

DECLINING AMPHIBIAN POPULATIONS: THE PITFALLS OF COUNT DATA IN THE STUDY OF DIVERSITY, DISTRIBUTIONS, DYNAMICS, AND DEMOGRAPHY

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Most data used in the study of the demography, dynamics, distributions, diversity, and declines of amphibians are count data that are not adjusted for detection probabilities, which are generally variable and low. Such unadjusted count data are unreliable for understanding amphibian ecology, amphibian declines, or when developing conservation and management strategies. In the future, detection probabilities should be estimated and counts adjusted accordingly. This could be achieved by using capture-mark-recapture, distance sampling or novel Bayesian methods.

Key words: conservation, detection probability, population census, survey methods

INTRODUCTION

Amphibians are declining locally and globally for a variety of reasons (Cooke, 1972; Beebee, 1973; Blaustein & Wake, 1990; Alford & Richards, 1999; Corn, 2000; Houlahan *et al.*, 2000). If we want to understand why amphibians are declining and how we can halt and reverse the negative trends, then we must improve our understanding of amphibian ecology. In particular, we should strive to better understand the demography and dynamics of amphibian populations and the factors that govern the distribution of species and species diversity at particular sites. Collecting reliable field data is an important step towards understanding these basic elements of amphibian ecology. Here, I argue that most field data on the ecology of amphibians are of limited use because they are unadjusted counts. Next, I suggest estimating detection probabilities to adjust the counts and improve data quality. High-quality field data are needed to complement experimental studies on the causes of amphibian declines, to parameterise population models, and for better quantification of declines.

THE PITFALLS OF UNADJUSTED COUNT DATA

Counts are commonly used in the study of amphibian ecology. Unadjusted counts are not reliable in amphibian ecology because they underestimate the true population parameters of interest because some individuals, populations, or species are not detected. Additionally, variation in detection probabilities generates variation in the counts which obscures true variation in ecological processes (Burnham, 1981; Nichols & Pollock, 1983; Martin *et al.*, 1995; Anderson, 2001). Nichols's (1992) simple formula indicates the relationship between a count, C , and the population parameter of interest, N (which may be a de-

mographic rate, population size, the number of populations in an area, or the number of species at a site):

$$E(C) = Np, \quad (1)$$

where p is a detection probability and E indicates an expected value. Obviously, it is impossible to detect all individuals, populations, or species in a given area (e.g. Preston, 1979); therefore, p is < 1 and C always underestimates N to an unknown degree (Nichols & Pollock, 1983). The detection probability will depend on what is being counted. For example, counts of egg masses are probably more reliable (i.e. on average higher – and more importantly – less variable p) than counts of adult newts within a pond. The count C is commonly known as 'return rate' when dealing with demographic rates and as a 'population index' or 'relative abundance' when dealing with population size, density, or abundance (Martin *et al.*, 1995; Anderson, 2001).

A comparison of two (or more) counts is problematic because one must assume that the detection probabilities are constant. A comparison of two counts, a trend, is given by:

$$E(C_1/C_2) = N_1 p_1 / N_2 p_2 \quad (2)$$

$E(C_1/C_2)$ equals N_1/N_2 only if $p_1 = p_2$ (Yoccoz *et al.*, 2001; Pollock *et al.*, 2002). This is unlikely. Anholt *et al.* (2003), for instance, showed that detection probabilities of two species of frogs were sex-, site-, and time-, but not species-specific. Bailey *et al.* (2004a,b) provide evidence for strong variation in detection probabilities in salamanders. If $p_1 \neq p_2$, then the comparison (the trend) is biased to an unknown degree and even the direction of bias is unknown. If $C_1 \neq C_2$, it is not known whether $N_1 \neq N_2$, $p_1 \neq p_2$, or both are different (i.e. are variable). With unadjusted counts, it cannot be determined which elements of the equation are variable.

Data from a capture-mark-recapture study on green turtles (*Chelonia mydas*; Chaloupka and Limpus, 2001)

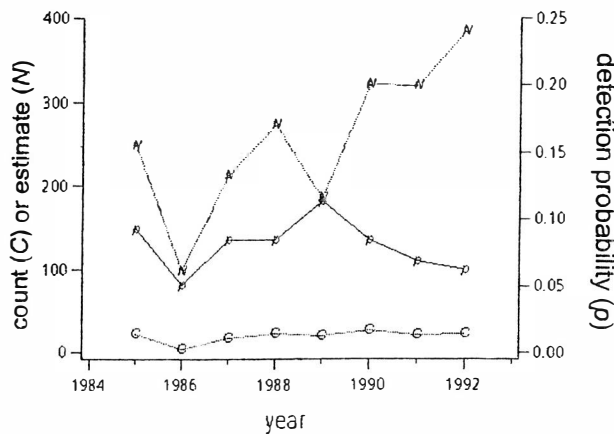


FIG. 1. C , $\hat{N}$, and $\hat{p}$ of male green turtles (*Chelonia mydas*) living in Great Barrier Reef, Australia, taken from the capture-mark-recapture study of Chaloupka and Limpus (2001). $\hat{N}$ was calculated as $C/\hat{p}$.

where C , N , and p were estimated serve to illustrate problems associated with unadjusted counts (Fig. 1): the unadjusted counts C seriously underestimate true population size (N) and suggest that the population is stable (i.e. stationary) while it is in fact increasing (the number of turtles fluctuates greatly because there are many transients). This happens because p is low, variable, and declines towards the end of the study period. Throughout the study period p remains between ca. 0.05 to 0.1. This suggests that even seemingly small fluctuations in p may lead to large errors when using C as an index for N (note that in fact there is a two-fold difference in detection probabilities). Temporal trends in detection probabilities may not be uncommon (e.g. Funk & Mills, 2003).

Herpetologists are well aware of the fact that it is impossible to capture all individuals or detect all populations or species. For instance, Hairston & Wiley (1993) argue that fluctuations in the apparent abundance of terrestrial salamanders are due to variation in student motivation to search for salamanders, i.e. variation in detection probabilities, rather than true variation in salamander abundance. Nevertheless, few amphibian ecologists seem aware of the problems caused by variation in detection probabilities, and often fail to take detection probabilities into account when estimating demographic rates or other population parameters (e.g. Schmidt & Anholt, 1999). Return rates (C) are often treated as if they were survival probabilities (e.g. Berven, 1990; Parris & McCarthy, 2001), 82% and 95% of the time series used by Alford & Richards (1999) and Houlahan *et al.* (2000), respectively, are unadjusted counts, and there are very few studies on the species distribution or diversity of amphibians that take detection probabilities into account (MacKenzie *et al.*, 2002, 2003). The use of unadjusted count data is not unique to herpetology. Most population data of fish, birds, and mammals consists of unadjusted counts (Preston, 1979; Nichols & Pollock, 1983; Martin *et al.*, 1995; Bjørnstad & Grenfell, 2001; Rosenstock *et al.*, 2002).

The most common solution to dealing with variation in detection probabilities is to standardize sampling methods (Heyer *et al.*, 1994). Standardization, it is (tac-

itly) argued, reduces variability in p such that C becomes a reliable index of N . This may not always be the case. Hyde & Simons (2001) compared several standard methods for sampling terrestrial salamanders. They found that correlations between the counts obtained using different standard methods were generally weak. No method was clearly the best and at least some of the methods are apparently unreliable. Hyde & Simons (2001) concluded that none of the standard methods was suitable for long-term monitoring of salamander populations (see also Bailey *et al.*, 2004a,b).

In addition to the use of standard methods, environmental variables that may affect p are often measured and used to adjust or calibrate the counts. This may solve the problems associated with unadjusted counts to some extent but is clearly not an easy task. Sauer & Link (1998, 2002) provide examples where environmental variables (in their studies primarily observer effects) are used to adjust counts from the North American Breeding Bird Survey. Standardization and the use of environmental variables are clearly valuable and should be used or collected, respectively, whenever possible; however, it is not possible to control for every factor that may affect detection probabilities. For example, some surveys use the number of calling males as an index of population size. In the natterjack toad (*Bufo calamita*), for instance, some males only call when few males are present and calling. In large populations, some males adopt a satellite strategy (Arak, 1988). Thus, the very focus of the survey – population size – affects the index through the behaviour of individuals. The behaviour of individuals is very difficult to standardize.

USING DETECTION PROBABILITIES TO ADJUST COUNTS

Detection probabilities are needed to adjust counts. Estimation-based methods (such as capture-mark-recapture and distance sampling methods) are the only reliable methods for amphibian population ecology because detection probabilities (p) are estimated and used to adjust C to obtain estimates of N (Buckland *et al.*, 2001; Williams *et al.*, 2002). These methods also accommodate detection probabilities that vary in space and time, for instance because effort is variable. The basic idea underlying all of these methods is simple: first, they estimate a detection probability, $\hat{p}$, and then use it to adjust the count:

$$\hat{N} = C/\hat{p} \quad (3)$$

(Pearson, 1955; Nichols, 1992; Yoccoz *et al.*, 2001; Pollock *et al.*, 2002; Williams *et al.*, 2002). Currently, capture-mark-recapture methods are available for the estimation of demographic rates, population dynamics, distributions, and species diversity and turnover (e.g. Pollock *et al.*, 1990; Lebreton *et al.*, 1992; Nichols & Conroy, 1996; Schwarz & Arnason, 1996; Nichols *et al.*, 1998; MacKenzie *et al.*, 2002; 2003; see also Preston, 1979; Kéry, 2002). There are many recent

TABLE 1. Results of linear regressions between counts (C), population size estimates ($\hat{N}$), and censuses for various amphibians. R^2 and F tests (PROC GLM in SAS) are from the full model. Asterisks indicate significance at $\alpha = 0.05$. Estimators used are Jolly-Seber for *Cryptobranchus alleganiensis*, various closed population estimators for *Plethodon cinereus*, Lincoln-Peterson for *Scaphiopus holbrookii*, *Scaphiopus couchii*, and *Hyla arenicolor*.

Species	Life stage	Studied in	Intercept	Slope	R^2	F	Reference
Between count and estimate							
<i>Cryptobranchus alleganiensis</i>	Adults	Natural streams	1.68	0.20	0.09	0.5	Peterson <i>et al.</i> , 1988
<i>Plethodon cinereus</i>	Adults	Terrestrial plots	120.62	1.78	0.27	3.0	Jung <i>et al.</i> , 2000
<i>Scaphiopus holbrookii</i>	Adults	Terrestrial enclosure	57.71	0.30	0.71	20.2*	Pearson, 1955
<i>Scaphiopus holbrookii</i>	Adults	Terrestrial enclosure	4.69	0.87	0.97	102.4*	Pearson, 1955
<i>Hyla arenicolor</i>	Tadpoles	Natural ponds	-36.98	1.93	0.59	25.1*	Jung <i>et al.</i> , 2002
<i>Scaphiopus couchii</i>	Tadpoles	Mesocosms	28.85	1.10	0.95	192.2*	Jung <i>et al.</i> , 2002
Between count and census							
<i>Hyla arenicolor</i>	Tadpoles	Natural ponds	-13.92	1.73	0.66	34.21*	Jung <i>et al.</i> , 2002
<i>Scaphiopus couchii</i>	Tadpoles	Mesocosms	12.44	1.17	0.96	283.1*	Jung <i>et al.</i> , 2002
Between estimate and census							
<i>Hyla arenicolor</i>	Tadpoles	Natural ponds	18.35	0.87	0.97	1005.0*	Jung <i>et al.</i> , 2002
<i>Scaphiopus couchii</i>	Tadpoles	Mesocosms	15.25	0.94	0.99	1509.0*	Jung <i>et al.</i> , 2002

developments in capture-mark-recapture methodology and some may contribute substantially to understanding amphibian ecology. Important examples include the direct estimation of population growth rate and the demographic contributions to it (Pradel, 1996; Nichols *et al.*, 2000; Nichols & Hines, 2002), and population size estimation when not all individuals are present simultaneously at the sampling site (e.g. when the sampling site is a breeding site; Schwarz & Arnason, 1996). Methods are also available for situations in which only a subset of the individuals can be marked or when some members of the population are not available for capture (Pollock, 1982; Lebreton *et al.*, 1999; Dreitz *et al.*, 2002; Kendall & Nichols, 2002). Some recent capture-mark-recapture models were developed specifically to analyse amphibian data (e.g., MacKenzie *et al.*, 2002; 2003; Bailey *et al.*, 2004c; Royle, 2004b).

Several amphibian studies report C , N (i.e. $\hat{N}$), and sometimes a census ($= N$ because $p = 1$ by definition; Pearson, 1955; Peterson *et al.*, 1988; Jung *et al.*, 2000; 2002). The correlations between C and $\hat{N}$ are often high, but they are also highly variable (Table 1). In these examples, the population estimates $\hat{N}$ are much closer to the census values than the C , suggesting that the capture-mark-recapture estimates are better than the unadjusted counts. These results have two main implications. First, if the only goal is to have a rough idea of N , then the C may be a useful first approximation. C may be sufficient if the purpose is to assign populations to size classes such as ‘small’, ‘medium’, or ‘large’ if one is willing to accept the risk that some large populations are assigned incorrectly to a smaller size class (Corn *et al.*, 2000). However, a strong linear relationship between C and N should not be assumed. The data of Jung *et al.* (2002) suggest that such relationships may be curvilinear rather than linear. Clearly, an index C must be calibrated (see

Jung *et al.*, 2000; 2002 for examples). Thus, when using C , researchers should provide evidence that the C is actually a reliable index of N (MacKenzie & Kendall, 2002). If costs prevent the estimation of detection probabilities at all sites in a large-scale monitoring program, then detection probabilities may be estimated and counts calibrated at only a subset of the sites (Pollock *et al.*, 2002).

Capture-mark-recapture methods are often considered not useful because they are labour-intensive and therefore expensive (e.g. Donnelly & Guyer, 1994). This may be true, but it is questionable whether collecting C data means that time and money are better invested. A solution may be to estimate detection probabilities only at a subset of the sites (Pollock *et al.*, 2002). Capture-mark-recapture approaches are unlikely to be more time-consuming or expensive when analysing distributions or patterns of species diversity because all that is required for a capture-mark-recapture analysis is multiple visits to a site or several sites. Populations or species are then treated analogously to individuals in the analysis of demographic parameters (Nichols & Conroy, 1996; Nichols *et al.*, 1998; MacKenzie *et al.*, 2002, 2003).

Recent Bayesian models may allow the estimation of population size and demographic parameters without marking individuals. These models may be especially useful when individuals cannot be marked or when costs of marking are prohibitively high. Royle (2004a) developed new models for estimating the size of a closed population based on counts of individuals. Royle’s (2004a) model uses mixture models to estimate both detection probabilities and population size based on spatially and temporally replicated counts. Dodd & Dorazio (2004) developed these models further and used them successfully to estimate abundance of several

species of salamanders in Great Smoky Mountains National Park, USA. Using a related Bayesian approach, Link *et al.* (2003) describe methods to estimate survival and recruitment from information on age classes such as “juveniles” and “adults”.

Unadjusted counts are sometimes regarded as better than capture-mark-recapture estimates because the latter often have wide confidence intervals (Alford & Richards, 1999). While this may be true, the width of the confidence interval indicates whether an estimate is good or poor. With unadjusted counts, there is no way of knowing whether the counts are good or poor.

People argue against the use of capture-mark-recapture and related methods because these methods make assumptions whereas counts make no assumptions. The assumptions underlying capture-mark-recapture methods can be tested and the models used for parameter estimation can be adjusted accordingly (Lebreton *et al.*, 1992; for an example, see Schmidt *et al.*, 2002). If assumptions are not met, then the magnitude and direction of bias are known or can be approximated using simulation (e.g., Manly *et al.*, 1999). The assumptions underlying unadjusted counts cannot be tested and the magnitude and direction of bias remain unknown. A single count of, say, a population makes no assumptions. A comparison between two unadjusted counts makes a strong, and untested, assumption: the assumption that detection probabilities are exactly equal (see equation 2). This assumption is probably never met (Anderson, 2001; MacKenzie & Kendall, 2002). Counts are almost always compared and therefore assumptions are made. For example, if an observer counts 20 salamanders in pond A and 50 salamanders in pond B then most people would believe that population B is larger than population A. Such uncritical use of count data is widespread.

DISCUSSION

Amphibian populations are declining for a variety of reasons which we need to understand if we are to halt or reverse the declines (Alford & Richards, 1999; Corn, 2000; Houlahan *et al.* 2000). Most amphibian population data for demography, population dynamics, patterns of distributions and species richness are unadjusted counts (Schmidt *et al.*, 2002; Schmidt, 2003). Such data provide a weak basis for understanding ecological processes because true biological variation is confounded with variation in detection probabilities. Variation in detection probabilities can obscure causal ecological relationships and can generate variability when there is actually none (Pollock *et al.*, 1990; Link & Nichols, 1994; Martin *et al.*, 1995; Anderson, 2001; Cam *et al.*, 2002; Shenk *et al.*, 1998; Yoccoz *et al.*, 2001; Pollock *et al.*, 2002). As Burnham (1981) and Nichols & Pollock (1983) pointed out a long time ago, it is important to use methods that remove variation due to detection probability differences (e.g. capture-mark-recapture or distance sampling methods).

Field data on amphibian populations and communities that take detection probabilities into account will

better our understanding of amphibian population declines. Experimental studies have shown that stressors, such as increased UV-B radiation, can affect some life history stages (Blaustein *et al.*, 1994; Kiesecker *et al.*, 2001) but we do not know yet whether these effects translate into population declines. In fact, UV-B may not induce strong mortality in most populations and where it does, UV-B-induced egg mortality may not affect population dynamics at all (Palen *et al.*, 2002; Vonesh & De la Cruz, 2002). Thus, establishing a link between population growth rate and UV-B radiation through time series analysis (e.g. Dennis & Otten, 2000) and estimating the contribution of the larval, juvenile, and adult stage to population growth rate (McPeck & Peckarsky, 1998; Nichols *et al.*, 2000; Biek *et al.*, 2002; Forbes & Calow, 2002) would strengthen the conclusions drawn from experiments. Capture-mark-recapture data and the associated estimation methods are likely the most suitable methods for this kind of research because they contain no variation that is due to variation in detection probabilities and many parameters of interest can be estimated directly from the data. Unadjusted count data probably fail to uncover the subtle differences that may determine whether a population is declining or growing (Fujiwara & Caswell, 2001).

Scaling-up from small-scale experiments to population-level processes is an important task. To fulfil this task and for a more comprehensive understanding of population declines, we need a better general understanding of the demography and dynamics of amphibian populations. Most experiments in amphibian ecology are on tadpoles (Wilbur, 1997), but several recent studies suggest that the juvenile or adult stages are more important determinants of population growth than the tadpole stage (Taylor & Scott, 1997; Biek *et al.*, 2002; Hels & Nachman, 2002; Loman, 2002; Vonesh & De la Cruz, 2002). Despite the fact that all of these studies seem to agree on the importance of the terrestrial stage(s), the relative contribution of different life history stages to population growth requires further study. For instance, both Biek *et al.* (2002) and Loman (2002) analysed population dynamics of the frog *Rana temporaria* and concluded that the terrestrial stages are more important than the tadpole stage. In contrast, Meyer *et al.* (1998) argued that a population of *Rana temporaria* declined because tadpole-eating fish were introduced into the breeding site. There is no consensus yet on which factors and stages are most important for amphibian population dynamics and which dynamical patterns we should expect (e.g. Alford & Richards, 1999; Alford *et al.*, 2001 vs. Houlahan *et al.*, 2001; Green, 2003). Clearly, more studies are needed to resolve these issues and we need reliable methods for the collection of demographic and population dynamic data. Again, capture-mark-recapture methods are probably the most reliable methods.

An explicit focus on detection probabilities would also help when quantifying the extent of amphibian declines. For example, Skelly *et al.* (2003) describe the

effects of survey length on the inferred magnitude of decline, e.g. when resurveying sites where a species was known to occur in the past. In their case study, a (re)survey conducted during one year resulted in an inferred decline of 45% whereas a (re)survey done in two years resulted in an inferred decline of only 28%. If sites are (re)surveyed over a period of five years, then the inferred decline was only 3%. Skelly *et al.* (2003) provided two explanations for this result: a species may be missed at site or species are only present at a site intermittently. Skelly *et al.* (2003) argued that they missed no species that was actually present (i.e., $p = 1.0$) and intermittent presence of species at sites was the best explanation. Skelly *et al.* (2003) discuss the challenges posed by intermittent presence of species. I focus here on the implications of imperfect surveys, where $p < 1.0$. Most surveys are less intense than Skelly *et al.*'s (2003) survey, such that most surveys likely miss species. If one assumes that species are present but imperfectly detected, say, during 60% of the visits to a site, then one would reach a conclusion similar to Skelly *et al.*'s (2003). If sites are visited only once during a survey, then the species is detected at 60% of the sites where it occurs. Thus, the inferred decline after a single visit to each site is 40%. If the sites are visited once per year, then the inferred decline is $0.4^2 = 0.20$ after two years and $0.4^5 = 0.02$ after five years. Obviously, with only one or two visits to a site, researchers would infer a decline although the species is present. This is because in most surveys detection of species is imperfect. The calculations above lead naturally to the approaches for inferring the absence of a species (Preston, 1979; Kéry, 2002; MacKenzie *et al.*, 2002) and the methods for estimating turnover in animal communities (Nichols *et al.*, 1998; MacKenzie *et al.*, 2003). Skelly *et al.* (2003) recommend that "resurveys should extend for long enough to estimate the value of additional data". Knowing detection probabilities allows one to disentangle whether a species is missed or absent from a site and allows investigators to estimate the number of visits (or years) necessary for a resurvey that is "long enough".

Detection probabilities *per se* are uninteresting nuisance parameters. Nevertheless, they are of major importance in the study of the demography, population dynamics, distributions, species diversity, and decline of amphibians. Only if we are aware of the pitfalls of unadjusted count data and use estimates of population and community parameters that are adjusted for detection probabilities, shall we understand the ecology and decline of amphibians.

ACKNOWLEDGMENTS

I would like to thank T. Halliday and R. Griffiths for organising and inviting me to the symposium on global amphibian declines at the Canterbury meeting of the Society for Conservation Biology. I am grateful for support from the Schweizerischer Nationalfonds (grant no. 31-55426.98 to J. Van Buskirk), the Forschungskredit of the University of Zürich, and a travel grant from the

Swiss Zoological Society. Last but not least, many thanks to L. Bailey, A. Cooke, C. Cummins, R. Griffiths, P. Pearman, and M. Schaub for helpful comments on the manuscript.

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Accepted: 30.7.03