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PERSPECTIVES ON AMPHIBIAN POPULATION DECLINES: DEFINING THE PROBLEM AND SEARCHING FOR ANSWERS.

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ABSTRACT. — Impressions of amphibian population decline are rarely backed with historical or demographic data and are expressed either as a concern over declining sizes of populations or as a concern over declining numbers of populations. All instances in Canada where amphibians are considered to be in decline are due to population number losses, as is true elsewhere in the world. A research program broadly aimed at identifying demographic declines in population size is not practicable and monitoring methods designed to estimate population sizes are largely unreliable. Populations normally fluctuate in size over time periods ranging from years to decades thus rarity and population size reductions are not equivalent to declines and are not good predictors of population extinction. To study the problem, declines must be defined in terms of population numbers, not size. These declines may be ascertained by examining relative gains and losses of populations from year to year using verified presence/absence data from monitoring surveys. Current absence does not imply former presence at any particular site and the loss of populations is not related to the sizes of the populations that remain. Due to the potential of environments to recover and of amphibians to disperse, local habitat destruction over the short term does not necessarily imply permanent amphibian population loss. There is a general paucity of information about natural amphibian populations under normal conditions and this information is needed to understand why declines in population number occur. Population changes are influenced by local conditions which may be possible to identify and are, in any case, usually specific and local. Amphibian populations are not universally declining. A single cause, or multiple synergistic causes, for global declines is elusive because it is difficult to prove that a particular factor involved in population loss is a primary or secondary agent. Amphibians' frequently complex life-histories, high reproductive potential, and high mortality rates, require that conservation efforts concentrate on habitat preservation, including all stages of ecological succession, as well education and informed land use practices.

RÉSUMÉ. — Il est rare que des données historiques ou démographiques confirment l'hypothèse d'un déclin des populations d'amphibiens; par déclin on entend soit une décroissance des effectifs soit une décroissance du nombre de populations. Au Canada comme ailleurs dans le monde, le déclin des populations d'amphibiens prend la forme d'une déperdition au niveau du nombre de populations. Le programme de recherche qui vise essentiellement à identifier les déclin démographiques dans les effectifs n'est pas réaliste et les méthodes de surveillance conçues pour évaluer les effectifs manquent globalement de fiabilité. Les effectifs connaissent normalement des fluctuations qui peuvent durer plusieurs années voire plusieurs dizaines d'années. Par conséquent, la rareté et la réduction des effectifs ne sont pas nécessairement le signe d'un déclin de la population en question et ne peuvent pas permettre de prédire sa disparition. Pour étudier le problème, le déclin doit être défini en termes de nombre de populations et non d'effectifs. Ces déclin doivent être évalués en examinant les gains et les pertes relatives de populations d'années en années sur la base de données sur les présences/absences dûment vérifiées dans le cadre d'études de surveillance. L'absence d'une espèce ne signifie pas nécessairement sa présence à une date antérieure et le déclin démographique n'est pas nécessairement lié aux effectifs qui restent. Étant donné le potentiel des environnements à se régénérer et celui des amphibiens à se disperser, la destruction des habitats locaux à court terme n'entraîne pas nécessairement la disparition permanente des populations d'amphibiens. Les données sur les populations naturelles d'amphibiens dans des conditions normales sont d'une manière générale aussi pauvres qu'elles sont nécessaires pour comprendre les causes du déclin démographique observé dans certaines populations. Les changements démographiques dépendent des conditions locales qu'il est possible d'identifier et qui sont en règle générale à caractère très spécifique et localisé. Les populations d'amphibiens ne sont pas toutes en voie de disparition. Une cause

unique ou des causes synergiques multiples ne suffisent pas à expliquer les phénomènes de déclin car il est très difficile de prouver qu'un facteur en particulier de déclin démographique est un agent primaire ou secondaire. Le cycle de vie des amphibiens est souvent très complexe et dans la mesure où leur potentiel reproducteur et leur taux de mortalité sont très élevés, il est essentiel que les efforts de conservation soient axés sur la protection de l'habitat, à toutes les étapes de la succession écologique, ainsi que sur l'éducation et l'adoption de pratiques raisonnables d'utilisation des sols.

When we discuss declines in amphibian populations, what do we mean? Is it a worry over the number of toads in a Toronto garden or the number of species of toads in Canada? the presence of salamanders across a wide region of Canadian Prairie or the presence of a particular salamander in a particular Québec bog? population change in a common frog in British Columbia or preservation of an endangered frog in Southern Ontario? Are our concerns local, regional, or global? Can we identify a decline when it is real and avoid labelling something a decline when it is not? And how can we identify and remedy the conditions that lead to declines when we see them?

Seventeen species of Canadian amphibians have been identified as having suffered losses of populations (Weller and Green, this volume). Among them, *Ambystoma tigrinum* has declined in south central British Columbia (Orchard, 1992) and losses of *Bufo hemiophrys* populations in Alberta have occurred over a decade (Roberts, 1992), with lowered numbers of sightings of these toads reported from Manitoba as well (Koonz, 1992). *Acris crepitans* and *Bufo w. fowleri* populations have been extirpated in Ontario from Pt. Pelée and Pelée Island in western Lake Erie (Oldham and Weller, 1992; Green, 1989). Drastic declines in *R. pipiens* abundance have been noted throughout the western portion of its range from British Columbia through to northern Ontario (Roberts, 1992; Seburn, 1992; Didiuk, this volume; Koonz, 1992; Oldham and Weller, 1992). *Pseudacris triseriata* is now rare throughout the St. Lawrence Valley in southwestern Québec, where it was common in the 1950's (Bonin, 1992; Daigle, this volume). At least eight species are losing population numbers in British Columbia alone, considered to be threatened by forestry practises and land conversion. This echoes the greater numbers of declines seen in the western US (Corn, 1994) compared to the eastern US (Pechmann et al., 1991). The population losses do not include those in habitats that are obviously disturbed by urbanization or intensive agricultural use. No one is considering the eradication of habitat in downtown Montréal, Toronto, or Vancouver, for instance, although amphibians surely once lived there. But neither has anyone seriously tested if the apparent declines are a significant departure from random or from normal levels of extinction.

There has been mixed opinion on precisely what is a decline and what is not. It is unfortunately easy to misinterpret biodiversity data of the sort that has so far been available (Rodda, 1993) and a nagging problem for the Declining Amphibian Populations (DAP) initiative has been to define these terms of reference (Pechmann and Wilbur, 1994; McCoy, 1994). For example, declines in numbers of populations of *Dicamptodon tenebrosus* and *Ascaphus truei* in southwestern British Columbia have justifiably been attributed to habitat destruction, largely by logging (Orchard, 1992), yet Farr (1989) expressed doubt that there was sufficient evidence to make a firm assessment or conclude that the declines were permanent. Although populations of some Canadian species have certainly been lost, there is no firm evidence that the sizes any remaining Canadian populations have permanently declined. It may appear to be paradoxical but population extinction is not necessarily preceded by prior decline in population size (Blaustein et al, 1994a). As reported in this volume, the Canadian DAP group undertook both wide-scale censusing to search for population loss and in-depth studies of particular populations to try to assess demographic decline. The results of these studies have shown how to define the problem more precisely and suggest the manner in which declining amphibian populations may be approached.

TYPES OF DECLINE

The demographic approach.

There are really two sorts of declines to consider: declines in the *size* of populations and declines in the *number* of

populations. Declines in population size may be addressed with quantitative, demographic data and involves the estimation of N , the census population size, or even more importantly, N_e , the effective population size. Heightened mortality, lowered fecundity, and/or lowered recruitment may all lead to lowered abundance. In this vein, Vial and Saylor (1993) defined a decline, pertaining to amphibian populations, as:

"a definite downward trend in numbers over a span of time appropriate to the species' life history, shown to be in excess of the normal fluctuations in population size".

This is a demographic definition requiring us to know amphibian life histories, understand the extent of normal fluctuations in abundance, be able to accurately census population size, and be able to model the parameters of viable populations. It further requires charting the change in population size over time, ΔN , merely to establish what is the normal range of fluctuation while neglecting the natural processes of local population extinction and recolonization.

But declines fitting this demographic definition are not entirely what have inspired the DAP initiative ([Barinaga, 1990](#); [Blaustein and Wake, 1990](#); [Wyman, 1990](#); [Wake, 1991](#)). The phenomenon most at issue is not necessarily demographic population size reductions but decrease in the numbers of populations due to extinctions over a broad scale. For instance, high abundance in a few populations does not mean that a species is holding its own if those are the only populations that remain. Therefore the Vial and Saylor definition does not encompass the whole of the phenomenon of concern regarding declining amphibian populations.

The diversity approach.

The other concern regarding declining amphibians is thus the decrease in population number, as seen among the 17 identified declining species in Canada. Local extinctions, extirpations, and range reductions are at issue, rather than demographic parameters. These are qualitative and discrete phenomena, best assessed with good presence/absence data, in contrast to the quantitative data at the level within populations. Because of the stochastic nature of within-population parameters, the relationship between demographic variability and the probability of population extinction is not at all obvious ([Goodman, 1987](#); [Schoener and Spiller, 1992](#)). Under normal, unstable conditions, and mindful of some amphibians' high fecundities, a reduction in N cannot be considered to lead inevitably to population loss, nor to be the singular hallmark of impending population loss. Thus another definition, complimentary to that of [Vial and Saylor \(1993\)](#), needs to be proposed:

A decline is the condition whereby the local loss of populations across the normal range of a species so exceeds the rate at which populations may be established, or re-established, that there is a definite downward trend in population number.

This prescribes a much different research program. In order to assess losses in the number of populations, we need to understand normal extinction and recolonization rates and be concerned, at this inter-population level, with landscape variability and the connections within metapopulation structures. All populations inevitably go extinct and the stability of individual populations can be very difficult to judge ([Goodman, 1987](#)) so this implies assessing the persistence of populations and relative rates of loss and gain over large areas. The two different research programs engendered by the two different definitions of population declines each may contribute to understanding the phenomenon.

THE DEMOGRAPHIC RESEARCH PROGRAM: CHARTING FLUCTUATING POPULATION SIZE

There is considerable scope for increasing our understanding of amphibian population biology. Many of the models used to assess and conserve mammalian or avian populations, for instance, may be of limited use with the high fecundity, high mortality, and iteroparity of pond-breeding anurans. Different species of amphibians have very different life history strategies, and thus reactions to perturbations affecting their numbers. They may also react quite differently to impacts at different times of the year ([Berven, 1990](#)). For a short-lived species with high fecundity and high mortality, such as *Rana sylvatica* or *Pseudacris triseriata*, large losses of tadpoles and juveniles are always expected. The animals of greatest importance to the continuance of the population are the breeding adults in spring. So long as there is production and survival of breeding adults, the population is likely to persist. Therefore the critical stage in the life history, and the one most critical to protect, is the adult in early

spring at the onset of the breeding season. Their chances of breeding a second time are often so low that losses of adults at any other time of year will have only minimal impact. However, for a long-lived, low-fecundity, low mortality species, like *Plethodon cinereus*, losses of any individuals, especially the dispersing juveniles, may be more severely felt by the population as a whole. Nevertheless, both reproducers and dispersers are important for population persistence and the colonization of new populations.

Amphibians also confound standard population models where they exhibit biphasic life histories. Many ranid frogs overwinter as tadpoles and can survive as populations despite losses of adults (Bradford, 1991). Contrarily, total reproductive failures due to massive die-offs of tadpoles may be masked by the presence of dispersed juveniles from other localities (Seburn et al., this volume). Thus amphibian population demographics need to be studied in rigorous fashion (Shirose and Brooks, this volume; Green, this volume) to discern in more detail amphibian survivorship, effective population size, minimum viable population size, and inbreeding, and determine how these demographic parameters affect metapopulation structure (Lande and Barrowclough, 1987; Meffe and Carroll, 1994). Many effects are density dependent. Although die-offs of tadpoles or metamorphs may be spectacular and alarming, epidemics of disease can only happen when population size is large enough for a pathogen to spread (Crawshaw, this volume).

Estimating population size.

Although counting numbers is in itself insufficient for understanding population viability, the fundamental parameter remains how many individuals there are in a population. Mark/recapture methods and removal sampling may be sufficient to produce analyzable data (Donnelly and Guyer, 1994). There are many methods and much literature on the subject. A Lincoln/Peterson index based upon two samples is both simple and unreliable. All animals captured in the first sample are marked and released. The second sample assumes that the ratio of recaptured marked animals to the whole of the second sample is proportional to the ratio of the first sample to whole of the population (ie. N). The assumptions are rarely met and there are better means, but all require greater sampling effort. The program CAPTURE, (available from Colorado Cooperative Fish and Wildlife Research Unit, 201 Wager Bldg., Colorado State University, Fort Collins, CO, 80523 USA) can yield more reliable estimates of total numbers in closed populations based on repeated mark/recapture data (Rexstad and Burnham, 1991; White et al., 1982). A closed population, where there is no immigration, emigration, birth or death, seems like a mere abstraction yet, for practical purposes, an anuran breeding chorus may approach the “closed” condition for the brief time the chorus endures. The Jolly-Seber method embodied in the program JOLLY (available from Dr. James E. Hines, Patuxent Wildlife Research Center, Laurel, MD 20708, USA) can apply to open populations (Pollack et al., 1990) but may not return the required total population size if used for mark-recapture within a single breeding season. It is valid for periodic sampling but may be hampered by low year to year recapture rates if survivorship is limited.

Sampling methods only aim to estimate the census size of the population, N_c , the absolute total number of animals present. The accuracy of estimating N_c depends upon the quality of the data, the model used, and the assumptions taken. But for judging the viability of a population and its real trends, N_c is not entirely adequate. The effective population size, N_e , is more pertinent to the continuation of a population because not all individuals share equally in the total reproductive effort (Lande and Barrowclough, 1987). But N_e is notoriously difficult to measure as it is governed by numerous factors, including bias in the effective sex ratio, variance in clutch size, and relative survival of offspring to maturity. Only a small proportion of individuals breed, for instance, and N_e contains only those which genetically contribute to the next generation. The formula

$$N_e = (4N_m \times N_f) / (N_m + N_f)$$

(Meffe and Carroll, 1994) might be applied to the data of Bertram and Berrill (this volume) on breeding success in *Hyla versicolor*. Although the census size of the population was 87, 34, and 83 individuals in each of three years, the numbers of amplexant pairs was considerably less than this — 10, 4, and 19, respectively — and therefore the effective population size was at most only 20, 8, and 38 individuals. But this reckoning still fails to account for a

further reduction in N_e when some males breed more than once.

The variance in the numbers of successfully raised offspring per female, σ^2 , also affects N_e . The greater the variance, the lower the value of N_e . In pond-breeding anurans, this may be significant since the variance in clutch sizes may be considerable. According to Gilhen (1984), clutch sizes ranged from 396 - 1581 eggs ($n = 87$) for *Pseudacris crucifer* and from 1401 - 5289 eggs ($n = 10$) for *Rana clamitans* in Nova Scotia. In contrast, *Plethodon cinereus* was recorded with clutch sizes only from 4 to 17 eggs ($n = 58$). However, lacking data on survivorship, calculating the variance in the distribution of progeny among females that is needed for this estimation of N_e is not possible.

Effective population size estimates calculated with demographic data complement those derived using genetic information. Fluctuations in population size decrease genetic N_e because each crash to a small population size produces a bottleneck and a reduction in the genetic diversity available for the subsequently expanding population. Over time, the harmonic mean of populations sizes estimates genetic N_e and thus a single population crash can greatly reduce its value. Many pond-breeding anurans experience such crashes (Bradford, 1991; Pechmann et al., 1991). Nevertheless, this allows genetic methods to also be employed to estimate population parameters (Galbraith, this volume). Because heterozygosity is influenced by genetic effective population size, change in heterozygosity per generation (ΔH) allows an indirect estimation of N_e using allozyme or molecular data. The importance of such genetic analyses should not be underestimated. Until sufficient demographic and genetic data are at hand for any species, it will not be possible to determine the true vulnerability of populations because we will be unable to estimate when a population may be approaching the critical minimum effective number of individuals required for population viability. We have no information on minimum viable population size from any Canadian amphibian.

Monitoring population demographics.

The one effective way to establish population demographic parameters is via intensive, long-term study. Yet which demographic variables to monitor depends upon the questions being asked. According to Blaustein et al. (1994a), demographic variables need monitoring on a landscape scale for metapopulations. Demographic information such as age/stage distributions, natality and mortality schedules, immigration and emigration are seldom stable in real populations and rarely known with accuracy. Yet these must be monitored on a real-time basis in order to have any predictive value. For example, it now appears that the number of calling adult male *Bufo fowleri* is dependent to an important but varying extent upon the numbers of yearling males joining the chorus (Green, this volume). Therefore, to predict chorus size for the following year, it may be best to monitor growth rate of juveniles during the summer. The number of calling males in one year has proven to be a poor predictor of the number calling the next year.

For many reasons, extensive monitoring of anuran choruses, as tested by numerous researchers in Canada, is too crude an estimation method of population size to enable meaningful evaluation of within-population parameters. Road call-counts are not useful as estimators of absolute animal abundance (Bonin et al., this volume,a; Bishop et al., this volume; Lepage et al. this volume). The scheme adopted experimentally by several Canadian monitoring studies used a scoring system for frog chorus intensity: 0 = no calls, 1 = individuals heard plainly, 2 = countable numbers but overlapping calls, 3 = full chorus with uncountable numbers. In truth, the score of 0 is a negative datum that often merely indicates a non-observation. Negative data require confirmation before they can be accepted as probably true. Even scores of 1 or 2, under sub-optimal weather conditions, may be considered negative data indicating *absence* of a full chorus of the males present. Unless all possible males are calling, these scores do not really quantify the numbers of animals even within earshot. The subjectivity of these two categories in practise leaves considerable latitude for observer bias. Inadequately motivated or overwhelmed volunteers may not rigorously adhere to complicated protocols for data collection, and thus may provide unreliable data. Anecdotal reportage almost always consists only of occurrence records, not reports of absences or losses.

Repeated observations at precisely the same locations are vital to verify the truth of "0" data.

A call-count score of 3 is not quantitative. Anuran choruses saturate with callers as densities increase (Arak, 1983). Once the air is full of calls, additional animals may be satellites or active searchers, depending upon species, and are in either case undetectable by ear. The relationship of the calling adult population to the total population also varies according to age structure, which may change from year to year. Furthermore, what constitutes a saturated chorus varies with species. A small number of toads of a species with a long call duration, such as *Bufo cognatus* or *B. americanus*, can easily fill the air near a listener whereas species with short call durations, such as *Pseudacris crucifer* or *Hyla regilla* may be more easily counted even in moderately large choruses. All monitoring groups operating in eastern Canada reported difficulty using the scoring scheme with *Rana pipiens*, which does not form tight choruses of closely spaced individuals. A full chorus of *Rana clamitans* is unlikely ever to be scored 3.

Time of night, relative humidity, and temperature also affect both the calling attitude of individual frogs or toads as well as the acoustic carrying capacity of the air. Weather conditions absolutely control whether or not there will be calls heard on any particular night and the proportion of animals calling, even at the height of a breeding season. In 1995, I and my students scored chorus strength on the 0 - 3 scale for both *Bufo americanus* and *B. fowleri* and estimated numbers of toads by ear (unpublished data) in conjunction with the Ontario Marsh Monitoring Program (see Bishop et al, this volume). We then waded into the chorus and counted all toads by intensive visual search. For both species, the aural estimates consistently underrated the real number of toads and there was no correlation between the two measures ($p < 0.001$). Within limits, call-count intensity data may be useful as a relative measure of population size from year to year, but listening for calls is likely to work best as a source of presence/absence data for monitoring population loss or gain, not for demographic estimation of within-population parameters.

For amphibians that do not call, or do not call loudly, other methods must be used to obtain a census. Terrestrial salamanders present particular problems for determining population size but the use of artificial cover objects (Davis, this volume, Bonin and Bachand, this volume) may allow mark/recapture studies to proceed with reduced impact on microhabitats. However, assessing numbers of tadpoles and salamander larvae by any means is both difficult and largely inapplicable to monitoring the health or persistence of a population (Wassersug, this volume).

The inherent unpredictability of population size.

The research program specified by the Vial/Saylor definition of declines is, for many species of amphibians, impossible to fulfill. The size of an animal population N at some time t is always a balance between gains of individuals by birth (B) and immigration (I) against losses by death (D) and emigration (E):

$$N_t = N_{t-1} + (B+I) - (D+E).$$

In species with the Type III survivorship curves that are typical of most North Temperate anurans, where both fecundity and mortality rates are very high, population parameters B and D are so inflated as to render it very difficult to establish population size based upon previous years' data. For long-lived species with low fecundities, like mammals, birds, or some terrestrial plethodontid salamanders and tropical frogs, populations may be stable enough that population growth models may be more predictive. But many species such as *Bufo fowleri* (Breden, 1988; Kellner and Green, 1995), *Bufo americanus* (Acker et al, 1986; Kalb and Zug, 1990), *Rana pipiens* (Leclair and Castanet, 1987) or *Rana sylvatica* (Bastien and Leclair, 1992) mature in only one or two years and have very short natural life spans. *Bufo fowleri*, for example requires an early successional habitat of dunes and ponds that are free from overgrowing vegetation (Green, this volume). These conditions often occur after major storms which also wreak catastrophic mortality upon the population yet are nevertheless necessary for population growth. Like other amphibians (Wassersug, 1975), the toads, then, are trapped in a perpetually and unpredictably fluctuating environment and respond in kind. Other species, such as *Hyla versicolor*, also require early or mid-succession habitats and thus find disturbed environments advantageous (McAlpine, this volume). Predator

populations are subject to weather-mediated stochasticity. The variable growth rates of amphibians between individuals and between years influence maturation rates. Thus unpredictability is inherent and population viability theory predicts that small and/or fluctuating populations are more prone to random extinction (Soulé, 1987). There is little chance within a human lifetime to identify what is the normal range of fluctuation in population size for many species of amphibians and therefore no way to know if a population has deviated from this norm.

THE DIVERSITY RESEARCH PROGRAM: CHARTING DECLINES IN POPULATION NUMBER

Despite the demographic stochasticity of many amphibian populations, especially those suffering declines, a diversity research program based upon population number may be feasible. The number of species or populations present in a region over time depends upon a dynamic balance between their gain and loss (MacArthur and Wilson, 1967; Levins, 1969; Hanski and Gilpin, 1991). Levins' (1969) metapopulation model considered the proportion of habitat patches occupied by a species at any time, modelling that to depend upon colonization of new patches (m) minus extinctions from occupied patches (e). But this concept can be simplified for our purposes by considering only numbers of populations rather than occupancy of habitat patches. Cast in the style of the previous equation describing change in population size, the numbers of populations (P) at time (t) can be seen to depend upon gains of new populations (G) minus losses of established populations (L):

$$P_t = P_{t-1} + (G - L).$$

Obviously, stable numbers of populations are achieved where $G - L = 0$, declining numbers occur where $G - L < 0$, and increases occur where $G - L > 0$. The flux, or amount of turnover (T) among populations is:

$$T = G + L$$

and the rate of change in population number ΔP is:

$$\Delta P = \Delta G - \Delta L$$

which reflects the rates of colonization (ΔG) and extinction (ΔL). This is clearly distinct from changes in population size, ΔN , since that is not necessarily tightly coupled with the chance of extinction (Blaustein et al. 1994a; Schoener and Spiller, 1992).

All populations go extinct eventually and the single loss of a population may or may not be meaningful depending upon the number of populations to begin with and the rate of population turnover. Demographic uncertainty, environmental uncertainty, genetic uncertainty, and catastrophe all lead to local extinctions. But similar uncertainties also lead to local recolonizations. Over a landscape scale, minimum viable population size is not so readily estimated as ΔP and T , and not so vital as the probability that all populations will go extinct over a given number of years.

Monitoring population turnover.

Hecnar (this volume) used intensive methods to study population turnover in southwestern Ontario. But, despite its problems when applied to assessing population demography, extensive monitoring and the compilation of atlases may also be used effectively for determining presence or absence and thereby gauge the contraction or expansion of ranges and the persistence of viable populations. But short-term presence/absence data or anecdotal reports of raw numbers are likely inadequate. One of the most valuable outcomes of extensive monitoring programs is the compilation of reliable, annual, presence/absence reports into new atlases. Several atlas projects are being pursued in Canada, the oldest being the Ontario Herpetofaunal Survey (Oldham and Weller, 1992) and the Atlas des amphibiens et reptiles du Québec (Bider and Matte, 1994). Other projects inspired by the DAPCAN initiative aiming to compile accurate geographic records are continuing in Alberta, Saskatchewan, Manitoba, and New Brunswick. The value of atlas projects has suffered in the past from non-standardized protocols for data collection and from sometimes uncritical acceptance of anecdotal reports. With relatively few exceptions (McAlpine, this volume; Maunder, this volume), the historical database in Canada has not proven to be very useful as a basis for determining present declines. But organized monitoring schemes operating with proven, uniform protocols and providing rigorously verified data may make it possible for atlases in future to chart yearly

changes in amphibian occurrence and thereby estimate ΔP and T over regional and landscape scales. This will more credibly determine the real nature of declines in population numbers than any information presently available.

THE CAUSES OF POPULATION LOSSES: DEMOGRAPHICS AGAIN

There is no compelling evidence that global causes are behind amphibian declines in Canada and no evidence from Canadian investigators that ozone depletion, ultraviolet radiation, or acid rain are directly responsible (Brooks, 1992; Green, 1993; Seburn, 1994; Ovaska, this volume). Losses and declines of populations can be explained by local causes and the reaction of amphibians both to stochastic fluctuations and to human-mediated disruption and/or fragmentation of environments. Although excessive UV-B radiation, hyperacidity, and pesticides of course can be lethal or debilitating (Corn and Vertucci, 1992; Blaustein et al., 1994b; Bradford et al., 1992; Berrill et al., this volume), and global warming is undoubtedly likely to make conditions better in some places and worse in others (Peters and Lovejoy, 1992; Ovaska, this volume), the ultimate cause for today's rapid losses of biodiversity is human impact upon the environment (Diamond, 1989). Its effect profoundly influences the demographics, metapopulation structure, and physiological responses of the species involved (Beebee, 1977). Therefore, when we examine the population biology of amphibians we are in all cases looking at human-influenced population biology.

Habitat destruction, fragmentation, and degradation are all considered to be the leading causes of population losses (Meffe and Carroll, 1994; Vial and Saylor, 1993; Weller and Green, this volume). More precisely, these include the direct and indirect effects of urban encroachment, agricultural development, and logging. Outright, permanent destruction of habitats is obvious as a cause for population loss (Johnson, 1992) but the fragmentation of environments is an equally powerful, yet more insidious potential cause of population disappearance. Fragmentation may sever the connections between co-dependent local populations, curtailing dispersal needed to rescue nearby local extirpations (Laan and Verboom, 1990).

Normally, local populations are connected by immigration and emigration of individuals (Gill, 1978; Hanski and Gilpin, 1991; Sjögren, 1991). Some local populations with high recruitment will be sources of emigrating, excess individuals. Other populations at the same time may have low recruitment and be population sinks that exist only by continual restocking and rescue. These metapopulation relations are dynamic and germane to understanding whether local population loss is permanent or transitory. A metapopulation may consist of a single, large source population, in a lake for instance, and several peripheral sink populations in small surrounding ponds. Loss of the source population, perhaps through trout-stocking, over-building, or shoreline degradation, will inevitably invite loss of the surrounding local populations which depend upon its emigrants for continuation. More usually, a metapopulation may consist of two or more local populations in disequilibrium (Gill, 1978). Since the probability of extinction for any one population exceeds the probability of extinction of the metapopulation as a whole, any human intervention which severs their connection risks altering the metapopulation structure and the increasing probability of extinction for all local populations. Thus a local population may be driven to extinction even though it is in a protected area and experiences no direct human impact.

Degradation of habitats reduces population viability *in situ*. Pollution, acidity, and toxic substances introduced into environments result in declines of reproductive potential and viability (Freda, 1986; Bonin et al. this volume,b; Bertram et al., this volume). Pesticides may be lethal and/or teratogenic for amphibians in dosages present in polluted habitats. These compromises of the environment leave amphibians susceptible to secondary infections and other disease (Blaustein et al., 1994c; Bradford, 1991; Crawshaw, this volume). There have been die-offs reported (Nyman, 1986). I have received reports of tadpole mass mortality in Laurentian lakes in Québec and Scott (1993) has coined a "post-metamorphic death syndrome" to describe similar die-offs of froglets in Arizona. Density-dependence of epidemic disease may be a factor in these die-offs but they may be insignificant over the long-term so long as breeding stocks of adults persist.

Introduced alien competitors and predators, including humans, also degrade habitats. Introduced predatory fish clearly have detrimental impact upon frog populations (Liss and Larson, 1991; Sexton and Phillips, 1986; Hecnar, this volume). Introduced bullfrogs (*Rana catesbeiana*) have also been touted as debilitating predators upon native western frog populations (Moyle, 1973; Hammerson, 1982; Orchard, 1992) although Hayes and Jennings (1986) cast doubt about their real contribution to *Rana aurora* population losses in California. Hayes and Jennings (1986) argued that although there is a correlation between increased bullfrog abundance and declines in other frog species in California, there is no evidence of direct effect. The bullfrogs may merely have moved into marginalized, compromised, or unoccupied habitats previously made less suitable for the other species. Over-harvest by humans, in particular, has been implicated in the *Rana aurora* declines in California (Jennings and Hayes, 1985) but there is no evidence that harvesting has directly reduced frog populations in Canada. During the catastrophic decline of *Rana pipiens* in Manitoba during the 1970s, the "frog-pickers" reported large numbers of dead and dying frogs in the wild (Koonz, 1992). There were still many frogs, but few live ones left to catch.

Environmental alteration may have beneficial effects for some species, especially those prospering in newly cleared, early successional habitats (Banks and Beebe, 1987). The expansion of *Hyla versicolor* in southern New Brunswick may be due to newly opened, disturbed habitats providing additional breeding sites (McAlpine et al., 1991). Global warming may produce opportunities for some species to expand (Ovaska, this volume). Even forestry operations may leave behind new breeding sites for some species in the form of dugout ponds in cleared sites (Waldick, this volume), although these are initially of very low quality. Species requiring stable, late successional environments with climax vegetation, such as terrestrial salamanders in British Columbia requiring old-growth forests, will be most perturbed by human resource-use activities (Davis, this volume; Dupuis, this volume). But, ironically, species requiring disturbed habitats and early successional vegetation, such as species of *Bufo*, may be adversely affected by conservation efforts aiming to prevent turnover of climax communities.

Different amphibian species are decidedly not uniform in their reactions to environmental change and, therefore, in order to ascertain causes of declines and study their impacts, detailed knowledge of the population biology, physiology, and demographics of each species is required. Studies of this sort may be unable to identify declines as effectively as broad-scale presence/absence surveys but once the phenomena are known and characterized, only intensive study at the local level can identify cause.

WHAT IS NOT A DECLINE?

As well as understanding which aspect of decline we are considering, we must also take pains not to be mistaken by situations that only appear to be declines. Endangered species, short-term diminution of population size, contained local habitat destruction, and lack of distributional data should not be interpreted inappropriately.

Rarity alone does not equal decline.

A great fear about amphibian declines has been that rare and threatened species may go extinct. This serious concern gave the global Declining Amphibian Populations Task Force much of its initial impetus. Outright losses of species, even in protected areas (Crump et al., 1992; Czechura and Ingram, 1990), are rightly a cause for anxiety. But once a species has already declined to so perilously low a level as to render it endangered, it may be difficult to reconstruct how it got to that condition. Wholesale declines, to be detectable, must occur among species widespread and visible enough that they are noticeable. Protection of endangered species is often a salvaging enterprise and a race against the extinction of only one or a few populations. Thus the factors that identify a species as endangered are not the same as those that may identify it as declining. Endangered species may in fact recover under careful management.

Furthermore, a species may be classified as rare simply because the extent of its range and abundance has not yet been gauged. Many amphibian species are considered rare and extremely localized in Canada. *Plethodon*

idahoensis is only known from a few sites in southeastern British Columbia. Although it appears on British Columbia's "Red List" of endangered species (Munro, 1993) there is no information about population trends despite fears that its fragmented range resulted from logging activities (Orchard, 1992). In Ontario, both *Desmognathus fuscus* and *Gyrinophilus porphyriticus* are known from only a very few specimens. There is not sufficient information from the few reports of *Bufo cognatus* in Manitoba and Saskatchewan upon which to base any assessment of numbers. *Desmognathus ochrophaeus* (Sharbel and Bonin, 1992) and *Rana pretiosa* species A (Green et al., 1996) are likewise only marginal in Canada. Therefore, from its beginning, the Canadian DAP Working Group did not involve itself heavily in concerns over presently endangered species. The working mission of the group was explicitly to document and research declines in amphibian populations. Because of the necessity of conducting research over landscape scales, the lessons to be learned about declines are to be found among erstwhile abundant species.

Population fluctuations are not declines.

Natural population fluctuations have to be distinguished from persistent declines in population viability across regions. Populations of amphibians normally may show apparently random variations in size simply because of their own population dynamics (Wissinger and Whiteman, 1992; Weitzel and Panik, 1993). Populations vary in their response to ecological changes in the environment, especially succession, and the unpredictable vagaries of the weather. Most Pond-breeding, North Temperate amphibians have high intrinsic rates of increase and should be able to rebound successfully after population decline as seen, for instance, in *Bufo fowleri*, at Long Point, Ontario (Green, this volume). Even long-term assessments of population fluctuations may be inadequate to identify them as declines since the stochasticity of these fluctuations makes any predictions about future population sizes unreliable.

Local habitat destruction does not signify permanent population loss.

Habitat destruction is rightly blamed for many losses of populations (Johnson, 1992) but not all habitat destruction may be permanent. There is little chance that downtown urban centres will be made hospitable to amphibian populations any time soon but, in many cases, habitats that have been destroyed may recover, and recovering habitats may be recolonized by certain species (Waldick, this volume). The destruction of a southwestern British Columbia stream due to logging, rendering it uninhabitable for *Dicamptodon tenebrosus* or *Ascaphus truei*, does not mean necessarily that there has been a permanent loss of these species. Amphibians do have the power of dispersal. We must consider the wider metapopulation which may cover a greater landscape area and encompass this local stream. So long as the habitat may again become usable and dispersal routes are available, it may be possible for local habitats to regain their ecological diversity. However, this optimism can only go so far. If the source populations are destroyed, or if the whole region is destroyed, or if dispersal routes are destroyed, then habitat loss may indeed result in permanent population loss. More important than the local destruction of any one habitat, therefore, is the regional interconnection of habitats and populations.

Current absence does not imply former presence.

Several species have been suspected of having suffered declines decades ago for which there is no current evidence. In some cases, it may be reasoned indirectly that species once existed in certain heavily disturbed urban or agricultural areas but little chance that these losses can now be studied. The clearing of forests for early European settlement in extreme southwestern Ontario permanently destroyed most habitats suitable for *Ambystoma maculatum*, *Plethodon cinereus*, or *Notophthalmus viridescens*, all of which are common and widespread elsewhere in the southern portion of the province yet extremely uncommon in this region (Hecnar, this volume; Weller and Green, this volume). This clearing took place long before occurrences of amphibians were systematically recorded and so the historical database contains no pertinent information. The region once was covered by tall-grass prairie, marshland, swamp, and hardwood forest (Bakowsky and Riley, 1994) which, logically, should have provided high-grade amphibian habitat. But no declines are presently detectable and historic losses from the region are now largely outside the scope of present investigations. Neither is it possible, at

this late date, to assess the true impact of pre-colonial aboriginal land use practises on other habitats, particularly in eastern Canada. Aside from a few subfossil remains (Holman and Cloutier, 1995), the lack of information means that it is not possible to determine for certain which species ever existed in particular regions.

CONSERVATION OF DECLINING AMPHIBIANS

Protection of amphibians.

Management practises must bear in mind the metapopulation structure of amphibian populations and preserve both source habitats and the connections between local populations. Modern forestry practice of smaller clear-cuts, preservation of wide margins around streams, especially small streams devoid of commercial fish, and corridors between un-cut stands is to be encouraged (Dupius, this volume; Waldick, this volume). Other possible measures may include "toad-tunnels" of appropriate design under new roads in critical areas or the rerouting of roads to avoid sensitive dispersal routes. Preservation of wetlands, establishment of forest preserves and maintenance of streams are all desirable. Parks and reserves must be extensive enough to buffer populations from surrounding development and encompass entire metapopulations. With better understanding and considered management practice, the problem of amphibian population loss might be forestalled.

The knowledge needed is readily apparent. We must identify critical life-history stages for species, identify metapopulation structures and habitat requirements, comprehend minimum sustainable population sizes, movements, and migrations, and chart population turnover, gains, and losses. We must gauge the impact of environmental stressors including UV-B radiation, acid precipitation, pesticide pollution, and habitat fragmentation. And we must identify vulnerable populations such as those which are isolated, in the way of urban or agricultural development, or affected by pollutants and toxic substances. With this knowledge, we may enact management plans that may have effect.

Status evaluations.

The status of species which may be at risk must be determined and so an evaluation of all species should be conducted. This partly has been the aim and intention of COSEWIC, the Committee on the Status of Endangered Wildlife in Canada, administered through Environment Canada. Reports on ten salamander species and four anurans have been commissioned yet only a handful have been completed (*Bufo fowleri*, *Ambystoma texanum*, *Dicamptodon tenebrosus*, *Acris crepitans*). Even so, COSEWIC only has a mandate to investigate *endangered* wildlife, not *declining* wildlife populations. All species in Canada need to be assessed, not just the rarities.

Land use.

Critical habitats necessary for maintenance of populations must be known and adequately protected. This will require extensive knowledge of the population biology of each species. This will also require clear assessment of the environmental impact of development or if the rate of habitat recovery is not as great as the rate of habitat destruction. Past environmental impact studies have provided only minimal information usable to assess, and mitigate, perturbations upon amphibian populations. They generally go unnoticed in favour of more overtly commercial and recreational fish, birds and mammals. In fairness, the lack of attention to amphibians in environmental impact assessment reflects their secretive behaviour and low visibility. But periodic or seasonal breeding, limited vagility, congregation of breeding assemblages, and sensitivity to habitat fragmentation can render amphibians particularly vulnerable to land use changes. Government agencies can take the lead to provide resources to assess populations of amphibians on public lands, determine those species at risk of decline, and determine habitat requirements of those species for incorporation into land management plans.

Education.

Additional resource materials are required to portray the diversity and range of adaptations of amphibians and to deliver conservation-oriented messages to young people. The inherent fascination with amphibians can provide an opportunity to attract and hold the interest of school children. Texts, videos, and films can supplement school

classroom curricula but field trips and participation by school groups in monitoring efforts and/or in local conservation projects would be especially valuable (Johnson, 1992). The Metro Toronto Zoo's "Adopt-a-Pond" program encourages individual and school participation in wetland conservation with its package of tape recordings, project ideas, stickers, posters, and information aimed at school children. Members of natural history societies, professors, teachers, and wildlife agency staff can and should also participate actively in school programs and offer activities. For instance, a reptile and amphibian display for school groups is being developed by Nature Saskatchewan, a provincial conservation organization, and a travelling display on frogs and toads in Québec has been put together by the Redpath Museum of McGill University in Montréal. Reports, media interviews, and popular articles can help inform the public regarding amphibians. Popular guides to amphibians (and often reptiles) written for particular provinces (Cook, 1966; Gilhen, 1984; Green and Campbell, 1984; Johnson, 1989; Melançon, 1961; Preston, 1982; Russell and Bauer, 1993) are instrumental in public education about amphibians. Despite the methodological and scientific difficulties of large-scale, volunteer-based monitoring of amphibian populations, one certain benefit is public education. Volunteers can realize that they are part of an important enterprise so long as the research programs they participate in are designed to yield useful data from their efforts.

And, finally, the Declining Amphibian Populations Task Force has, in itself, inspired unprecedented interest in the biology of amphibians. The annual conferences of DAPCAN and the work of its national, regional, and provincial co-ordinators has stimulated the involvement of government agencies in amphibian conservation biology and inspired new graduate research. If humans are the problem, they are also the solution.

THE FINAL WORD

Are amphibians declining? Of course they are. All manner of species are declining, not just frogs and salamanders, because there is no place left on Earth that is truly pristine and untouched by the effects of human hands (Diamond, 1989; Pounds and Crump, 1994). When we discuss declines in amphibian populations we must continue to encompass concerns over toads in gardens and across Canada, salamander populations over the prairie and in particular bogs, and population changes in both common and endangered frogs. The fears are global; the causes are local or regional. It is possible, with good information, to identify a decline when it is real and ultimately to identify and remedy the conditions that are its cause. That is because there is no special, overarching cause for frogs and salamanders to decline, nor even a need to presuppose one, unless we are prepared to accuse ourselves. All declines of amphibian populations depend upon how the animals are affected by the myriad ways in which we humans can affect the landscape. This is cause for hope. If the universal cause was global, we as individuals may only be able to wring our hands in despair, with little hope ourselves of effecting a remedy. Yet, if there is a lesson, it is that no matter how widespread a causative factor may be, the population biology of amphibians is intensely local. And since local conditions breed local responses, we may act to preserve amphibians, a region at a time.

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