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The ecology of extinction: population fluctuation and decline in amphibians

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Abstract

Even among widespread species with high reproductive potentials and significant dispersal abilities, the probability of extinctions should be correlated both with population size variance and with the extent of population isolation. To address how variation in demographic characteristics and habitat requirements may reflect on the comparative risk of species decline, I examined 617 time series of population census data derived from 89 amphibian species using the normalized estimate of the realized rate of increase, ΔN, and its variance. Amphibians are demonstrably in general decline and exhibit a great range of dispersal abilities, demographic characteristics, and population sizes. I compared species according to life-history characteristics and habitat use. Among the populations examined, census declines outnumbered increases yet the average magnitudes for both declines and increases were not demonstrably different, substantiating findings of amphibian decline. This gives no support for the idea that amphibian population sizes are dictated by regimes featuring relatively rare years of high recruitment offset by intervening years of gradual decline such that declines may outnumber increases without negative effect. For any given population size, those populations living in large streams or in ponds had significantly higher variance than did populations of completely terrestrial or other stream-dwelling amphibians. This could not be related to life-history complexity as all the stream-breeding species examined have larvae and all of the wholly terrestrial species have direct development without a larval stage. Variance in ΔN was highest amongst the smallest populations in each comparison group. Estimated local extinction rates averaged 3.1% among pond-breeding frogs, 2.2% for pond-breeding salamanders, and negligible for both stream-breeding and terrestrial direct-developing species. Recoveries slightly exceeded extinctions among European pond-breeding frogs but not among North American pond-breeding frogs. Less common species had greater negative disparities between extinctions and recoveries. Species with highly fluctuating populations and high frequencies of local extinctions living in changeable environments, such pond- and torrent-breeding amphibians, may be especially susceptible to curtailment of dispersal and restriction of habitat.
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Keywords: Population declines; Population variation; Extinction risk; Amphibians; Life history

1. Introduction

Population decline leading to local or complete extinction of species is explicitly or implicitly the focus of conservation initiatives and conservation research. Population decline can be considered a downward trend in numbers of individuals (Vial and Saylor, 1993) but confirming this in any species with even moderate population fluctuations is problematic. Populations of species with high potentials for increase (*r*) tend to show fluctuations and should therefore have increased risk of chance extinction at low population sizes (Belovsky, 1987). But, in some cases, fluctuating population sizes are not necessarily tightly coupled with the chance of extinction (Blaustein et al., 1994a; Schoener and Spiller, 1992) and thus it is the interplay of the demographic characteristics of populations with changes in their particular environments, coupled with the interconnectivity of populations over landscapes, that determines how populations will behave and survive (Bolger et al., 1991; Opdam et al., 1993; Hanski, 1998; Marsh and Trenham, 2001). The probability of local extinctions should be correlated both with high variance in population size and with habitat alterations that have severed or attenuated dispersal between local populations (Thrall et

al., 2000). Although these effects have been shown in particular cases (Gibbs, 1998; Cooper and Walters, 2002), their generality has not been thoroughly examined.

There is real concern over broad scale declines, for instance, in numbers of amphibians (Houlahan et al., 2000; Alford and Richards, 1999). Investigations into the plight of amphibian populations have been directed towards discerning decreases in numbers of individuals within populations and by documenting possible proximate causes (Blaustein, et al., 1994a; Corn, 2000; Kiesecker et al., 2001). Emerging infectious diseases (Cunningham et al., 1996; Lips, 1999; Morell, 1999), parasitic infections (Sessions and Ruth, 1990; Johnson et al., 1999), ultra-violet radiation (Blaustein et al., 1994b), chemical pollutants (Berrill et al., 1997; Bonin et al., 1997; Harte and Hoffman, 1989), introduced predators (Liss and Larson, 1991; Bradford et al., 1993; Morgan and Buttemer, 1996), habitat destruction (Blaustein et al., 1994a; Green, 1997a; Corn, 2000), and climate change (Pounds et al., 1999; Kiesecker et al., 2001) have all been touted as explanations for declines in amphibian populations. Each is plausible, all are likely, but none is mutually exclusive nor apt to be the single underlying cause.

The condundrum is that amphibian declines occur neither everywhere nor among all species. In some amphibians, declines have not been detected (Hairston and Wiley, 1993) and in others, trends cannot be detected at all (Pechmann et al., 1991). Some have argued (Pechmann and Wilbur, 1996, Alford et al., 2001) that declines in amphibian abundances may be more apparent than real. Alford and Richards (1999) proposed a model whereby fluctuating amphibian populations are dictated by the occasional year of high recruitment offset by intervening years in which reproducive success is low. Therefore, population declines could outnumber population increases without indicating overall decline in the population's status. The corollary to this is that the average magnitude of the declines should be less than the average magnitude of the increases. But this particular model may not be general (Houlahan et al., 2001) and, as stated by Alford et al. (2001), more detailed analysis is required.

Understanding the causes of population declines in any group of organisms is likely to be hampered if the ecology of the organisms themselves is insufficiently considered. Amphibians are often depicted as particularly susceptible to the adverse effects of habitat alteration. They are routinely stereotyped as small and damp, and possessing only limited powers of dispersal. It is true that most of the nearly 5000 species of amphibians are small and damp yet they also are abundant, adaptable, and resilient. Amphibians exhibit a great range of dispersing abilities (Marsh and Trenham, 2001) and demographic characteristics (Stebbins and Cohen, 1995). Their populations cannot all be presumed to behave in a similar fashion when confronted with environmental dangers.

Because of the stochasiticity entailed in extinction events, the variance in population change must be accounted for in order to predict susceptibility to decline and population loss. For example, it may be predicted that pond-breeding frogs which disperse widely should have better capacity for maintaining cohesion within metapopulations but, on the other hand, may have more need to do so because they have greatly fluctuating populations. Populations of species with limited dispersal abilities may or may not be more at risk of decline and/or extinction than similarly-sized populations of highly fecund, dispersing species. Is population size variance dependent upon the relative stability of habitats, particularly breeding habitats, or is it correlated with recruitment or fecundity? To address how variation in demographic characteristics and habitat requirements may reflect on the comparative risk of decline in amphibians, and to comprehend the relative degrees of variance among changes in amphibian population sizes, I examined 617 time series of population census data derived from 89 amphibian species, largely from North America and Europe. I considered if species with expected high intrinsic rates of increase, notably those pond-breeding amphibian species with biphasic life-histories and the highest fecundities, have more highly fluctuating populations and higher rates of local extinctions. Specifically I predicted that populations of direct-developing species in stable terrestrial habitats would exhibit decreased population variance relative to pond-breeding amphibians subject to greater demographic and environmental stochasticity.

2. Methods

2.1. Data sets

The data were amassed from published sources as listed in the North American Amphibian Monitoring Program (NAAMP) database and the dataset used by Houlahan et al. (2000), as well as unpublished sources as used also by Houlahan et al. (2000). I only looked at time series of 5 years or greater duration. In cases where the census values were given as densities rather than as counts or estimates of actual animal numbers, I multiplied the density values by the sizes of the areas studied, where available, to derive counts. Population estimates which were obviously gross approximations, sporting values rounded to the nearest 100 or 1000, were eliminated. The majority of the data were not population size estimates with high degrees of confidence. For the most part, they were merely counts of numbers of individuals. In some instances, counts of breeding individuals may

further underestimate population size as not all individuals may breed each year (Trenham et al., 2000). Nevertheless, as I was interested in population change rather than precise population size, and because capture probabilities within data sets can be assumed to be more or less consistent from census to census, count data were appropriate for my purposes.

I divided the species represented into different groups for comparison (Table 1) based on life- history (Duellman and Trueb, 1986; Kuzmin, 1999; Maeda and Matsui, 1989; Petranka, 1998; Stebbins and Cohen 1995; Thorn, 1968; Tyler, 1989; Wright and Wright, 1949). Species with biphasic life histories (aquatic larvae and terrestrial adults) were assorted into pond-breeding ($n = 549$) vs. stream-breeding species ($n = 24$). Species with uniphasic life histories were divided into terrestrial direct-developing species ($n = 43$), and permanently aquatic, paedomorphic species ($n = 1$). There were sufficient numbers of data sets among pond-breeders to enable me to further divide them into frogs ($n = 454$) vs. salamanders ($n = 95$) and individually characterize *Bufo bufo* (Common toad; $n = 93$), *B. calamita* (Natterjack; $n = 36$), *Rana temporaria* (Common frog; $n = 139$), *R. arvalis* (Moor frog; $n = 35$), *R. sylvatica* (Wood frog; $n = 20$), and *Hyla arborea* (European treefrog; $n = 22$). Based upon the outcome of the analysis of stream-dwelling species, I further divided them into logical groups based upon habitat. I did not attempt any phylogenetically based comparisons using independent contrasts beyond considering frogs and salamanders separately in some cases. Direct-development amongst amphibians may not necessarily always be a derived condition (Bogart, 1981) and the evolution of that character was not the focus of this analysis.

2.2. Statistical measures

I calculated the mean population size and its variance for each time series. I correlated population size variance against mean population size for each comparison group. I compared the slopes of the resultant regressions by testing for homogeneity of slope after linearizing the relationships by taking the logarithms of all data. Relationships can be directly compared provided their slopes are not significantly different. Any comparison group with a relationship between mean population size and variance that was significantly different in slope from the other groups was further analyzed to determine the cause of the difference.

I measured change in population size using ΔN (Houlahan et al. 2000), a normalized estimate of the realized rate of increase, *R*:

$$\Delta N = \log(N + 1)_t - \log(N + 1)_{t-1}.$$

ΔN is positive when populations increase and negative when they decline. Average ΔN and its variance, $V_{\Delta N}$, were calculated for each time series to give a measure of that population's trend. For each time series, I also calculated a coefficient of variation (CV), which is the standard deviation of population size divided by the mean, as used by Marsh and Trenham (2001) and Welsh and Droege (2001). The CV, however, has little biological significance and assumes, incorrectly, that each census value is independent. A further measure of population size change, r_t (Turchin, 1999), which is equal to $\ln(N_{t+1}/N_t)$, cannot be calculated for a population recovery following a crash to zero and was not used.

Table 1
Summary of the direction of population changes, with percentages, for over 4,482 census intervals derived from 617 time series of amphibian population census data[a]

	Census intervals	Decreases	Increases	No change
Total	4482	2270 (50.6%)	2020 (45.1%)	186 (4.1%)
Pond breeding species	4031	2058 (51.1%)	1804 (44.8%)	169 (4.2%)
Anura	3319	1681 (50.6%)	1502 (45.3%)	136 (4.1%)
Bufo bufo	758	394 (52.0%)	360 (47.5%)	4 (0.5%)
Bufo calamita	396	206 (52.0%)	164 (41.4%)	26 (6.6%)
Hyla arborea	122	51 (41.8%)	54 (44.3%)	17 (13.9%)
Rana arvalis	210	88 (41.9%)	98 (46.7%)	24 (11.4%)
Rana sylvatica	121	74 (61.2%)	47 (38.8%)	0 (0.0%)
Rana temporaria	990	497 (50.2%)	460 (46.5%)	33 (3.3%)
all other frogs	722	371 (51.4%)	319 (44.2%)	32 (4.4%)
Caudata	712	377 (52.9%)	302 (42.4%)	33 (4.6%)
Stream breeding species	149	72 (48.3%)	74 (49.7%)	3 (2.0%)
Terrestrial direct-developing species	296	140 (47.3%)	142 (48.0%)	14 (4.7%)
Aquatic paedomorphic species	6	4	2	0

[a] Sources of data: Beebee et al. 1996; Bertram and Berrill, 1997; Berven and Grudzien, 1990; Berven, 1990; Bruce, 1995; Dodd, 1991, 1992; Elmberg, 1990; Gittins, 1983; Green, 1997b and unpublished; Hairston, 1983; Hairston and Wiley, 1993; Halley et. al. 1996; Harte and Hoffman, 1989; Houlahan et al., 2000; Husting, 1965; Jaeger, 1980; Kagarise Sherman and Morton, 1993; Macan, 1977; Meyer et al. 1998; Mierzwa, 1998; Olson, 1989; Ramotnik, 1997; Raymond and Hardy, 1990; Schlupp and Podloucky, 1994; Semlitsch et al. 1996; Shirose and Brooks, 1997; Shoop, 1974; Sinsch, 1996; Sredl et al., 1997; Stebbins, 1954; Stromberg, 1995; Stumpel, 1987; Waringer- Loschenkohl, 1991; Weitzel and Panik, 1993.

I compared the range and magnitudes of the values of ΔN for the different groups to examine if declines outnumbered increases and/or differed in magnitude, as had been predicted by Alford and Richards (1999). However, I did not seek to establish if there was an overall decline in amphibian abundance, as was investigated by Houlahan et al. (2000) and discussed by numerous other authors (Pechmann et al., 1991; Blaustein et al., 1994a; Alford and Richards, 1999). Rather, I concentrated on measures of variance in population size and population change, i.e. $V_{\Delta N}$, to establish and compare levels of population fluctuation and thereby investigate the likelihood of population persistence. I compared the variance in population size, coefficient of variation, and $V_{\Delta N}$ against mean population size for the different life history groups.

It may be expected that larger populations should exhibit decreased variance in ΔN. To determine whether variance in population change was related to population size, I correlated $V_{\Delta N}$ against mean population size for each comparison group. I then examined $V_{\Delta N}$ among the groups, restricting the analysis to populations with mean size <250, i.e. within the range where demographic stochasticity may be expected to play a role (Lande, 1988, 1993; Burgman et al., 1993).

I estimated local extinction rates for each of the comparison groups and the six individually examined species by counting the number of occasions when any population census fell to zero and dividing that count by the total number of census intervals ($=$ the number of ΔN values) to arrive at a "crash rate". Repeated values of 0 were not included. Similarly, I determined local recovery rates by counting the number of occasions when there was a positive census count after a 0. As local crash and recovery rates, through direct examination, were no greater than about 3%, no attempt was made to calculate them on data sets with fewer than 100 intervals.

3. Results

3.1. Changes in population size

Among the 617 time-series, there were 4482 census intervals in total. Declines (50.6% of changes) overall outnumbered increases (45.1%), in accordance with the general downward trend detected by Houlahan et al. (2000), however this result is greatly influenced by the preponderance of pond-breeding frogs in the data set. Both the terrestrial direct developers and stream-breeding species exhibited more increases than decreases; their populations increased 48.0 and 49.7% of the time, respectively, versus 47.3 and 48.3% for declines. Pond-breeding species increased 44.8% of the time and decreased 51.1% of the time. Rarely did populations remain constant in size from one census to the next: only 4.1% of changes overall. In general, terrestrial direct developers more often showed no change (4.7% of intervals) compared to pond-breeding species (4.2%) and stream-breeding species (2.0%). The greatest stability was seen in *H. arborea*, which did not change population size 13.9% of the time and increased (44.3%) more often than it decreased (41.8%). *R. sylvatica*, however, always underwent change, mainly to decrease (61.2%).

3.2. Population size variance

Predictably, population size variance was highly correlated with mean population size (Fig. 1) according to allometric, power relationships with R^2 values around 0.9. The slopes of the lines (exponents) of the initial comparison groups were not homogeneous. Slopes for pond-breeding frogs, pond-breeding salamanders, and direct developers, equaling 1.70, 1.76 and 1.76, respectively, were not significantly different from each other ($P \gg 0.05$) but the slope of the relationship for stream-breeders, at 1.92, was steeper than for other groups and was significantly different from the pond-breeding frogs ($P = 0.026$). The stream-breeding species thus appeared either to be obeying a different rule from other amphibians or else comprised a group of samples that was not a natural assemblage. Some of the stream-breeding populations inhabited small streams (i.e. trickles and rivulets) whereas others, with the largest population sizes, were found in large streams (i.e. rivers and torrents). Once divided into these two sub-categories, the slopes of the relationships for species breeding in small streams ($y = 0.53x^{1.51}$; $n = 16$) and large streams ($y = 10.30x^{1.43}$; $n = 8$) were not significantly different from each other, nor from the other comparison groups ($P > > 0.05$) and the analysis could proceed.

Although the slopes of the regressions could be homogeneous, population variance for any given population size was significantly different between certain groups of species, as indicated by the respective y-intercept values for the regression lines: 10.30 for large-stream breeding species, 1.71 for pond-breeding frogs, 1.01 for pond-breeding salamanders, 0.53 for small-stream breeding species, and 0.29 for direct developers. Thus for a given average population size, the large-stream-breeding species and then the pond-breeding species exhibited higher levels of population variance than did either the terrestrial direct-developing species or the remaining stream-breeding species.

For populations of pond breeding species, the coefficient of variation averaged 0.750 ± 0.037 (S.E.), slightly but not significantly ($P = 0.803$) higher for frogs (0.757 ± 0.041) than for salamanders (0.721 ± 0.089). The average values for stream breeding species (0.443 ± 0.104) and terrestrial direct-developing species
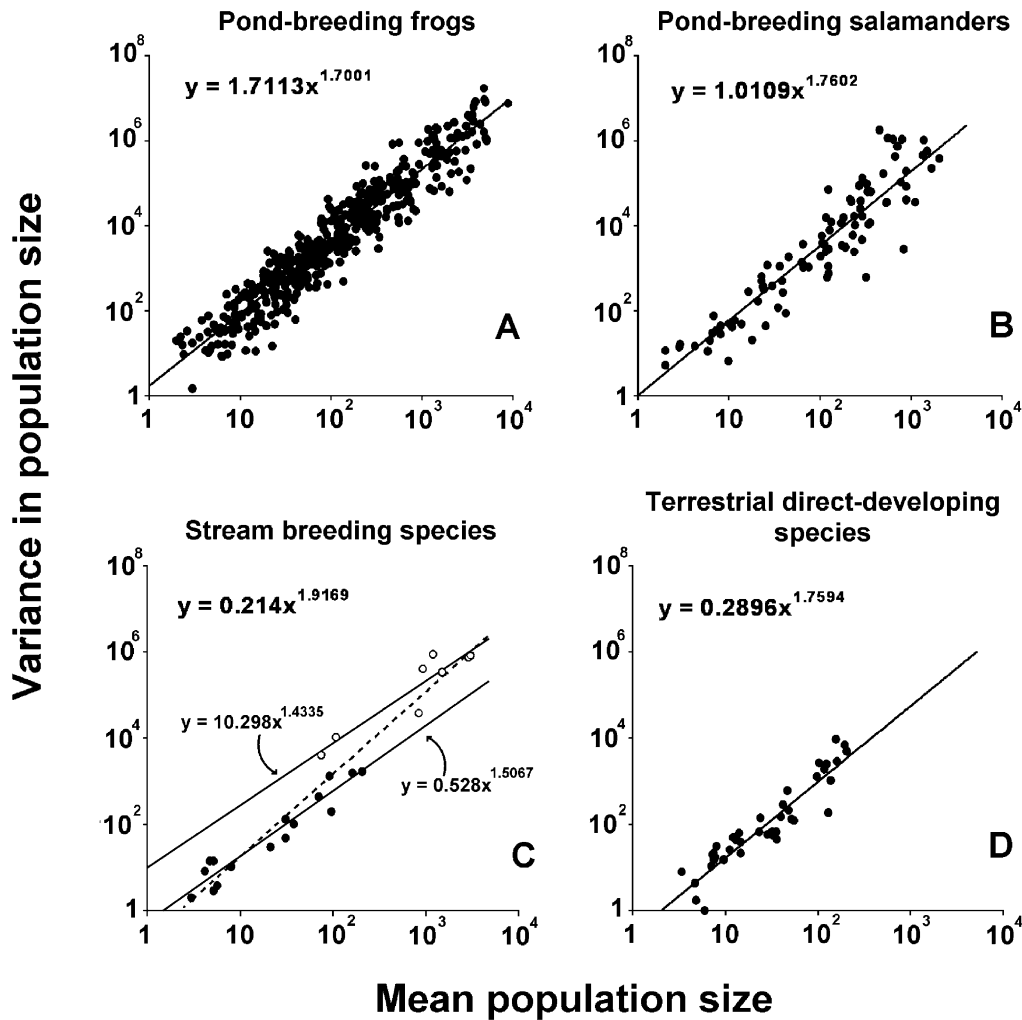
Fig. 1. Variance in population size versus mean population size (log/log plots) for amphibian species of different life histories: (A) pond-breeding frogs, (B) pond-breeding salamanders, (C) stream-breeding species, which are further divided into those inhabiting large streams, i.e. torrents and rivers (open circles), versus those inhabiting small streams, i.e. rivulets and trickles (dots), (D) terrestrial direct-developing species. The slopes of the power functions describing these relationships are not significantly different, except for stream-breeding species overall (dotted line in C). All correlations are highly significant ($P < 0.01$). The large-stream breeding species and pond-breeding frogs have the highest population size variances for a given population size whereas terrestrial species have the least.

(0.403 ± 0.067) were considerably and significantly lower than for the pond-breeding species ($P < 0.001$), but not significantly different from each other ($P = 0.541$). The coefficient of variation for species in small streams (average $= 0.384 \pm 0.049$) and species in large streams average $= 0.560 \pm 0.101$) were not significantly different ($P = 0.087$).

The mean values of ΔN were slightly negative in pond-breeding frogs (-0.018 ± 0.007), pond-breeding salamanders (-0.018 ± 0.013), and stream-breeders (-0.033 ± 0.030), and not significantly different one from each other ($P < 0.01$). However, among the stream-breeding species, those populations in large streams averaged a decline in population size according to mean ΔN (-0.113 ± 0.080) whereas those populations in small streams averaged a slight increase (0.007 ± 0.011). Among the pond breeding species, only

Rana arvalis showed a significant tendency towards population increase (mean $\Delta N = 0.126 \pm 0.042$). The average ΔN calculated for terrestrial, direct-developing species, whether frogs or salamanders, was slightly positive (0.007 ± 0.011), frogs faring slightly better than salamanders (mean $\Delta N = 0.016 \pm 0.027$ compared to 0.002 ± 0.009).

The distribution of ΔN values for all groups of species examined (Fig. 2) was symmetrical around a median class of values centered on zero. The range of ΔN values (Fig. 2) was much the greatest for pond-breeding species, especially the frogs (minimum $= -2.634$, maximum $= 2.340$) and then the salamanders (range $= -1.934$ to 1.661), followed by the stream-breeding species overall (range $= -2.137$ to 0.477) and then the terrestrial, direct-developing species (range $= -0.903$ to 0.727). The smallest range of values,
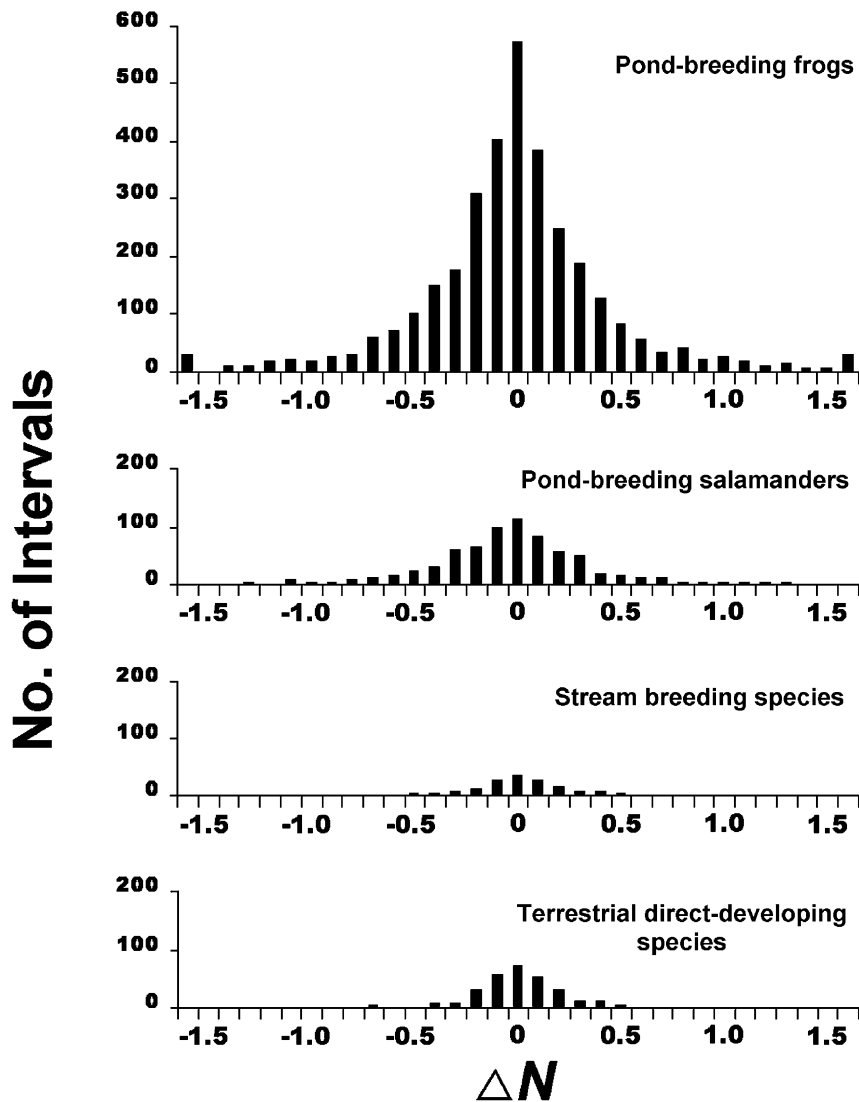
Fig. 2. Distribution of ΔN values for amphibian populations. Pond-breeding frogs have much the greatest range of values of ΔN, reflecting the great population size variance. In contrast, populations of terrestrial, direct-developing species show much lesser magnitudes of change from one census to the next.

however, belonged to those species breeding in small streams (range = −0.802 to 0.454).

The pond-breeding frogs had the highest variance in ΔN (mean $V_{\Delta N} = 0.306 \pm 0.022$ S.E.), followed by pond-breeding salamanders (mean $V_{\Delta N} = 0.158 \pm 0.021$) and stream-breeding species [mean $V_{\Delta N} = 0.106 \pm 0.044$ (small stream species mean $V_{\Delta N} = 0.062 \pm 0.016$, large stream species mean $V_{\Delta N} = 0.194 \pm 0.129$); Fig. 3a]. The terrestrial direct-developing species had the lowest variance in ΔN on average (mean $V_{\Delta N} = 0.045 \pm 0.007$), lower than the single time-series from a paedomorphic species ($V_{\Delta N} = 0.051$). The pond-breeding frogs, pond-breeding salamanders and terrestrial direct-developing species were significantly different from each other in terms of $V_{\Delta N}$ ($P < 0.001$) but the stream-breeding species as a whole were not significantly different from either pond-breeding salamanders or direct-developing

species ($P = 0.29$ and $P = 0.19$, respectively), likely due to the differences between species breeding in small streams (mean $V_{\Delta N} = 0.062 \pm 0.016$; $n = 16$) versus species breeding in large streams (mean $V_{\Delta N} = 0.194 \pm 0.129$; $n = 8$). Tested separately, $V_{\Delta N}$ of species breeding in small streams was significantly different from $V_{\Delta N}$ of pond-breeding frogs ($P = 0.039$) but not significantly different from pond-breeding salamanders ($P = 0.060$) or direct-developing species ($P = 0.292$). Conversely, $V_{\Delta N}$ of species breeding in large streams was not significantly different from $V_{\Delta N}$ of pond-breeding frogs ($P = 0.514$) or pond-breeding salamanders ($P = 0.652$) but significantly different from direct-developing species ($P = 0.010$).

Among those pond-breeding anuran species examined individually, *H. arborea*, *R. temporaria*, *R. sylvatica* and *B. calamita* had mean values of $V_{\Delta N}$ similar to
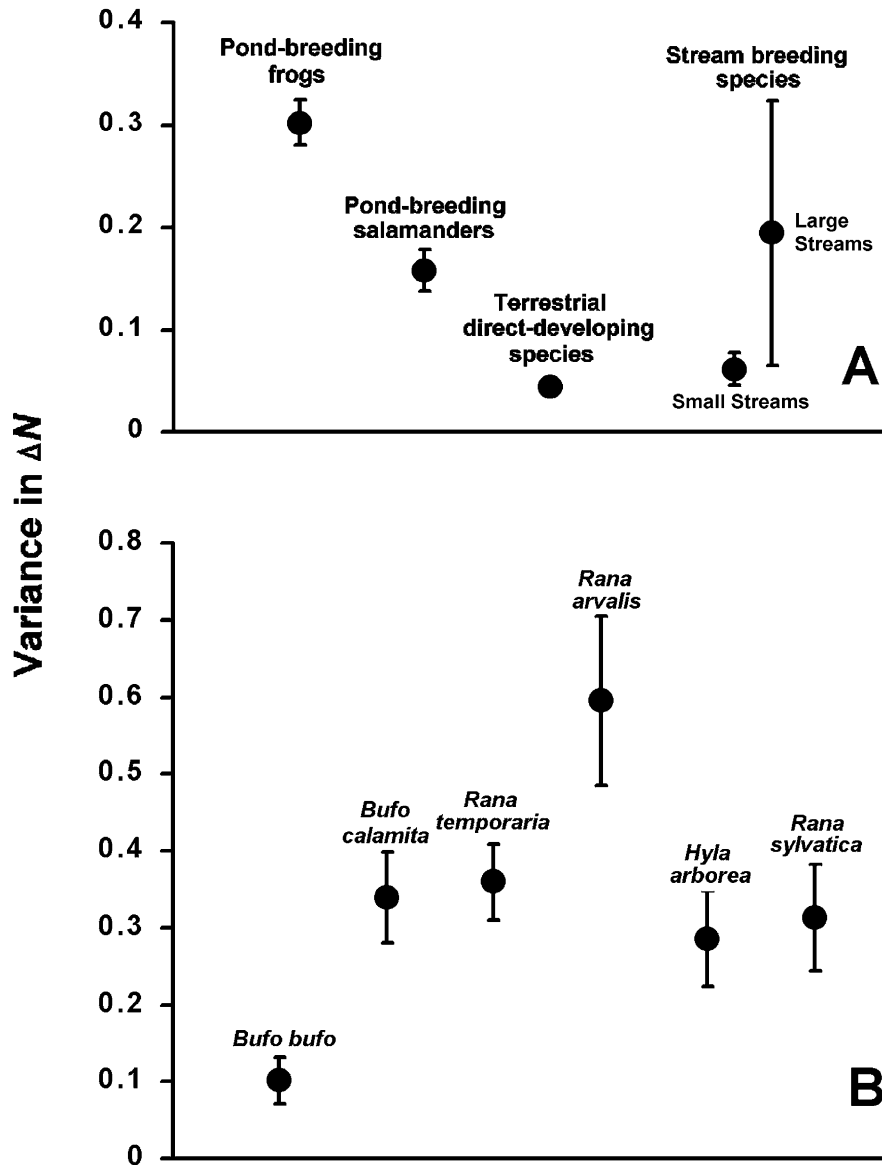
Fig. 3. Variance in ΔN (mean and standard error) for amphibian populations. (A) Amphibian species of different life histories. Pond-breeding frogs, pond-breeding salamanders, and terrestrial, direct- developing species were significantly different from each other ($P < 0.01$). The stream-breeding species taken together had a great diversity of population sizes and were not significantly different in variance in ΔN from either pond-breeding salamanders ($P = 0.29$) or terrestrial direct-developing species ($P = 0.19$). Those species breeding in small streams were not significantly different from terrestrial direct-developing species ($P = 0.29$) or pond-breeding salamanders ($P = 0.06$), and significantly different from pond breeding frogs ($P = 0.04$). Conversely, those species breeding in large streams were significantly different from terrestrial direct-developing species ($P = 0.01$) and not significantly different from pond-breeding salamanders ($P = 0.65$) or pond breeding frogs ($P = 0.51$). (B) Six pond-breeding anurans with $n \geqslant 20$. Four of the six species cluster around typical values of population size and variance for pond-breeding frogs. *Rana arvalis*, however, exhibits an unusually high variance whereas *Bufo bufo* exhibits an usually low variance.

the overall average for the group (Fig. 3b). The exceptions were *R. arvalis*, which had relatively high levels of population variance, and *B. bufo*, which was comparatively low. European pond-breeding species of frogs and salamanders exhibited less variance in ΔN (mean $V_{\Delta N} = 0.296 \pm 0.031$ for frogs and 0.131 ± 0.021 for salamanders) compared to their North American counterparts (mean $V_{\Delta N} = 0.353 \pm 0.058$ for frogs and 0.229 ± 0.073 for salamanders) but the differences were not significant ($P < 0.01$).

The significance of these overall comparisons is compromised because variance in ΔN was considerably damped in large populations (Fig. 4). Most of the populations of the pond-breeding anuran, *B. bufo*, in particular, were very large (mean $= 1382 \pm 145$ individuals; Fig. 3b), as were all estimates of abundance for the torrent-dwelling Mallorcan midwife toad, *Alytes muletensis* ($n = 5$). *A. muletensis* had populations averaging 1885 ± 993 individuals, with a mean $V_{\Delta N}$ of 0.020.
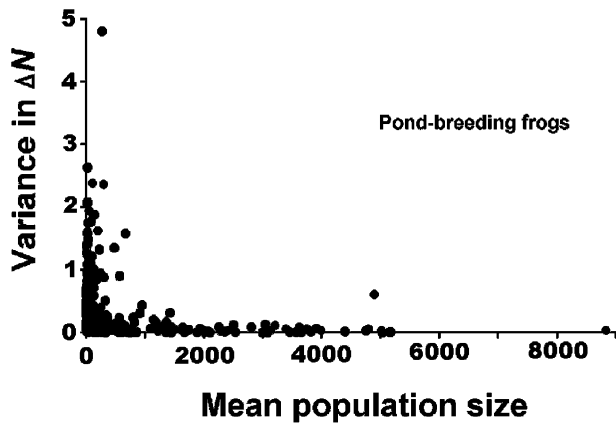
Fig. 4. Variance in ΔN versus mean population size for 454 populations of 47 species of pond-breeding frogs illustrating a significantly greater mean variance among smaller populations.

Large population sizes were the exception, however. Because of the damping effect of large population size, I re-analyzed the data restricting the comparison of $V_{\Delta N}$ between life-history groups to populations with mean sizes under 250 individuals (Fig. 5). The restriction on population size in the analysis had the effect of eliminating from the set of stream-breeding species six of the eight data series for species dwelling in large streams but none of the data for species dwelling in small streams. I therefore used only the value for species dwelling in small streams, previously calculated as mean $V_{\Delta N} = 0.062 \pm 0.016$, in order make a comparison. Population estimates for terrestrial, direct-developing species were all under 250 individuals and thus the previously calculated value of mean $V_{\Delta N} = 0.045 \pm 0.007$ was also used. Mean $V_{\Delta N}$ for pond-breeding frog

populations under a mean size of 250 was 0.372 ± 0.026 ($n = 306$) and for pond-breeding salamanders it was 0.164 ± 0.025 ($n = 63$). These were significantly different ($P < 0.001$). Mean $V_{\Delta N}$ among the small-stream dwellers was found to significantly different from both pond-breeding frogs ($P = 0.006$) and salamanders ($P = 0.049$) but not from the terrestrial direct developers ($P = 0.292$). The terrestrial direct developers were likewise found to significantly different from both pond-breeding frogs and salamanders ($P < 0.001$). Only three populations of *B. calamita* and one population of *H. arborea* averaged more than 250 individuals and therefore estimates of mean $V_{\Delta N}$ in those species changed little. When populations > 250 individuals were excluded, estimates of $V_{\Delta N}$ in *R. temporaria* (mean $V_{\Delta N} = 0.411 \pm 0.047$; $n = 104$), *R. arvalis* (mean $V_{\Delta N} = 0.686 \pm 0.120$; $n = 30$) and *R. sylvatica* (mean $V_{\Delta N} = 0.345 \pm 0.101$; $n = 13$) rose considerably. In *B. bufo,* however, there was a reduction in variance (mean $V_{\Delta N} = 0.092 \pm 0.020$; $n = 18$) when considering only those population < 250 individuals.

3.3. Local extinction and recovery

The population crash rate was 0.031 among pond-breeding frogs ($n = 3008$ census intervals), 0.022 for pond-breeding salamanders ($n = 712$), and negligible for both stream-breeding and terrestrial direct-developing species (Table 2). The European ($n = 2,290$) and North American ($n = 590$) pond-breeding frogs both had a crash rate of 0.032. However, whereas recoveries (rate $= 0.034$) slightly exceeded crashes among European pond-breeding frogs, they were decidedly less than crashes among North American pond-breeding frogs (rate $= 0.020$). Neither *B.*

Table 2
Crash (population count $= 0$) and recovery rates for amphibian populations

	No. of species	Population changes	Crashes		Recoveries	
			Number	Rate	Number	Rate
Pond breeding species	*65*	*10 320*	*311*	*0.03*	*292*	*0.028*
Anura	47	3008	93	0.031	90	0.03
Europe	12	2290	74	0.032	78	0.034
Bufo bufo	1	758	0	0	0	0
Bufo calamita	1	396	13	0.033	11	0.028
Rana temporaria	1	615	36	0.059	33	0.054
Rana arvalis	1	210	17	0.081	26	0.124
Hyla arborea	1	122	4	0.033	6	0.049
all other species	7	189	4	0.021	2	0.011
North America	29	590	19	0.032	12	0.02
Rana sylvatica	1	121	0	0	0	0
all other species	28	469	19	0.041	12	0.026
Caudata	18	712	16	0.022	11	0.015
Europe	6	503	11	0.022	8	0.016
North America	10	185	5	0.027	3	0.016
Stream breeding species	*10*	*149*	*1*	*0.007*	*0*	*0*
Terrestrial direct-developing species	*13*	*296*	*0*	*0*	*0*	*0*

bufo ($n=758$) nor *R. sylvatica* ($n=121$) exhibited any crashes whereas *R. temporaria*, with a rate of 0.059 ($n=615$), and *R. arvalis*, with a rate of 0.081 ($n=210$), were at the high end of the scale. The crash rate of 0.033 in *H. arborea* closely agreed with local extinction rates recorded by Carlson and Edenhamn (2000). In the main, recovery rates were at levels that matched crashes (Table 2). Despite its high crash rate, *R. arvalis* had an even higher recovery rate of 0.124. The greatest negative disparities between crashes and recoveries were among the more rarely sampled pond-breeding frogs from both Europe and North America and among pond-breeding salamanders (Table 2).

4. Discussion: population variance and population persistence

Contrary to the expectations of Alford and Richards (1999), the distribution of ΔN values was not consistent with any particular pattern of population rises and declines within populations. Although populations rarely remained precisely the same size, most of the time they changed little from one census to the next. Large increases and large decreases were both rare. Alford and Richards (1999) had predicted that amphibian populations are dominated by few, but large positive ΔN values amidst many, but small negative ΔN values. Corrobortaing Houlahan et al. (2001), my analysis shows that this is not the general case. Declines (i.e., ΔN is negative) outnumber increases (i.e., ΔN is positive) yet the average magnitudes for each are not different. The indication is that the pattern proposed by Alford and Richards (1999) is not general and that amphibian populations are, overall, declining.

The heightened levels of $V_{\Delta N}$ detected among smaller populations of amphibians may be evidence of the effects of demographic stochasticity upon population size. Demographic stochasticity should increase population size variance at effective population sizes, N_e, less
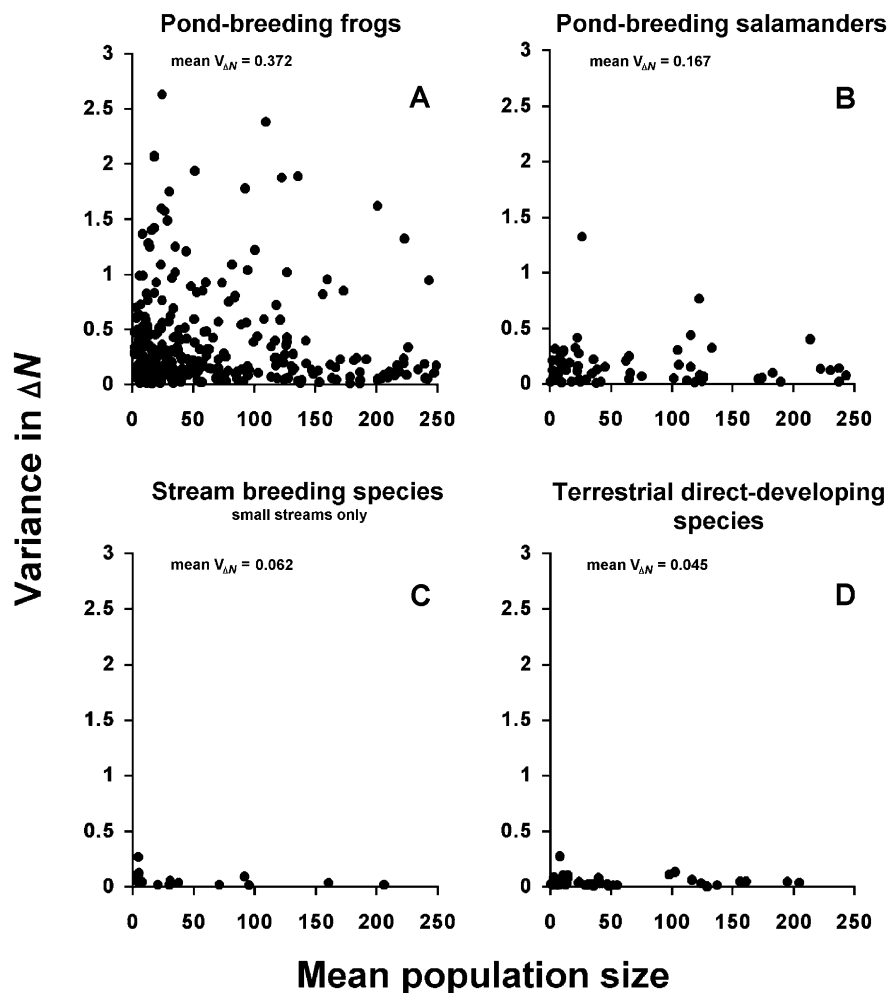

Fig. 5. Variance in ΔN versus mean population size for populations of amphibians under 250. Mean $V_{\Delta N}=0.372\pm0.026$ for pond-breeding frogs ($n=306$), 0.164 ± 0.025 for pond-breeding salamanders ($n=63$), 0.062 ± 0.016 for small-stream breeding species ($n=16$) and 0.045 ± 0.007 for terrestrial direct-developing species ($n=43$).

than 100 (Lande, 1988, 1993; Burgman et al., 1993) and for many pond-breeding amphibian populations, N_e is considerably smaller than the census population size (Vucetich et al., 1997; Vucetich and Waite, 1998; Scribner et al., 1997). Among the 549 populations of pond-breeding species examined here, 48.8% averaged fewer than 100 censussed individuals and 78.3% averaged fewer than 500 individuals. Demographic stochasticity is predicted be higher for a given census population size among species with fluctuating populations compared to species with comparatively long lives and low fecundities in stable populations (Kokko and Ebenhard, 1996). This is borne out by comparison of pond-breeding amphibian species with direct-developing and paedomorphic species.

My analysis indicates that high population variance is not necessarily causally related to life-history complexity. Species with complex life histories are expected to have complex population dynamics (Wilbur, 1980) and populations of assorted amphibian species with biphasic life histories have been seen to fluctuate, sometimes over orders of magnitude (Banks and Beebee, 1988; Berven, 1995; Alford and Richards, 1999). Yet among the large number of populations I examined, for any given population size those amphibian populations living in large streams and ponds had the highest population variance. The most stable populations were those inhabiting small streams, trickles and rivulets, or which were wholly terrestrial. This is not related to the presence or absence of a complex life-history as all the stream-breeding species examined have indirect development with larvae whereas the wholly terrestrial species do not. Furthermore, the observed differences in population size variation have no taxonomic bias either, especially for frogs versus salamanders. Plethodontid salamander species, with or without larvae, have less fluctuating populations than do most hylid, ranid, or bufonid frogs, and they also fluctuate significantly less than salamandrid or ambystomatid salamanders. That same relative population stability is also true for frogs of the genus *Eleutherodactylus* and other species of both frogs and salamanders with terrestrial, direct development. Although Hairston (1987) stated that salamanders, in general, have stable populations, it is evident this stability applies to terrestrial and stream-breeding species not to pond-breeding species, regardless of taxonomic group or life-history complexity. Variance in population size appears to be a function of the stability of the immediate environment.

Certain of the species examined are abundant, widespread and secure throughout their ranges but have differing dynamics of population size. Populations of *B. bufo*, the common toad of Europe, are large compared to other species and its population size variance, even among its smaller populations, is relatively low for a pond-breeding species. *R. sylvatica* has a local extinction rate of zero, as reported previously by Berven (1995). However, population stability is not required for persistence. *R. arvalis,* exhibits a very high population variance but its estimated recovery rate is greater than its estimated rate of local extinction. Whereas previous authors had recorded no local extinctions in *B. calamita*, (Sinsch, 1997) or *R. temporaria* (Meyer et al., 1998), they do in fact appear to have significant local extinction rates, matched by recoveries. Species such as *B. bufo* and *R. temporaria* may have adapted themselves particularly well to human-altered landscapes (Beebee and Griffiths, 2000) in part due to their dispersal abilities and demographic characteristics. Other, less common species of pond-breeding frogs, for which there were not enough populations in the data set to characterize individually, differed from the six common species in having collectively a much higher crash rate than recovery rate. Therefore, as expected for a thriving species (Sjögren, 1991; Hanski, 1999), local population extinctions, at whatever level, are counteracted by recolonizations made possible by dispersal. Some amphibians, particularly those which breed in temporary ponds, require complex habitats. Numerous pond-breeding amphibians have been demonstrated to have considerable abilities to disperse (Ash, 1997; Dupuis, 1997; Waldick, 1997; Marsh and Trenham, 2001; Reimchen, 1991; Schlupp and Podloucky, 1994). But their evident reliance upon dispersal should render pond breeding species prone to the effects of permanent habitat fragmentation. Pond-breeding, forest-dependent amphibian species, such as *R. sylvatica* and the spotted salamander, *Ambystoma maculatum*, have been show to disappear from progressively more fragmented habitats which leave the strictly terrestrial red-backed salamander, *Plethodon cinereus*, unaffected (Gibbs, 1998).

Habitat fragmentation is widely and rightly invoked in the decline of biodiversity (Harrison and Bruna, 1999; Fischer, 2000). Its effects are frequently considered in terms of inbreeding depression and reduction of genetic variability in small, isolated populations (Hitchings and Beebee, 1997; Young and Clarke, 2000; Dudash and Fenster, 2000), which leads to unadaptability in the face of environmental change and thus, in the long run, to reduced population viability and local extinction. The likelihood that this will happen depends also upon population size fluctuation (Vucetich and Waite, 1999) and dispersal (Gilbert et al., 1998), especially when population decay is rapid (Gaggiotti and Smouse, 1996). Amphibians exhibit a great range of dispersing abilities (Stebbins and Cohen, 1995). Pond-breeding anurans of all sorts disperse widely as juveniles (Marsh and Trenham, 2001), which has been demonstrated to be important in maintaining populations (Sinsch, 1997; Seburn et al., 1997; Pope et al., 2000; Semlitsch, 2000). Red-legged frogs, *R. aurora*, are

reported to disperse up to 2.4 km in a year (Hayes et al, 2001). Both, *R. sylvatica* and Pacific treefrogs, *H. regilla*, can move 2.5 km/year (Berven and Grudzien, 1990; Reimchen, 1991), and *H. arborea* can move up to 12.6 km/year (Stumpel and Hanekamp, 1986). *R. lessonae* have been marked and then recaptured up to 15 km away (Tunner, 1992). Terrestrial, direct-developing salamanders, though, may be extremely sedentary and territorial (Mathis, 1989; Thurow, 1976; Welsh and Droege, 2001). Thus the pond-breeding species should have better capacity for maintaining cohesion within metapopulations but, with their complex habitat requirements, may have more need to do so because of their more greatly fluctuating populations. Without the effect of rescue from neighboring populations, a species with a high turnover of local populations and dependent upon dispersal for its persistence should suffer greater cumulative extinctions of local populations in fragmented landscapes regardless of any eventual loss of genetic variation.

One of the puzzles of population declines among amphibians is that they have also occurred in apparently undisturbed sites and among highly fecund species (Blaustein et al., 1994a; Corn, 2000; Alford and Richards; 1999), those very species presumed to be least affected by habitat alteration. Highly fecund pond-breeding amphibians fluctuate in population size to a great extent, correlated with high rates of local population extinctions. Yet not all pond-breeding species of amphibians are widespread. Species with restricted or fragmented ranges within the genus *Bufo* in North and Central America, for example, include *B. houstonensis, B. baxteri, B. periglenes, B. canorus, B. exsul,* and *B. californicus* and all of these species are either endangered or recently gone extinct. The conclusion is that curtailment of recolonizations in an obligately dispersing species with highly fluctuating populations and high frequencies of local extinctions, such pond-breeding amphibians, is likely to be affected rapidly and catastrophically by habitat fragmentation.

Acknowledgements

References

Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30, 133–165.

Alford, R.A., Dixon, P.M., Pechmann, J.H.K., 2001. Global amphibian population declines. Nature 412, 499–500.

Ash, A.N., 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge mountains. Conservation Biology 11, 983–989.

Banks, B., Beebee, T.J.C., 1988. Reproductive success of natterjack toads *Bufo calamita* in two contrasting environments. Journal of Animal Ecology 57, 475–492.

Beebee, T.J.C., Griffiths, R.A., 2000. Amphibians and Reptiles. A Natural History of the British Herpetofauna. HarperCollins Publishers, London.

Beebee, T.J.C., Denton, J.S., Buckley, J., 1996. Factors affecting populations densities of adult natterjack toads *Bufo calamita* in Britain. Journal of Applied Ecology 33, 263–268.

Belovsky, G.E., 1987. Extinction models and mammalian persistence. In: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, New York, pp. 35–37.

Berrill, M., Bertram, S., Pauli, B., 1997. Effects of pesticides on amphibian embryos and tadpoles. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, MO, pp. 233–245.

Bertram, S., Berrill, M., 1997. Fluctuations in a northern population of gray treefrogs, *Hyla versicolor*. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, MO, pp. 57–63.

Berven, K.A., 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71, 1599–1608.

Berven, K.A., 1995. Population regulation in the wood frog, *Rana sylvatica*, from three diverse geographic localities. Australian Journal of Ecology 71, 1599–1608.

Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44, 2047–2056.

Blaustein, A.R., Wake, D.B., Sousa, W.P., 1994a. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8, 60–71.

Blaustein, A.R., Hoffman, P.D., Hokit, D.G., Kiesecker, J.M., Walls, S.C., Hays, J.B., 1994b. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines. Proceedings of the National Academy of Sciences, USA 91, 1791–1795.

Bogart, J.P., 1981. How many times has terrestrial breeding evolved in anuran amphibians? Monitore Zoologico Italiano (N.S.) Supplement 15, 29–40.

Bolger, D.T., Alberts, A.C., Soulé, M.E., 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. American Naturalist 137, 155–156.

Bonin, J., Ouellet, M., Rodrigue, J., Desgranges, J.-L., Gagné, F., Sharbel, T.F., Lowcock, L.A., 1997. Measuring the health of frogs in agricultural habitats subjected to pesticides. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 258–270.

Bradford, F.Tabatabai, Graber, D.M., 1993. Isolation of remaining populations of the native frog, *Rana muscusa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conservation Biology 7, 882–888.

Bruce, R.C., 1995. The use of temporary removal sampling in a study of population dynamics of the salamander *Desmognathus monticola*. Australian Journal of Ecology 20, 403–412.

Burgman, M.A., Ferson, S., Akçakaya, H.R., 1993. Risk Assessment in Conservation Biology. Chapman and Hall, New York.

Carlson, A., Edenhamn, P., 2000. Extinction dynamics and the regional persistence of a tree frog metapopulation. Proceedings of the Royal Society of London B 267, 1311–1313.

Cooper, C.B., Walters, J.R., 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. Conservation Biology 16, 471–478.

Corn, P.S., 2000. Amphibian declines: review of some current hypotheses. In: Sparling, D.W., Linder, G., Bishop, C.A. (Eds.), Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, Florida, pp. 633–696.

Cunningham, A.A., Langton, T.E.S., Bennett, P.M., Drury, S.E.N., Gough, R.E., MacGregor, S.K., 1996. Pathological and microbiological findings from incidents of unusual mortality of the common frog (*Rana temporaria*). Philosophical Transactions of the Royal Society, London B 351, 539–1557.

Dodd, C.K., 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. Journal of Herpetology 25, 296–301.

Dodd, C.K., 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1, 125–142.

Dudash, M.R., Fenster, C.B., 2000. Inbreeding and outbreeding depression in fragmented populations. In: Young, A.G., Clarke, G.M. (Eds.), Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, pp. 35–53.

Duellman, W.E., Trueb, L., 1986. Biology of Amphibians. McGraw-Hill, New York.

Dupuis, L., 1997. Effects of logging on terrestrial-breeding amphibians on Vancouver Island. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 258–270.

Elmberg, J., 1990. Long-term survival, length of breeding season, and operational sex ratio in a boreal population of common frogs, *Rana temporaria* L. Canadian Journal of Zoology 68, 121–127.

Fischer, M., 2000. Species loss after habitat fragmentation. Trends in Ecology and Evolution 15, 396.

Gaggiotti, O.E., Smouse, P.E., 1996. Stochastic migration and maintenance of genetic variation in sink populations. American Naturalist 147, 919–945.

Gilbert, F., Gonzalez, A., Evans-Freke, I., 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proceedings of the Royal Society, London B 265, 577–582.

Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 113, 263–268.

Gittins, S.P., 1983. Population dynamics of the common toad (*Bufo bufo*) at a lake in mid-Wales. Journal of Animal Ecology 52, 981–988.

Green, D.M., 1997a. Perspectives on amphibian population declines: defining the problem and searching for answers. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 291–308.

Green, D.M., 1997b. Temporal variation in abundance and age structure in Fowler's toads (*Bufo fowleri*) at Long Point, Ontario. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 258–270.

Hairston, N.G.Sr., 1983. Growth, survival and reproduction of *Plethodon jordani*: trade-offs between selective pressures. Copeia 1983, 1024–1035.

Hairston, N.G.Sr., 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge.

Hairston, N.G., Wiley, R.H., 1993. No decline in salamander (Amphibia: Caudata) populations: a twenty-year study in the southern Appalachians. Brimleyana 18, 59–64.

Halley, J.M., Oldham, R.S., Arntzen, J.W., 1996. Predicting the persistence of amphibian populations with the help of a spatial model. Journal of Applied Ecology 33, 455–470.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.

Hanski, I., 1999. Metapopulation Biology. Oxford University Press, Oxford.

Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22, 225–232.

Harte, J., Hoffman, E., 1989. Possible effects of acidic deposition on a Rocky Mountain population of the tiger salamander *Ambystoma tigrinum*. Conservation Biology 3, 149–158.

Hayes, M.P., Pearl, C.A., Rombough, C.J., 2001. *Rana aurora aurora*. movement. Herpetological Review 32, 35–36.

Hitchings, S.P., Beebee, T.J.C., 1997. Genetic substructuring as a result of barriers to gene flow in urban *Rana temporaria* (common frog) populations—implications for biodiversity conservation. Heredity 79, 7117–7127.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian decline. Nature 404, 752–755.

Houlahan, J.E., Findlay, C.S., Meyer, A.H., Kuzmin, S.L., Schmidt, B.R., 2001. Houlahan et al. reply. Nature 412, 500.

Husting, E.L., 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965, 352–359.

Jaeger, R.G., 1980. Density-dependent and density-independent causes of extinction of a salamander population. Evolution 34, 617–621.

Johnson, P.T.J., Lunde, K.B., Ritchie, E.G., Launer, A.E., 1999. The effect of trematode infection on amphibian limb development and survivorship. Science 284, 802–804.

Kagarise Sherman, C., Morton, M.L., 1993. Population declines of Yosemite Toads in the eastern Sierra Nevada of California. Journal of Herpetology 27, 186–198.

Kiesecker, J.M., Blaustein, A.R., Belden, L.K., 2001. Complex causes of amphibian declines. Nature 410, 681–684.

Kokko, H., Ebenhard, T., 1996. Measuring the strength of demographic stochasticity. Journal of Theoretical Biology 183, 169–178.

Kuzmin, S.L., 1999. The Amphibians of the Former Soviet Union. Pensoft Publishers, Sofia.

Lande, R., 1988. Genetics and demography in biological conservation. Science 241, 1455–1460.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142, 911–927.

Lips, K.R., 1999. Mass mortality and population declines of anurans at an upland site in western Panama. Conservation Biology 13, 117–125.

Liss, W.J., Larson, G.L., 1991. Ecological effects of stocked trout on North Cascades naturally fishless lakes. Park Science 11, 22–23.

Macan, T.T., 1977. A twenty-year study of the fauna in the vegetation of a moorland fishpond. Archives of Hydrobiology 81, 1–24.

Maeda, N., Matsui, M., 1989. Frogs and toads of Japan. Bin-ichi Sōgō Shuppan, Tokyo.

Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15, 40–49.

Mathis, A., 1989. Do seasonal spatial patterns in a terrestrial salamander reflect reproductive behavior or territoriality? Copeia 1989, 788–791.

Meyer, A.H., Schmidt, B.R., Grossenbacher, K., 1998. Analysis of three amphibian populations with quarter-century long time-series. Proceedings of the Royal Society of London Series B Biological Sciences 265, 523–528.

Mierzwa, K.S., 1998. Status of northeastern Illinois amphibians. In: Lannoo, M.J. (Ed.), Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA, pp. 115–124.

Morell, V., 1999. Are pathogens felling frogs? Science 284, 728–731.

Morgan, L.A., Buttemer, X., 1996. Predation by the non-native fish *Gambusia holbrooki* on small *Litoria aurea* and *L. dentata* tadpoles. Australian Zoology 30, 143–149.

Olson, D.H., 1989. Predation on breeding western toads (*Bufo boreas*). Copeia 391–397.

Opdam, P., Van Apeldoorn, R., Schotman, R., Kalkhoven, J., 1993. Population responses to landscape fragmentation. In: Vos, C.C., Opdam, P. (Eds.), Landscape Ecology of a Stressed Environment. Chapman and Hall, London, pp. 147–171.

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Campbell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253, 892–895.

Pechmann, J.H.K., Wilbur, H.M., 1996. Putting declining amphibian populations in perspective, natural fluctuations and human impacts. Herpetologica 50, 65–84.

Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington.

Pope, S.E., Fahrig, L., Merriam, N.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81, 2498–2508.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398, 611–615.

Ramotnik, C. A. 1997. Conservation Assessment of the Sacramento Mountain Salamander. Gen. Tech. Rep. RM-GTR-293. USDAFS, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Raymond, L.R., Hardy, L.M., 1990. Demography of a population of *Ambystoma talpoideum* (Caudata: Ambystomatidae) in northwestern Louisiana. Herpetologica 46 (4), 371–382.

Reimchen, T.E., 1991. Introduction and dispersal of the Pacific Treefrog, *Hyla regilla*, on the Queen Charlotte Islands, British Columbia. Canadian Field-Naturalist 105, 288–290.

Schlupp, I., Podloucky, R., 1994. Changes in breeding site fidelity: a combined study of conservation and behavior in the common toad *Bufo bufo*. Biological Conservation 69, 285–291.

Schoener, T.W., Spiller, D.A., 1992. Is extinction related to temporal variability in population size? An empirical answer for orb spiders. American Naturalist 139, 1176–1207.

Scribner, K.T., Arntzen, J.W., Burke, T., 1997. Effective number of breeding adults in *Bufo bufo* estimated from age-specific variation at mini-satellite loci. Molecular Ecology 6, 701–712.

Seburn, C.N.L., Seburn, D.C., Paszkowski, C.A., 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 258–270.

Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64, 615–631.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W., 1996. Structure and dynamics of an amphibian community. In: Cody, M.L, Smallwood, J.A. (Eds.), Long-term Studies of Vertebrate Communities. Academic Press, San Diego, pp. 217–250.

Sessions, S.K., Ruth, S.B., 1990. Explanation for naturally occurring supernumerary limbs in amphibians. Journal of Experimental Biology 254, 38–47.

Shirose, L.J., Brooks, R.J., 1997. Fluctuations in abundance and age structure in three species of frogs (Anura: Ranidae) in Algonquin Park, Canada, from 1985 to 1993. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, St. Louis, pp. 16–26.

Shoop, C.R., 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology 55, 440–444.

Sinsch, U., 1996. Population dynamics of natterjack toads (*Bufo calamita*) in the Rhineland: a nine-years study. Verlandlungen der Deutschen Zoologischen Gesellschaft 89, 1–127.

Sinsch, U., 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112, 42–47.

Sjögren, P., 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnaean Society 42, 135–147.

Sredl, M.J., Collins, E.P., Howland, J.M., 1997. Mark-recapture of Arizona leopard frogs. In: Sredl, M.J. (Ed.), Ranid Frog Conservation and Management. Nongame and Endangered Wildlife Program Technical Report 121. Arizona Game and Fish Department, Phoenix, AZ, pp. 1–20.

Stebbins, R.C., 1954. Natural history of the salamanders of the Plethodontid genus *Ensatina*. University of California Publications in Zoology 54, 47–124.

Stebbins, R.C., Cohen, N.W., 1995. A Natural History of Amphibians. Princeton University Press, Princeton.

Stromberg, G., 1995. The yearly cycle of the Jumping Frog (*Rana dalmatina*) in Sweden. A 12 year study. Scientia Herpetologica 1995, 185–186.

Stumpel, A.H.P., 1987. Distribution and present numbers of the Tree Frog *Hyla arborea* in Zealand Flanders, The Netherlands (Amphibia, Hylidae). Bijdragen tot de Kierkunde 57, 151–163.

Stumpel, A.H.P., Hanekamp, G., 1986. Habitat and ecology of *Hyla arborea* in the Netherlands. In: Roček, Z. (Ed.), Studies in Herpetology. Charles University, Prague, pp. 409–441.

Thorn, R., 1968. Les Salamandres d'Europe, d'Asie et d'Afrique Nord. Editions Paul Lechevalier, Paris.

Thrall, P.H., Burdon, J.J., Murray, B.R., 2000. The metapopulation paradigm: a fragmented view of conservation biology. In: Young, A.G., Clarke, G.M. (Eds.), Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, pp. 75–95.

Thurow, G.R., 1976. Aggression and competition in eastern *Plethodon* (Amphibia, Urodela, Plethodontidae). Journal of Herpetology 10, 277–291.

Trenham, P.C., Shaffer, H.B., Koenig, W.D., Stromberg, M.R., 2000. Life history and demographic variation in the California Tiger Salamander (*Ambystoma californiense*). Copeia 2000, 365–377.

Tunner, H.G., 1992. Locomotion behavior in water frogs from Neusiedlersee. In: Korsós, Z., Kiss, I. (Eds.), Proceedings of the Sixth Ordinary General Meeting of the Societas Europaea Herpetologica. Hungarian National Museum, Budapest, pp. 449–452.

Turchin, P., 1999. Population regulation: a synthetic view. Oikos 84, 153–159.

Tyler, M.J., 1989. Australian Frogs. Viking O'Neil, Ringwood, Australia.

Vial, J.L., Saylor, L. 1993. The Status of Amphibian Populations: a Compilation and Analysis. Declining Amphibian Populations Task Force, IUCN/SSC, Working Document 1, 1–98.

Vucetich, J.A., Waite, T.A., 1998. Number of censuses required for demographic estimation of effective population size. Conservation Biology 12, 1023–1030.

Vucetich, J.A., Waite, T.A., 1999. Erosion of heterozygosity in fluctuating populations. Conservation Biology 13, 860–868.

Vucetich, J.A., Waite, T.A., Nunney, L., 1997. Fluctuating population size and the ratio of effective to census population size. Evolution 51, 2017–2021.

Waldick, R., 1997. The impact of forestry practices upon amphibian populations in eastern North America. In: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a Global Problem, pp. 258–270.

Waringer-Loschenkohl, A., 1991. Breeding ecology of *Rana dalmatina* in Lower Austria: a 7-years study. Alytes 9, 121–134.

Weitzel, N.H., Panik, H.R., 1993. Long-term fluctuations of an isolated population of the Pacific Chorus Frog (*Pseudacris regilla*) in northwestern Nevada. Great Basin Naturalist 53, 379–384.

Welsh Jr., H.H., Droege, S., 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conservation Biology 15, 558–569.

Wilbur, H.M., 1980. Complex life cycles. Annual Review of Ecology and Systematics 11, 67–93.

Wright, A.H., Wright, A.A., 1947. Handbook of Frogs and Toads of the United States and Canada. Comstock Publishing Associates, Ithaca, NY, USA.

Young, A.G., Clarke, G.M. (Eds.), 2000. Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge.