

Forum

Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads

Benedikt R. Schmidt¹, Michael Schaub^{2,3}, Bradley R. Anholt⁴

¹ Zoologisches Institut, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
e-mail: bschmidt@zool.unizh.ch

² CEFE/CNRS, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France

³ Present address: Zoologisches Institut, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

⁴ Department of Biology, University of Victoria, P.O. Box 3020 STN CSC, Victoria BC V8W 3N5, Canada

The global decline of amphibians (Blaustein and Wake, 1990; Houlihan et al., 2000) has created an urgent need to better understand amphibian population dynamics (Meyer et al., 1998; Wake, 1998). Measuring basic demographic parameters, such as survival probabilities, is essential to parameterize population models (e.g., Halley et al., 1996; Griffiths and Williams, 2000; Fujiwara and Caswell, 2001). In recent years, estimation of survival probabilities based on capture-recapture (hereafter CR) has made enormous progress and these methods are currently the most reliable (e.g., Burnham et al., 1987; Pollock et al., 1990; Lebreton et al., 1992; Buckland et al., 2000). So many additional population and community parameters can be estimated based on CR methodology (e.g., Nichols et al., 1998a; Nichols et al., 1998b; Thompson et al., 1998; Schwarz and Seber, 1999; Lebreton et al., 1999; Nichols et al., 2000; Schaub et al., 2001), that Begon (1979) is now clearly outdated. Williams et al. (2002) is a recent comprehensive review of CR methods.

Capture-recapture methods are widely used in fisheries, ornithology, and mammalogy. Unfortunately, they are not yet widely used in herpetology, despite the fact that amphibian ecologists contributed early to CR methodology (e.g., Wilbur and Landwehr, 1974). CR methods are sometimes considered not to be useful in herpetology (e.g., Wilbur, 1984). Only ca. 5% of the 936 time series used by Houlihan et al. (2000) were based on CR methods and there are CR survival estimates for only a few amphibian species (Gittins, 1983; Nichols et al., 1987; Wood et al., 1998; Holenweg Peter, 2001; there are a few for reptiles). When we read Kuhn's (1994) paper on the life history of female common toads (*Bufo bufo*) in which he claimed that survival probabilities cannot be estimated from CR data (Kuhn, 1994: 18), we decided to analyse the raw data that he published, hoping that we could promote the use of CR methods in herpetology (Schmidt and Anholt, 1999). We do not

want to imply that Kuhn (1994) is better or worse than other amphibian studies. Challenging the analyses and conclusions of published studies is a part of science (e.g., Arthur, 2001). Kuhn (1994) used a standard method in herpetology, drift fences around a pond, and assumed that the drift fence would sample the entire population without bias (Kuhn, 1994: 17). Hence, his data set is a good example of how much more valuable information could be extracted from many similar studies where amphibians are individually marked. We agree with Henle et al. (1999: 95) that “estimates” of population parameters that are not based on sound statistical methods should be called suppositions rather than estimates and they should not be trusted.

Recently, Henle (2001) commented on our analysis of Kuhn’s (1994) data. In reply to Henle’s (2001) comments, we will first discuss the main reason why CR analysis methods should be used, even though the superiority of CR methods is not questioned by Henle (2001). The goal is to show the limits of non-CR methods and that bias is likely and larger than when using CR methods. With CR methods, the magnitude of bias can be estimated and is known to be small. We will also discuss some other points raised by Henle (2001), namely temporary emigration, bias, overdispersion, and breeding probabilities. While we largely disagree with Henle (2001), we accepted his challenge, reanalysed a subset of the data, present nearly unbiased estimates of survival probabilities, and estimate the proportion of toads that skip breeding opportunities. By doing so, we reject Henle’s (2001) claim that a meaningful analysis of Kuhn’s (1994) data is not possible. Our conclusion is that CR methods should be used because they provide robust estimates, and, equally important, a measure of the precision of those estimates.

Why use capture-recapture methods?

It is impossible to capture all the members of a population. This simple fact is why CR methods should be used if you want to estimate population size or survival probabilities. It is generally true that $C_i = N_i^* p_i$, where C_i is a count statistic, N_i is the true number of animals, and p_i the sampling fraction at time and place i (Nichols, 1992). Researchers can try to standardize methods such that p_i is constant and C_i becomes a reliable index for N_i . Standard methods are clearly valuable (Heyer et al., 1994), yet p_i may depend on, for example, weather conditions that cannot be standardized. CR methods estimate p_i and allow testing of whether it is variable in time and/or space.

Like any other method, CR methods need to be used carefully. The methods are well documented (e.g., Burnham et al., 1987; Pollock et al., 1990; Lebreton et al., 1992; Cooch and White, 2001) and software for the analysis of CR data is available (e.g., White and Burnham, 1999) and can be downloaded from the internet (currently <http://www.phidot.org/software/>). The assumptions of the models can be tested and, if necessary, the models can be modified because CR methods and the associated software are sufficiently flexible (e.g., White and Burnham, 1999). Most importantly, CR methods offer a standard framework for assessing how well the data support alternative scientific hypotheses (Lebreton et al., 1992; Burnham and Anderson, 1998, 2002).

A common critique of CR methods is that they are very time-consuming (e.g., Wilbur, 1984; Donnelly and Guyer, 1994; Jung et al., 2000). However, checking a drift fence daily or more often for several months is a heavy workload as well. Disappointingly, this enormous effort does not guarantee that all animals are captured and consequently, most population parameters of interest are of unknown quality. In fact, Freilich et al. (2000) show that when using CR methods you may expend less effort in the field but get better estimates nevertheless.

As noted by Henle (2001), Pollock’s (1982) robust design would probably be a better approach to collecting data on amphibian populations than the standard drift fence where individuals are captured only during immigration and emigration (Kendall et al., 1997, also comment on amphibian studies). Freilich et al. (2000) and Savarie et al. (2001) are recent studies where the robust design was used to estimate survival and population sizes of tortoises and snakes, respectively. However, recent advances in CR theory (Lebreton et al., 1999) are likely to offer alternatives to the robust design.

Why not use alternatives to CR methods? A common method for estimating survival is the enumeration or minimum number alive method (e.g., Pollock et al., 1990: chapter 5.2). It works like this. You mark 100 frogs in the first year. You recapture 17 frogs in the second year. Therefore, the minimum survival probability, also known as the return rate, is $17/100 = 0.17$. Therefore, true survival must be between 0.17 and 1. Since true survival is very likely to be larger than 0.17, this estimate is usually biased to an unknown degree. It can be shown that the survival estimates from the enumeration method are always smaller or equal to the CR survival estimates (appendix to Nichols and Pollock, 1983). If survival is constant over time and recapture probabilities vary, then

the enumeration method will generate variability in survival estimates when none exists. In contrast, CR methods eliminate this bias (e.g., Pollock et al., 1990: fig. 5.2; see also Martin et al., 1995).

It is possible to estimate survival probabilities or maximum lifespan from a stable age distribution (Krebs, 1999: chapter 14; see also Kremenetz et al., 1989, for a discussion of the value of maximum lifespan estimates). However, the study by Sinsch et al. (2001) on the demography of *Bufo achalensis*, for example, shows that the age structure of a population may be highly variable. Evidently, the assumption of a stable age distribution is unlikely to be met, making the value of survival estimates derived from an age distribution questionable.

Addressing the comments of Henle (2001)

We believe that Henle's (2001) arguments are insufficient and oversimplifying because he takes facts out of context. To see why Henle's (2001) objections fail, we must examine the context in each case. For example, Henle (2001) argues that temporary emigration causes bias. Whether bias matters depends very much on the context of the analysis: which model is used to estimate parameters, which parameter is biased (survival or capture probability), and the size of the bias and standard errors. We agree that no bias is the ideal, but when biases are associated with nuisance parameters (capture probabilities) or the biases are small relative to standard errors of the estimates, this deviation from the ideal is not important.

Model assumptions and recapture probabilities. Schmidt and Anholt (1999) found strong variation in capture probabilities despite the fact that Kuhn (1994) used the same method in all years. We provided a list of factors that may lead to variable capture probabilities. Henle (2001) argued that most factors are not applicable to Kuhn's (1994) study. We did not want to imply that all these factors acted in the study of Kuhn (1994). We apologize for any confusion that we may have caused. Our intent was to point out that capture probabilities may be affected by many factors and that standardization does not necessarily solve the problem. One may standardize the method (e.g., the drift fence) but many other factors that may affect capture probabilities, like weather, cannot be standardized. Henle's (2001) table 1 tacitly supports our conjecture. In his table 1, Henle (2001) reports minimum capture probabilities. Minimum capture probabilities range from 52.8% to 85.4%; they i) are well below 100%, ii) vary among years, and iii) vary among populations. This is a disturbing amount of variation given the use of the same standardized method in all populations and a species that has "a very high catchability once they hit the drift fence" (Henle, 2001: 381). Rather than discussing whether capture efficiencies at a drift fence are high and invariant and invoking the clumsiness of the study species, one should estimate capture probabilities and their variation and assess whether this variation needs to be included in the CR analysis (Lebreton et al., 1992; Burnham and Anderson, 1998; see Jung et al., 2000, for a similar approach).

In his table 1, Henle (2001) (section "Evidence for irregular breeding") compares minimum capture probabilities with Schmidt and Anholt's (1999) CR capture probabilities. In our opinion, this comparison is not meaningful. First, the minimum capture probabilities and CR capture probabilities are fundamentally different quantities. The minimum capture probability is the ratio (number of marked toads emigrating/number of marked toads during immigration). The CR capture probability is the probability of capturing an animal, given that it is alive *and* at the study site (in this case the pond). The CR capture probability is thus the product of the probability of breeding and the probability of being caught at the fence. In contrast to minimum capture probabilities, the CR capture probabilities also account for toads that trespass the fence undetected during both immigration and emigration or toads that arrive at the fence but return to the summer habitat without breeding. Second, Henle (2001) claims that there is non-random temporary emigration, which is known to negatively bias estimates of capture probabilities by 20% or more (Kendall et al., 1997). Given this suspected bias, it is not surprising that the capture probabilities of Schmidt and Anholt (1999) are lower than Henle's (2001) minimum capture probabilities.

Evidence for irregular breeding. This section and the associated table 2 of Henle (2001) contain major errors. In a thought experiment, Henle (2001) constructs two data sets. In one data set (table 2a), he assumes that both the capture and survival probabilities are 50%. In the other (table 2b), some toads show temporary emigration, the survival probabilities are lower (33.8%, 47.0% and 39% for the first, second, and third year, respectively), and the capture probability at the pond is 100%. Henle's (2001) message is that the incidences of the *observable* capture histories are the same in both tables even though very different processes generated the data, suggesting i) that goodness of fit tests cannot detect non-random temporary emigration and ii) that "using the approach of

Schmidt and Anholt (1999) one will get survival estimates of 50%” which is clearly wrong. Unfortunately, Henle (2001) makes two major errors. First, Henle’s (2001) distinction between observable and non-observable capture histories is wrong as is his claim that only observable capture histories would be used for CR analysis. Clearly, *toads* with a capture history of “1000” are never observed again after year 1, but you still observe the *capture history*, and its frequency is considered when the likelihood of the model is maximised. Note also the difference between observed and observable capture histories. Thus, the two populations in table 2a and 2b can easily be distinguished because the incidences of all capture histories matter (contra Henle, 2001: 383). For example, the capture history “1000” is observed 125 times in table 2a and 0 times in table 2b (i.e., 125 toads have capture history “1000” in table 2a whereas zero toads have this capture history in table 2b). By analogy, when analysing a two-by-two contingency table using a χ^2 , cells with a frequency of zero are retained in the analysis. However, Henle (2001: 383) drops these cells and then claims that “they receive a perfect fit ($\chi^2 = 0$)”. The second error is that Henle (2001) failed to correctly construct the CR capture histories. In Henle’s (2001) thought experiment, 8000 toads were marked in the first year. Thus, by definition, the sum of the incidences of all capture histories for this marking cohort must be 8000 in all years that follow. In Henle’s (2001) example, the sums of the incidences of the capture histories are 8000, 4000, 2000, and 1000. With an assumed survival of 0.5 and a capture probability of 0.5 (table 2a), 4000 toads die and are not observed anymore; 4000 toads survive, of which 50% are observed and 50% are not observed. Thus, the capture history “11” (“seen in both year 1 and year 2”) must occur 2000 times. Capture history “10” (“seen in year 1, not seen in year 2”) must occur 6000 times: 4000 animals died and cannot be seen anymore and 2000 of the surviving toads are not observed. In Henle’s (2001) table 2 both capture histories occur 2000 times. Henle (2001) makes the same error in all years of table 2a and 2b. In summary, if the nonsense distinction between observable and non-observable capture histories is abandoned and the capture histories are constructed correctly, then Henle’s (2001) arguments break down. The goodness of fit tests will detect that the assumptions of the standard CJS model are violated and correct survival estimates will be obtained.

Henle (2001: 383) argues that “independent data are preferable to a goodness of fit (GOF) test for analysing the adequacy of a model”. A GOF asks whether the structure of the data is such that the CR model can be used to analyse the data. It is clear that you must do a GOF with the data that you want to analyse. By analogy, in an analysis of variance, no one would test residuals for normality on a data set other than the one analysed.

In section “a reanalysis: model selection and parameter estimation”, we present a new approach to estimating breeding probabilities. This approach is clearly better than the analysis in table 5 of Schmidt and Anholt (1999) or Henle’s (2001) approach.

Are the survival estimates of Schmidt and Anholt (1999) biased and can the data be reanalysed?

Henle (2001) argues that temporary emigration causes bias and that the use of a variance inflation factor cannot solve the problem associated with the fact that the CJS model does not fit the data well. Because of these problems, the data should not be analysed. We discuss variance inflation factors and overdispersion first and temporary emigration second. We conclude that the data can be analysed.

Variance inflation factors are used if the data are more dispersed (overdispersed) than expected from a multinomial distribution on which CR statistics are based. What is overdispersion? Overdispersion is a form of lack of fit of the model to the data. CR models assume that the fates of all individuals are independent. Non-independence may cause overdispersion. Fates may not be independent if you mark, for example, 50 pairs of birds. Clearly, marking 50 pairs is different from marking 100 independent birds since pairs are likely to have similar fates (you are likely to catch or resight both partners). A simple calculation shows the effect of non-independence on variance. The model of binomial variation is $\text{var}(\hat{p}) = (p^*(1-p))/n$, where p is a probability and n sample size. Let n be 100 independent birds or 50 pairs with strong dependence of individuals. Then, $(p^*(1-p))/100 < (p^*(1-p))/50$. Thus, the estimated variance is too small and it needs to be “inflated”. This is done using \hat{c} , the variance inflation factor. \hat{c} can be estimated as (goodness of fit $\chi^2/\text{degrees of freedom}$) (Burnham et al., 1987; Lebreton et al., 1992).

Overdispersion has two consequences (e.g., Lebreton et al., 1992: 84 and 106-107). First, model selection needs to be based on a different information criterion, the quasi-likelihood Akaike Information Criterion, QAIC = $-2^*(\log\text{-likelihood}/\hat{c}) + 2^*$ (number of parameters in the model). If the data are not overdispersed, then $\hat{c} = 1$ and QAIC = AIC, where AIC is the standard model selection criterion derived from information theory (i.e., Kullback-Leibler distance; Burnham and Anderson, 1998, 2002). Second, overdispersion will lead to estimated

standard errors being too small. Consequently, the standard errors must be multiplied by \hat{c} . Lebreton et al. (1992: 85) recommend combining the excess residual structure into the error estimates. This is because the conceptual basis for a model is data = structure + residual. The structural part of a model can hold even if the residual shows excess variance (Lebreton et al., 1992: 84; see also Anderson and Burnham, 1999: 264). Correcting for overdispersion makes an analysis more conservative. However, the most important point is that overdispersion does not induce bias in the survival estimates.

How would overdispersion affect the analyses of Schmidt and Anholt (1999)? It would only lead to larger confidence intervals. It is easy to see that model selection in this analysis set is unaffected by even the largest estimate of \hat{c} ($\hat{c} = 1647/1270 = 1.29$; Schmidt and Anholt, 1999: 101). This amount of overdispersion is no reason for concern (Anderson and Burnham, 1999: 264). For these reasons, Schmidt and Anholt (1999) argued that the observed overdispersion did not affect the conclusions in any substantial way. Since \hat{c} is estimated from data, it may be $\neq 1$ by chance, like any estimate can be different from the true value of a parameter (see also Anderson and Burnham, 1999: 264).

The second major concern of Henle (2001) is that temporary emigration may cause bias in estimated survival probabilities. Henle (2001) argues that the data should not be analysed because it is not possible to estimate the bias even though Kendall et al. (1997) and Manly et al. (1999; both papers cited by Henle, 2001) estimated bias. We disagree with Henle's (2001) conclusion: The presence of temporary emigration does not preclude analysis of the data (J.D. Nichols, pers. comm.). What is temporary emigration? If you study an amphibian population at its breeding site, then individuals that do not breed will not migrate to the pond. Thus, they "emigrated" from the breeding population. Since they are likely to skip breeding only in some years, they are temporary emigrants. Because temporary emigrants cannot be captured at the pond (drift fence), there is variation among individuals in capture probabilities. This may violate an assumption of CR models and may cause bias in the estimates of survival and capture probabilities. However, in contrast to what Henle (2001: 380-381) seems to imply, heterogeneity in capture probabilities and temporary emigration may not have the same effect. Even if there is heterogeneity in capture probabilities, they are all assumed to be >0 . With temporary emigration, the capture probabilities of some individuals are zero by definition (D.L. Otis, pers. comm.).

There are two forms of temporary emigration, random and non-random (Markovian). Under random temporary emigration, all individuals have the same probability γ_i to be absent from the sampling area (i.e., the breeding site) at time i , irrespective of whether they were absent or not from the breeding site at the time $i - 1$. Random temporary emigration does not violate any assumption of the CJS models and causes no bias in the survival estimates (Kendall et al., 1997: table 1). Non-random temporary emigration means that the probability of being a temporary emigrant depends on last year's status (temporary emigrant or not). Under non-random temporary emigration, individuals that were temporary emigrants in time $i - 1$ and those that were not temporary emigrants (i.e., present at the pond) in time $i - 1$ have different probabilities of being temporary emigrants in time i , which are denoted γ' and γ'' , respectively (Kendall et al., 1997: 564). The analyses by Kendall et al. (1997) and the extensive simulations by Manly et al. (1999) clearly showed that although capture probabilities may have large biases, bias in survival estimates is minor and in the range of $\pm 2-3\%$ (Kendall et al., 1997: tables 2, 3) or -1.6% (Manly et al., 1999: table 3), when data are analysed with a model that does not account for non-random temporary emigration. These are the largest estimates of bias that we are aware of.

What is the effect of non-random temporary emigration on the survival estimates of Schmidt and Anholt (1999)? To answer this question, let us assume non-random temporary emigration. Assume that survival is 0.4 (pooled over sites, years, and marking cohorts). If we take the largest estimates of (proportional) bias reported in tables 2 and 3 of Kendall et al. (1997), then an unbiased estimate of survival would be $0.4 * 0.981 = 0.392$ (if $\gamma' > \gamma''$) or $0.4 * 1.031 = 0.412$ (if $\gamma' < \gamma''$). The largest absolute difference between biased and unbiased estimates is $0.412 - 0.4 = 0.012$. Cochran (1977: 12-15) showed that it is not the absolute magnitude of bias that counts, but the ratio (bias/standard error). In the analysis of Schmidt and Anholt (1999), the smallest standard error of a survival estimate of population A was 0.03. This gives a ratio bias/standard error of $0.012/0.03 = 0.4$. In this worst case scenario, there is a probability of ca. 7% that the true survival estimate is outside the 95% confidence interval (where, by definition, this probability should be 5%; see Cochran, 1977: table 1.1). For other estimates the standard errors are larger (s.e. = 0.06 and 0.08) such that there is a probability of ca. 6% that the true survival estimate is outside the 95% confidence interval. Thus, bias hardly matters. To be conservative, the 95% confidence intervals of Schmidt and Anholt (1999) should be viewed as 90% confidence intervals. If you believe that the new estimates in tables 3 and 4 are still biased, then use the 95% confidence intervals where overdispersion is assumed. These confidence intervals are enlarged, such that they are likely to cover the true mean.

Conclusion. As correctly pointed out by Henle (2001), temporary emigration may cause bias. This is true if the standard Cormack-Jolly-Seber model is used to estimate parameters. It is not clear how large bias is in the cohort model used by Schmidt and Anholt (1999). However, Henle's (2001) concern over bias is overly pessimistic. The presence of non-random temporary emigration is clearly not a reason to leave the data without analysis (J.D. Nichols, pers. comm.), since bias in the survival probability estimates is small (Kendall et al., 1997; Manly et al., 1999). If Henle (2001) believes that bias is larger, then we ask that he provides evidence. The magnitude and direction of bias can be estimated (Manly et al., 1999).

A reanalysis

In this section we present a reanalysis of a subset of the data, population A of Kuhn (1994). The major reason for a reanalysis is that the goodness of fit (GOF) tests of Schmidt and Anholt (1999) were wrong — a fact not noticed by Henle (2001) who refers repeatedly to these tests. The GOF of Schmidt and Anholt (1999) were partly based on the ratio deviance/d.f., which is a valid measure of model fit. However, the deviance used was the *relative* deviance provided by program SURGE. The relative deviance cannot be used for GOF. The new and correct GOF are the starting point for the new analysis.

Goodness-of-fit (GOF) tests. GOF were performed with U-CARE (Choquet et al., 2001), which is a modified version of program RELEASE (Burnham et al., 1987). U-CARE provides additionally specific “directional” tests for transience (Pradel et al., 1997) and trap-dependence (trap-happiness or -shyness; Pradel, 1993) derived from the contingency tables used in the GOF tests. These additional tests help with the interpretation of a significant GOF test result. The GOF tests have several components that are sensitive to different violations of the model assumptions (e.g., Cooch and White, 2001). Test 3.SR asks whether there is a difference in survival between individuals, depending on whether or not they were seen for the first time either before or on occasion i . This test may be significant if there is i) an age effect in survival, ii) occurrence of transients, iii) a marking effect, or iv) capture probability heterogeneity. Test 3.Sm asks “among those animals seen again, does when they were seen depend on whether they were marked on or before occasion i ?”. Reasons for a significant test 3.Sm include i) an age effect in survival, ii) a marking effect, or iii) capture probability heterogeneity. Test 2.Ct asks whether the probability of being seen at time $i + 1$ is dependent on whether the animals have been seen at time i , given that they survived from i to $i + 1$. This component of the GOF testing is significant if there is i) an immediate trap effect (on the capture probability) or ii) non-random temporary emigration. The fourth component GOF test (2.Cm) could not be performed here, because there were too few capture occasions.

We first tested the GOF of the standard Cormack-Jolly-Seber (CJS) model with time dependent survival and capture probabilities (ϕ_t, p_t). Several of the test components were significant (table 1), such that the CJS model is clearly rejected. Deciding which of the above mentioned possible reason(s) is/are responsible for the lack of fit is often a difficult task. This is especially true for data with strong heterogeneity and with few capture occasions, as here. As all test components were significant or nearly so, it is very likely that several reasons are responsible for the violation of the assumptions. The significant positive z-statistic of test 3.SR shows that more toads than

Table 1. Goodness of fit (GOF) tests for the capture-recapture data of population A of Kuhn (1994) using program U-CARE. All groups had sufficient data for the tests. Shown are the GOF test for the components of Tests 2 and 3 and the combined tests. χ^2 : test statistic of the single and overall tests, d.f. degrees of freedom, z: z-statistic of the directional tests.

Test	χ^2	d.f.	P	z	P
2.Ct2	10.01	1	0.0015		
Test 2	10.01	1	0.0015	3.18	0.014
3.SR2	11.92	1	0.0006	–	
3.SR3	7.01	1	0.0081	–	
3.Sm2	3.56	1	0.0592	–	
Test 3	22.49	3	0.0001	4.31	<0.001
Test 2 and 3	32.59	4	<0.0001	–	

expected (under the CJS model) are seen only once. A true age effect in the survival rates is unlikely, because the toads were of different, unknown age when they were marked. Another biological interpretation of this fact is the occurrence of transients. Transients would be toads that change the breeding site each year and are seen therefore only once at pond A (this, however, seems unlikely for Kuhn's (1994) study site). In Kuhn's (1994) short study, toads that skip breeding opportunities (i.e., are temporary emigrants) might occur as transients in the data, because the study is already over when they return from a one year absence to breed again. The significant positive z -statistic of test 2.Ct shows that fewer toads than expected were captured at the occasion following the last capture. Such a pattern emerges if the toads would avoid the pond the year after they have been caught because of an adverse effect of capture ("trap-shyness"). The same pattern would also emerge if the probability to return to the pond at t is lower for toads that have been at the pond already at $t - 1$ than for those that were not at the pond at $t - 1$ (non-random temporary emigration; Sandland and Kirkwood, 1981). This latter explanation seems most likely to us, since a likely biological interpretation is that a proportion of the toads skips breeding in some years.

The different biological interpretations for the lack of fit change the interpretation of the results, but have no influence on the calculations that follow. For instance, if we had interpreted the significant test 3.SR as an indication of a true age-effect, we would have fitted the same model for recovering this structure as if we interpreted it as indication of transients. But in the former case we would conclude that the toads in the first age class have survival rate $\phi_{\text{first_age}}$, and the toads in the second age class have a survival rate of $\phi_{\text{second_age}}$, whereas in the latter case we would conclude that the survival rate of the residents is $\phi_{\text{second_age}}$ ($\phi_{\text{first_age}}$ would be a dummy variable to adequately model the data).

Given our interpretation of the GOF test of the CJS model (table 1), we build a new starting model for the analysis that takes account of transients and temporary emigration and is written as (ϕ_{a2^*t}, p_{m^*t}) . The subscript "a2" in the survival model (ϕ) denotes that there are two age classes. Toads enter the first age class in the year after they are caught the first time and stay there for a year. Thereafter, they are in the second age class. This part of the model accounts for transients. The subscript "m" in the capture model (p) denotes that there are two groups: animals captured at the previous occasion and those not captured at the previous occasion. This part of the model accounts for temporary emigrants. In both the survival and capture model, "t" indicates that survival and capture probabilities can vary temporally and the asterisk (*) means that this temporal variation may vary among age classes or with temporary emigration status.

A GOF for model (ϕ_{a2^*t}, p_{m^*t}) requires two steps. The GOF of the transients model (ϕ_{a2^*t}, p_t) is computed first. This is just the sum of the overall GOF (table 1) without the elements 3.SR ($\chi^2 = 13.66$, d.f. = 2). Then the difference of the deviance and degrees of freedom of the models (ϕ_{a2^*t}, p_{m^*t}) and (ϕ_{a2^*t}, p_t) when fitted in MARK is calculated ($\Delta \text{dev} = 13.41$, $\Delta \text{d.f.} = 1$). The difference between these two statistics is approximately χ^2 -distributed and is an approximate GOF of the model (ϕ_{a2^*t}, p_{m^*t}) (see Lebreton et al., 1992, for more details). The GOF of model (ϕ_{a2^*t}, p_{m^*t}) is not significant ($\chi^2 = 13.66 - 13.41 = 0.25$, d.f. = 1, $p = 0.617$). Thus, the model is well suited as a starting model. Because the GOF is not significant, overdispersion is unlikely. Yet, as this GOF is only approximate and the power is low with only four capture occasions, we analysed the data with and without correcting for overdispersion. When correcting for overdispersion, we used the largest variation inflation factor that can be expected if there is very strong overdispersion ($\hat{c} = 4$; Anderson et al., 1994). Accounting for overdispersion in the data, even if there is likely none, conservatively chooses models with few parameters.

*Construction of model (ϕ_{a2^*t}, p_{m^*t}) .* To fit this model, a special arrangement of the data is required: the capture history of each individual is replaced by a compound capture history. There are as many component capture histories as there are capture events (see appendix 1; J.-D. Lebreton, pers. comm.). After capture, a component capture history ends and the individual is removed from the sample, and released again in a new component capture history. Furthermore, the component capture histories are allocated to two groups. The first one consists of transients and non-transients (residents), and the second one of residents only. A similar arrangement of the data for modelling immediate trap-dependence is described in detail in Pradel (1993). With these data the desired model can be fitted. In a fully time-dependent context (ϕ_{a2^*t}, p_{m^*t}) , an age and time-dependent structure in the survival rates for the transients/residents group and a time-dependent structure in the survival rate for the residents group is fitted, but where the parameters of the residents group are equal to those of the second age class in the first group (see appendix 2). An age and time-dependent structure with identical parameters for both groups is fitted to the recapture rates. In this fully time-dependent model and with only four capture sessions no parameter is separately estimable (Catchpole and Morgan, 1997). We had therefore to start from a model with an additive time structure (ϕ_{a2+t}, p_{m+t}) , where all parameters are separately estimable.

Model selection and parameter estimation. The selection of the best model from which to estimate survival and capture probabilities was done using program MARK (White and Burnham, 1999) and was performed in an exploratory way. Thus, all possible nested models of the starting model (ϕ_{a2+t}, p_{m+t}) were fitted. Although not recommended as the best model selection strategy for making strong inference (Burnham and Anderson, 1998), we have chosen this approach for being sure not to miss a model that might be a good description of the data. For comparison, we present the model selection results with and without correction for overdispersion. The models, their ΔQAICc and ΔAICc , respectively, the QAICc and AICc weights, respectively, number of parameters (K), and deviance are shown in table 2 (cf. Anderson et al., 2001; QAICc and AICc are information-theoretic model selection criteria for small samples; see Burnham and Anderson, 1998, 2002). Regardless of overdispersion, the best model was (ϕ_{a2+t}, p_m). Thus, we can have high confidence in this model. The parameter estimates are shown in table 3. The confidence intervals under the conservative approach with $\hat{c} = 4$ were much wider than when $\hat{c} = 1$. The “true” confidence intervals are between these estimates.

Survival varies considerably among years (table 3) with little overlap of the confidence intervals. The estimates are larger than Kuhn’s (1993) and in the range of the estimates of Schmidt and Anholt (1999) and Gittins (1983), but, for example, considerably lower than the values used in the population model of Halley et al. (1996). For comparison, and to illustrate model selection uncertainty (Burnham and Anderson, 1998: chapter 4), we also present parameter estimates from the AICc- and QAICc-selected second best model. In table 4 we present model averaged estimates of survival and recapture probabilities. Model averaging means that parameter estimates are based on simultaneous inference from more than one model. The influence of each model on parameter estimates is determined by its AICc or QAICc weight (see table 2). Model averaging is highly recommended if several models describe the data well (Burnham and Anderson, 1998, 2002; Anderson et al., 2000, 2001).

Estimates of capture and especially survival probabilities vary strongly among years (tables 3, 4). Concern over bias due to non-random temporary emigration seems unwarranted given this strong interyear variability.

If we assume that heterogeneity in the data was caused by transients (toads that breed only once during the period of the study) and non-random temporary emigrants (toads that skip breeding opportunities), then we can estimate further parameters from the new analysis. The survival estimates for the first age class (#1, #2, and #3 in appendix 2) are the product of the true survival probability times the probability of being a resident (Pradel et al., 1997). We can estimate the proportion of transients among the toads present using the parameters in appendix 2 as $1 - \#2/\#5$ or $1 - \#3/\#6$ (Pradel et al., 1997). This yields estimates of 0.43 (95% confidence interval 0.271-0.594 ($\hat{c} = 1$), 0.110-0.755 ($\hat{c} = 4$) for the year 1990 and 0.54 (0.322-0.755 ($\hat{c} = 1$), 0.106-0.971 ($\hat{c} = 4$)) for 1991; confidence intervals calculated using the delta method of Seber, 1982). We can also estimate the probability that a toad does not breed at $t + 1$ given that it has bred at t and given that it is still alive at $t + 1$ (analogous to the calculations above). This calculation requires an additional assumption: all toads that did not breed in year t breed

Table 2. Model selection for the capture recapture data of population A of Kuhn (1994). Models are ordered from best to worst (increasing ΔQAICc , decreasing QAICc weights). For comparison we also present ΔAICc and AICc weights, which assume no overdispersion ($\hat{c} = 1$). K is the number of estimated parameters for models assuming $\hat{c} = 1$. Add +1 to K when assuming $\hat{c} = 4$ (Burnham and Anderson, 2001). Note that ϕ_t, p_t is the standard Cormack-Jolly-Seber model. The best model of Schmidt and Anholt (1999) was $\phi_c, p_{(2,1)}$, with deviance = 2126.86, $K = 5$, and $\Delta\text{AICc} = 2.28$ in comparison to the new best model.

Model	K	Deviance	ΔQAICc	ΔAICc	QAICc weight	AICc weight
ϕ_{a2+t}, p_m	6	2122.57	0	0	0.40	0.63
ϕ_{a2}, p_{m+t}	6	2124.20	0.41	1.63	0.33	0.28
ϕ_t, p	4	2153.13	3.62	26.54	0.07	0.00
$\phi_{..}, p_t$	4	2154.30	3.91	27.70	0.06	0.00
ϕ_{a2+t}, p_{m+t}	8	2122.54	4.01	3.99	0.05	0.09
ϕ_t, p_{t+m}	6	2139.64	4.27	17.07	0.05	0.00
ϕ_{a2+t}, p_t	7	2135.96	5.36	15.39	0.02	0.00
ϕ_t, p_t	5	2153.06	5.61	28.47	0.02	0.00
ϕ_{a2}, p_m	4	2176.04	9.35	49.45	0.00	0.00
$\phi_{..}, p$	2	2209.04	13.59	78.43	0.00	0.00

Table 3. Survival, capture, and breeding probabilities of toads (*Bufo bufo*) of population A of Kuhn (1994) estimated from model (ϕ_{a2+t}, p_m) (QAICc-selected best model; see table 2) and the second best model (ϕ_{a2}, p_{m+t}). Note that the survival probability of the “residents from 1989 to 1990” cannot be estimated with the model used. Survival probabilities are #5 and #6 in the parameter index matrices in Appendix 2. Capture probabilities are #8 to #10.

Parameter	Mean	95% CI ($\hat{c} = 4$)	95% CI ($\hat{c} = 1$)
Model ϕ_{a2+t}, p_m			
Survival 1990 to 1991	0.487	[0.331, 0.646]	[0.407, 0.569]
Survival 1991 to 1992	0.214	[0.123, 0.346]	[0.164, 0.275]
Mean of the two years	0.351	[0.239, 0.463]	[0.295, 0.407]
Capture when captured at previous occasion	0.488	[0.365, 0.613]	[0.425, 0.552]
Capture when not captured at previous occasion	0.926	[0.162, 0.999]	[0.609, 0.990]
Model ϕ_{a2}, p_{m+t}			
Survival 1990 to 1991	0.445	[0.278, 0.626]	[0.357, 0.537]
Survival 1991 to 1992	0.445	[0.278, 0.626]	[0.357, 0.537]
Mean of the two years	0.445	[0.278, 0.626]	[0.357, 0.537]
Capture 1991 when captured at previous occasion	0.561	[0.348, 0.753]	[0.452, 0.664]
Capture 1991 when not captured at previous occasion	0.898	[0.241, 0.996]	[0.626, 0.979]
Capture 1992 when captured at previous occasion	0.200	[0.105, 0.347]	[0.146, 0.267]
Capture 1992 when not captured at previous occasion	0.633	[0.075, 0.973]	[0.276, 0.888]

Table 4. Model averaged survival, capture, and breeding probabilities of toads (*Bufo bufo*) of population A of Kuhn (1994). AICc weights used for model averaging are given in table 2. Survival and capture probabilities for the two best models are given in table 3. Model averaging was done assuming no overdispersion ($\hat{c} = 1$). Model averaged estimates assuming overdispersion ($\hat{c} = 4$) are available upon request from the authors.

Parameter	Mean	95% unconditional CI
Survival 1990 to 1991	0.474	[0.365, 0.585]
Survival 1991 to 1992	0.282	[0.112, 0.552]
Mean of the two years	0.378	[0.231, 0.525]
Capture 1991 when captured at previous occasion	0.483	[0.405, 0.561]
Capture 1991 when not captured at previous occasion	0.919	[0.604, 0.988]
Capture 1992 when captured at previous occasion	0.511	[0.386, 0.635]
Capture 1992 when not captured at previous occasion	0.842	[0.313, 0.984]
Probability that a toad does not breed in 1991	0.474	[0.339, 0.610]
Probability that a toad does not breed in 1992	0.393	[0.075, 0.710]

in year $t + 1$, given that they are still alive. With this assumption, the second capture probability (“capture when not captured at previous occasion” in tables 3 and 4) is the true (as defined for CJS models) capture probability (i.e., the probability of capture for an animal that is at the breeding site). The proportion of toads that skip breeding for one year is one minus the quotient of the two capture probabilities (in terms of appendix 2: $1 - \#8/\#10$ and $1 - \#9/\#11$). The proportions of toads that skipped breeding in 1990 and 1991 are given in table 4. Because these estimates also have associated confidence limits they are a marked improvement over the analysis of breeding patterns of Schmidt and Anholt (1999: table 5) or the calculations of Henle (2001: 384).

The capture probability “capture when not captured at previous occasion” is the probability that a toad is captured at the drift fence (assuming that toads skip breeding for only one year). The estimates in table 4 are higher than the ones estimated by Schmidt and Anholt (1999). Since temporary emigration causes strong bias in

the capture probabilities (Kendall et al., 1997), the difference between the estimates is not surprising. The new estimates are probably more realistic, but still not 1.0 and vary among years. Although the capture probability is not a direct measure of the efficiency of the drift fence, the high value for the capture probability “capture when not captured at previous occasion” suggests that many, but not all, toads that arrived at the drift fence were actually captured in Kuhn’s (1994) study. Nevertheless, the assumption that a drift fence captures all the animals is clearly not valid. Schmidt and Anholt (1999: 105) suggested that the low recapture probabilities they estimated could be evidence for toads that skip breeding if most toads that arrive at the fence are captured. Kuhn (1994) also measured several individual covariates, such as body size, on each toad. These data could be incorporated into a more sophisticated analysis that would shed light on which characteristics of the toads affect the probability of breeding.

Comparing the original analysis and reanalysis. We can compare the analyses in two ways: 1) The structure of the models or 2) the parameter estimates. Recent advances in GOF testing provided by U-CARE (Choquet et al., 2001) led us to consider an alternative model with a more adequate structure. The survival rate estimates from the best model in Schmidt and Anholt (1999) are difficult to compare with those developed here because Schmidt and Anholt (1999) used cohort-specific survival probabilities whereas they are time-specific in the present analysis (after correction for transients). We leave it to the reader to judge whether the difference between the cohort-specific survival estimates in Schmidt and Anholt (1999) and the time-specific survival estimates in table 4 are large or small. Although we do not think that the survival estimates in Schmidt and Anholt (1999) are wrong since bias is small and has a minor effect, we are convinced that the new analysis is better because it accounts and corrects for transients and temporary emigrants (capture heterogeneity). This analysis results in nearly unbiased estimates of the probability of survival. In addition, the model-averaged estimates account for model selection uncertainty.

Conclusion

We reject Henle’s (2001) claim that Schmidt and Anholt (1999) is an excellent example of the pitfalls arising when using CR methods. The problems that Henle (2001) identified are minor.

However, the new analysis is a clear improvement over the analysis of Schmidt and Anholt (1999). Schmidt and Anholt (1999: 105) could not identify why capture probabilities were low and variable. The new analysis can do so because it disentangles breeding probabilities and capture probabilities at the fence. Many toads skip breeding opportunities (table 4). In contrast to the conclusion of Schmidt and Anholt (1999: 105), the probability of breeding depends on whether a toad bred in the previous year (table 4). Capture probabilities at the fence are high, but not 100%, and variable between years (table 4). Survival probabilities estimated by Schmidt and Anholt (1999) and the estimates presented in table 4 are considerably higher than the ones presented by Kuhn (1994). The survival estimates suggest that common toads are not as long lived as commonly believed (e.g., Günther and Geiger, 1996). Taken together, these CR analyses improve our understanding of the life history of the common toad and provide direction for future research.

Capture probabilities are very likely to be variable, even when using standardized methods and this will cause potentially large biases. Therefore, it is better to use CR methods than other methods. As correctly pointed out by Henle (2001), temporary emigration may cause bias. This bias, however, is small in comparison to the standard errors and does not preclude an analysis of the data. As expected, the CR survival estimates are generally higher than what Kuhn (1994) reported, both in Schmidt and Anholt (1999) and table 4. Some, however, are within the range that he reported. This does not mean that both methods are equal. The CR analysis was done in a rigorous framework. This framework, GOF testing, model selection, and parameter estimation, can be critically evaluated by others and can thus be improved. Without Henle’s (2001) comments, we would not have reanalysed the data to get better estimates for survival and breeding probabilities. The new estimates of survival and breeding probabilities are distinctly better than the ones reported by Schmidt and Anholt (1999). This is the value of criticism in science.

Kuhn’s (1994) study represents an enormous effort to acquire reliable data to analyse the life history of the common toad. If we want to understand the demography and dynamics of amphibian populations, then we should use the most powerful methods at our disposal to arrive at the most reliable estimates of survival, rather than throw away this investment as Henle (2001) suggests.

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Appendix 1. Two examples of the preparation of the capture histories that allow simultaneous modelling of transients and immediate trap effects. The capture histories are given in MARK format (White and Burnham, 1999), where a count variable follows the capture history. Note that the original data did consist of a single group (one count variable; a count variable tells MARK how often a capture history was observed), whereas the arranged data consist of two groups (two count variables, the first one is for the group “transients and residents”, the second for the group “residents”). A negative sign in the count variables tells MARK that the animals are not released when captured for the last time.

Original capture history	Component capture histories, split into two groups
0101101 1;	0101000 -1 0; (transients and residents) 0001100 0 -1; (residents only) 0000101 0 -1; (residents only) 0000001 0 1; (residents only)
0100000 1;	0100000 1 0; (transients and residents)

Appendix 2. Parameter Index Matrices (PIM) for of model (ϕ_{a2^*t}, p_{m^*t}) in MARK (White and Burnham 1999) format. Each column denotes survival from one year to the next or a capture probability at a capture event. Each marking cohort is represented by one row. Fitting model (ϕ_{a2+t}, p_{m+t}) requires that certain parameters are constrained in a design matrix, such that the maximum number of estimated parameters (K) is 8.

Survival	Group transients and residents	1	5	6
			2	6
				3
	Group residents	4	5	6
			5	6
				6
Recapture	Group transients and residents	7	10	11
			8	11
				9
	Group residents	7	10	11
			8	11
				9

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Correction

Schmidt, B.R., Schaub, M., Anholt, B.R. (2002). Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. – *Amphibia-Reptilia* **23**: 375-388.

There is an error on page 379: “The standard errors must be multiplied by \hat{c} .” should read “The standard errors must be multiplied by $\sqrt{\hat{c}}$.”

\hat{c} is the *variance* inflation factor; it is the variance that should be multiplied by \hat{c} whereas the standard error must be multiplied by $\sqrt{\hat{c}}$.

The estimates and confidence intervals presented in our paper (tables 2, 3, and 4) are unaffected by this error as they were calculated correctly.

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