (Amherstburg, Ojibway, Albuna), increased in one (Harrow), decreased in two (McGregor Point, Allan Park), and no apparent trend was discernible in three (Bayfield, Hay, Parkhill). Multiple comparisons indicated complex changing patterns among years.

At the local scale (individual ponds) adult abundance ranged from 1 to 136 in 1992, 1 to 69 in 1993, and 1 to 100 in 1994. From 1992 to 1994 adult abundance (n = 90 ponds) was stable at 20% of ponds, increased at 17.8%, decreased at 14.4%, and no trend existed at 47.8%.

Repeated measures ANOVA, using scale as a factor, indicated that mean adult abundance did not differ significantly among local, sub-region or regional scales, among years, or in the interaction between scale and year (Ta-
Turnover

At the geographic scale, mean colonization rate was 0.09 ± 0.037 ponds/pond occupied/year for 1992 to 1993 and 0.04 ± 0.020 for 1993 to 1994, but did not differ significantly ($t_{8df} = 2.22, p = 0.057$; Fig. 6). Mean extinction rate was 0.09 ± 0.035 ponds/pond occupied/year in 1992 to 1993 and 0.16 ± 0.065 for 1993 to 1994, and also did not differ significantly ($t_{8df} = 1.481, p = 0.177$).

At the regional scale colonization rates varied from 0 to 0.20 and extinction rates varied from 0 to 0.35 (Fig. 3c,d). Nevertheless, variation in abundance decreased with increasing spatial and temporal scale (Fig. 3c,d).

Discussion

Determination of the status of green frogs is dependent on the spatial scale of investigation and the scale of data summary (Table 6). During our study the green frog was stable in terms of abundance and occupancy at the geographic scale. As spatial scale is reduced to regional, sub-regional, and finally to local, trends emerge, variation increases, and differences among locations increase. Our analyses revealed three important features of the green frog system (Table 6). First, abundance was quite variable and trends differed among regions, sub-regions, and local ponds. Second, occupancy was stable at the regional scale (two of three regions) and sub-regional scale (six of nine sub-regions) and at many local ponds (≥70%) (Table 6). Variance in both abundance and oc-
cupancy decreased as spatial scale increases. Although local extinctions commonly occurred, extinctions did not occur at larger spatial scales. This suggests that although green frog populations may undergo substantial fluctuations in local abundance, there is persistence at regional and sub-regional scales. The third important result was that inherent differences in the levels of abundance and occupancy exist among regions.

A prominent pattern was of lower abundance and occupancy in Essex than in the other regions. Essex is the most heavily affected region with the highest levels of habitat fragmentation, the most intensive agriculture, and the highest human population density (Hecnar 1997). Factors capable of reducing green frog population size in Essex may act through direct adult mortality, reduced reproductive effort, or reduced recruitment. Possible factors include chemical pollution, climate, or increased predation. Acid rain has been suggested as a possible cause of amphibian decline (Harte & Hoffman 1989; Beebee et al. 1990), but can be ruled out in southwestern Ontario where pond waters are hard, alkaline, and well-buffered against pH change (Hecnar & M’Closkey 1996a). Runoff or leaching of nitrogen fertilizers are a potential problem. Nitrates have toxic effects on amphibian larvae (Berger 1989; Baker & Waights 1993, 1994; Hecnar 1995), and concentrations in the field can reach levels toxic to green frog tadpoles (Hecnar 1995).

Table 3. Univariate and multivariate nested repeated measures ANOVA of adult green frog abundance among regions and sub-regions for 1992 to 1994.

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<th>Univariate source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
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<th>p</th>
<th>(P_{GG})</th>
<th>(P_{HF})</th>
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<td>Between subjects</td>
<td></td>
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<td>Region</td>
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<td>71</td>
<td>25.70</td>
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<tr>
<td>Sub-region</td>
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<td>11</td>
<td>4.04</td>
<td>&lt;0.010</td>
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</tr>
<tr>
<td>Error</td>
<td>200</td>
<td>72</td>
<td>3</td>
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</tr>
<tr>
<td>Year</td>
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<td>4</td>
<td>5.20</td>
<td>0.007</td>
<td>0.008</td>
<td>0.00</td>
</tr>
<tr>
<td>Year (\times) region</td>
<td>26</td>
<td>4</td>
<td>7</td>
<td>8.29</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.00</td>
</tr>
<tr>
<td>Year (\times) sub-region</td>
<td>20</td>
<td>12</td>
<td>2</td>
<td>2.13</td>
<td>0.019</td>
<td>0.021</td>
<td>0.01</td>
</tr>
<tr>
<td>Error</td>
<td>113</td>
<td>144</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<th>Multivariate source</th>
<th>Test</th>
<th>Hypothesis</th>
<th>Error</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>Wilk’s (\lambda) = 0.865</td>
<td>2</td>
<td>71</td>
<td>5.555</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Pillai trace = 0.135</td>
<td>2</td>
<td>71</td>
<td>5.555</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>H-L trace = 0.156</td>
<td>2</td>
<td>71</td>
<td>5.555</td>
<td>0.006</td>
</tr>
<tr>
<td>Year (\times) region</td>
<td>Wilk’s (\lambda) = 0.683</td>
<td>4</td>
<td>142</td>
<td>7.452</td>
<td>0.000</td>
</tr>
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<td></td>
<td>Pillai trace = 0.344</td>
<td>4</td>
<td>144</td>
<td>7.474</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>H-L trace = 0.424</td>
<td>4</td>
<td>140</td>
<td>7.428</td>
<td>0.000</td>
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<td>S = 2, (M = -0.5), (N = 34.5)</td>
<td>1</td>
<td>2.101</td>
<td>0.020</td>
</tr>
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<td>Year (\times) sub-region</td>
<td>Wilk’s (\lambda) = 0.721</td>
<td>12</td>
<td>142</td>
<td>2.101</td>
<td>0.020</td>
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<tr>
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<td>Pillai trace = 0.294</td>
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<td>2.069</td>
<td>0.022</td>
</tr>
<tr>
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<td>H-L trace = 0.365</td>
<td>12</td>
<td>140</td>
<td>2.132</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>theta = 0.227</td>
<td>S = 2, (M = 1.5), (N = 34.5)</td>
<td>1</td>
<td>2.132</td>
<td>0.018</td>
</tr>
</tbody>
</table>

\(a\) Greenhouse-Geisser epsilon = 0.9441.
\(b\) Huynh-Feldt epsilon = 1.000.

Figure 5. Mean adult green frog abundance among sub-regions from 1992 to 1994. The name of the sub-region and the region in which it occurs appears in each panel.
High levels of organochlorine pesticides and their residues from historic application persist in amphibians in the Essex region (Russell et al. 1995). Climate can be ruled out because it is similar among regions. Increased predation is also a possibility. Many studies have demonstrated or suggested that fish negatively affect amphibians (Heyer et al. 1975; Hayes & Jennings 1986; Bradford et al. 1993; Donnelly & Guyer 1994). Proportionately more ponds in Essex have predatory fish (e.g., sunfish, bass, trout) present than ponds in Stratford or Grey-Bruce (Hecnar 1997). Nevertheless, neither green frog distribution nor abundance is negatively affected by the presence of predatory fish in southwestern Ontario (Hecnar & M’Closkey 1996b, unpublished data). At an isolated pond, however, it is possible that efficient terrestrial vertebrate predators could substantially reduce frog population size.

Population viability theory suggests that small populations are more vulnerable to extinction than large populations (Richter-Dyn & Goel 1972; Leigh 1981). Our observations are consistent with this theory. Extinctions occurred only in small populations where adult abundance was less than 10. Small populations would be more susceptible to demographic or environmental stochastic events. Adult abundance indicated that population size was significantly lower in Essex than in the other regions and would thus account for the higher extinction rates and lower occupancy rates we found in Essex. The increasing trend in adult abundance in Essex may seem inconsistent with the high extinction rates; however, this occurs because of differing conditions at local ponds. Although poor conditions led to extinctions at some sites, favorable conditions led to population growth at other sites. Colonization rate also tended to be higher in Essex. This is not surprising because there are more permanent ponds in Essex (pers. obs.), resulting in inter-pond distances (0.3 ± 0.06 km) being less than potential dispersal distance (4.8 km, Schroeder 1976). We have commonly observed young green frogs far from

Table 4. Univariate and multivariate repeated measures ANOVA of green frog adult abundance among local, sub-regional and regional scales for 1992 to 1994.

<table>
<thead>
<tr>
<th>Unitivariate source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
<th>pGG</th>
<th>pHF</th>
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<tbody>
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<td>Between subjects</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>3</td>
<td>2</td>
<td>1</td>
<td>0.28</td>
<td>0.756</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>484</td>
<td>101</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Within subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>2</td>
<td>0.6</td>
<td>0.68</td>
<td>0.507</td>
<td>0.498</td>
<td>0.50</td>
</tr>
<tr>
<td>Year × scale</td>
<td>2</td>
<td>4</td>
<td>0.5</td>
<td>0.52</td>
<td>0.722</td>
<td>0.711</td>
<td>0.71</td>
</tr>
<tr>
<td>Error</td>
<td>187</td>
<td>202</td>
<td>0.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</table>

<table>
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<th>Multivariate source</th>
<th>Test</th>
<th>Hypothesis</th>
<th>Error</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>Wilk’s λ = 0.986</td>
<td>2</td>
<td>100</td>
<td>0.726</td>
<td>0.486</td>
</tr>
<tr>
<td></td>
<td>Pillai trace = 0.014</td>
<td>2</td>
<td>100</td>
<td>0.726</td>
<td>0.486</td>
</tr>
<tr>
<td></td>
<td>H-L trace = 0.015</td>
<td>2</td>
<td>100</td>
<td>0.726</td>
<td>0.486</td>
</tr>
<tr>
<td>Year × scale</td>
<td>Wilk’s λ = 0.982</td>
<td>4</td>
<td>200</td>
<td>0.462</td>
<td>0.764</td>
</tr>
<tr>
<td></td>
<td>Pillai trace = 0.018</td>
<td>4</td>
<td>202</td>
<td>0.465</td>
<td>0.761</td>
</tr>
<tr>
<td></td>
<td>H-L trace = 0.019</td>
<td>4</td>
<td>198</td>
<td>0.459</td>
<td>0.766</td>
</tr>
<tr>
<td></td>
<td>theta = 0.017</td>
<td>S = 2, M = −0.5, N = 49.0</td>
<td>0.693</td>
<td></td>
<td></td>
</tr>
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</table>

*Greenhouse-Geisser epsilon = 0.9394.

*Huynh-Feldt epsilon = 0.9755.

S.W. Ontario
Essex
Stratford
Grey-Bruce

S.W. Ontario
Essex
Stratford
Grey-Bruce

Figure 6. Mean colonization and extinction rates for green frogs in southwestern Ontario (geographic scale) and by regions in 1992-1993 (a) and 1993-1994 (b). Open bars represent colonization and closed bars represent extinction.
permanent sources of water and found that green frogs quickly colonized new ponds. The Essex region also has flat topography and is dissected by many deep ditches that may function as corridors and reduce pond isolation. Higher colonization rates may occur because more ponds are available when occupancy is lower.

Turnover rates were variable, but generally high at all spatial scales. Although its populations are highly dynamic, the green frog is widely distributed and has the highest occupancy of all pond-dwelling amphibian species in southwestern Ontario (Hecnar 1997). Although green frog occupancy was stable at the geographic scale, a slight decline occurred from 1993 to 1994. All four Essex sub-regions showed a pattern of declining occupancy from 1993 to 1994. Record cold temperatures combined with low snow cover in Essex during the winter of 1993–1994 (Environment Canada 1994) appears to have increased mortality because of winterkill (complete pond freezing and/or oxygen depletion) in the spring of 1994. Mortality caused by winterkill has been noted in green frogs (Collins & Wilbur 1979) and other ranid species (Manion & Cory 1952; Bradford 1983). The impact of environmental stochasticity is dependent on the degree of spatial correlation in environmental factors (Gilpin 1987; Harrison & Quinn 1989). The severe winter of 1993–1994 was a rare event and evidently some degree of spatial correlation existed because a regional pattern of decreased occupancy was observed in the Essex region. Nevertheless, populations in some ponds were not affected and mean abundance showed an increasing trend. The general patterns of status in both abundance and occupancy do suggest that a high level of asynchrony exists even at the local scale, which may help promote persistence at the regional scale.

Table 5. Green frog adult abundance and vulnerability to extinction.

<table>
<thead>
<tr>
<th>Abundance (n of adults)</th>
<th>Ponds surveyed (n)</th>
<th>Local extinctions (n)</th>
<th>Probability of extinction</th>
<th>Confidence interval* (95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤5</td>
<td>102</td>
<td>23</td>
<td>0.225</td>
<td>(0.1485–0.3180)</td>
</tr>
<tr>
<td>6–10</td>
<td>32</td>
<td>2</td>
<td>0.065</td>
<td>(0.0077–0.2071)</td>
</tr>
<tr>
<td>&gt;10</td>
<td>48</td>
<td>0</td>
<td>0.000</td>
<td>(0.0000–0.0594)</td>
</tr>
</tbody>
</table>

*Confidence interval for probability of extinction is based on the binomial distribution method for proportions.
We found that both extinction and colonization rate decreased with increasing occupancy. The negative relationship of extinction to occupancy can be explained by rescue effect (Brown & Kodric-Brown 1977; Hanski 1982). As the proportion of occupied ponds increased more dispersal among ponds may have saved ponds with small populations from extinction. The negative relationship of colonization rate to occupancy may at first seem counter-intuitive, but is consistent with the predictions of basic metapopulation models. In both Levins’ original model (Levins 1969) and Hanski’s modification (Hanski 1982), immigration decreases from moderate to high occupancy because fewer patches are available for colonization as occupancy increases. In our study green frog occupancy ranged from moderate to high. Gotelli (1991) incorporated the concept of propagule rain into his modification of Levins’ model. With propagule rain, immigration is highest at low occupancy and decreases to zero when all patches are occupied.

The dynamics of amphibian populations at expanded spatial scales have been investigated in two other studies. Stumpel (1987) studied tree frogs (Hyla arborea) in the Netherlands at 52 agricultural pools over 6 years and found fluctuating populations and a highly dynamic system in terms of changing patterns of presence and absence. Stumpel (1987) concluded that ponds were not totally isolated and that patterns of presence and absence would be explained by dispersal or migration. Although he did not estimate turnover rates, using the presence/absence data he reported in his Table 3, we calculated annual colonization and extinction rates and they varied from 0 to 1.857 and 0 to 0.38, respectively. Sjögren (1991, 1994) studied the regional distribution and dynamics of the pool frog (Rana lessonae) at 60 permanent ponds in Sweden and reported that occupancy ranged from 17% to 87% and that extinction rate averaged 0.021/ponds/year. Extinctions were of two types: those involving habitat loss resulting from either succession or pond drainage or extinctions related to fish predation and/or environmental and demographic stochasticity. Extinctions occurred at ponds isolated by greater than 1 km that could not be rescued by dispersers from neighboring populations.

Our results concur with those cited above. In general, these populations were spatially dynamic with local extinctions and recolonizations frequently occurring. These studies suggest that metapopulation structure may be a general feature of many amphibian species and clearly illustrate the importance of spatial scale in determining species status.

Based on occupancy and adult abundance, the status of the green frog can be described as common and stable at the geographic scale. Although this species is widely distributed and common among permanent water habitats, many of its populations are highly dynamic. We conducted our study near the center of the green frog’s range where it seems reasonable to assume that conditions would be most favorable, yet we found that a sizable proportion of populations showed declines and local extinctions. Nevertheless, although local extinctions were common, extinctions did not occur at larger spatial scales. Perception of the status of this species is clearly location- and scale-dependent regardless of whether abundance, turnover, or occupancy is viewed. Ecological investigations have generally been conducted at reduced spatial scales and conservation biology has often employed a narrow perspective or even failed to recognize the scale issue (but see Noss 1992). If we had restricted our analysis to the local scale, we could have found any of the entire gamut of possible results, increasing, decreasing, stable, or no trend (Table 6). Although processes that negatively affect a species may be occurring at the local scale, a large-scale perspective is necessary to determine status of a species. In species that live in isolated habitats and have high turnover (many amphibian species), the focus of persistence shifts from local populations to metapopulations (Gilpin 1987). The implication for species conservation is that efforts must also shift from local to regional scales. This increases the importance of factors related to fragmentation, such as isolation, dispersal, corridors, barriers, and also suggests that existing reserves may be too small for small vertebrates as well as large ones. Our results also emphasize the importance of cooperation between jurisdictions if species must be managed on regional or geographic scales.

The green frog is not presently a conservation concern in southwestern Ontario, but studying its spatial dynamics still yields valuable information for conservation. Conservation efforts are often directed toward species that are difficult to study by virtue of their rarity. Understanding spatial dynamics before species become rare may provide early warnings of species that are beginning to decline and give conservation biologists time and knowledge to develop effective management strategies.

Two approaches being used to study amphibian declines are comparing present with historic surveys (e.g., Clarkson & Rorabaugh 1989; Fellers & Drost 1993; Lanno et al. 1994) and investigating potential causal mechanisms on local scales (e.g. Blaustein et al. 1994a,b,c). Although it is interesting and informative to compare contemporary presence or absence with historic data, a caveat is that the number of times turnover occurred is unknown, therefore, calculated extinction rates would be conservative. Determining the plausibility of causal mechanisms is very important, but the results from local studies can neither be generalized to other sites, nor can their effects be extrapolated to larger scales without a high risk of error.

Assessments of the status of species would benefit from an expanded spatial perspective and from multi-scaled approaches. Investigations restricted to reduced spatial...
scales can lead to erroneous conclusions about species status. Although we advocate using expanded spatial approaches, we do not intend that they should replace long-term studies, but rather act as a necessary complement to them. A variety of approaches will be required to investigate species status and conserve target species, but increased attention to spatial scales is essential.

Acknowledgments

We thank D. Hecnar, T. Hecnar, J. Cotter, D. Chalcraft, R. Poulin, D. Peterson, A. Plante, J. Barten, and C. Watson for field assistance. S. and V. Hecnar provided field accommodations. The Ontario Ministry of Natural Resources; Ausable-Bayfield, Essex Region, St. Clair Region, and Saugeen Valley Conservation Authorities; Agriculture Canada, Parks Canada, and many private landowners, allowed access to their lands. Valuable comments on the manuscript were made by M. Donnelly, E. Berlow, and an anonymous reviewer. Funding was provided through a Natural Sciences and Engineering Research Council of Canada grant to R. T. M.

Literature Cited


