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Quantifying population declines based on presence-only records for red-list assessments

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Abstract

Accurate trend estimates are necessary for understanding which species are declining and which are most in need of conservation action. Imperfect species detection may result in unreliable trend estimates because this may lead to the overestimation of declines.

As many management decisions are based on population trend estimates, such biases could have severe consequences for conservation policy. We used an occupancy modelling framework to estimate detectability and calculate nationwide population trends for 14 Swiss amphibian species both accounting for and ignoring imperfect detection. Through application of IUCN Red List criteria to the different trend estimates, we assessed whether ignoring imperfect detection could impact on conservation policy. Imperfect detection was seen in all species and detection varied substantially among species, which led to the overestimation of population declines when detectability was ignored. Consequently, accounting for imperfect detection lowered the red-list risk category for 5 of the 14 species assessed. We demonstrate that failing to consider species detectability can have serious consequences for species management, and that occupancy modelling provides a flexible framework to account for observation bias and improve assessments of conservation status. A problem inherent to most historical records is that they contain presence-only data from which only relative declines can be estimated. A move towards the routine recording of non-observation and absence data is essential if we are to move beyond this towards accurate population trend estimation.
**Introduction**

The reliable assessment of trends in the distribution and abundance of species is a major concern for conservationists. Without an accurate measure of population trends it is challenging to identify those species most in need of conservation action or to measure the success of conservation action and policy (Butchart et al. 2010; Hoffmann et al. 2010). Given the large number of imperilled species and limited conservation funds, some sort of triage and priority setting is necessary (Bottrill et al. 2008, 2009). The use of red lists based on International Union for Conservation of Nature (IUCN) criteria to fill such a role has increased over past decades because the methods underpinning the red-listing process are transparent and quantitative and thus represent an objective method of assigning extinction threat (Lamoureux et al. 2003, Rodrigues et al. 2006, Collen et al. 2013). Red lists describe the extinction risk of species at the global scale or at smaller geographic scale (e.g., a continent or country). One of the red-list criteria used to determine extinction risk is magnitude of population decline over a defined period; species having undergone relatively greater declines receive higher red-list status (Gärdenfors et al. 2001, Mace et al. 2008). Yet, even though the quantification of declines is fundamental for red listing in particular and biodiversity conservation in general, it still remains a challenge (e.g., Yoccoz et al. 2001, Skelly et al. 2003, Tingley & Beissinger 2006).

To illustrate problems that conservation scientists and wildlife managers are likely to encounter when they attempt to quantify the decline of species in an area, we focused on changes in patch occupancy (i.e., the loss of local populations), a commonly used proxy for population declines. Patch occupancy is a state variable commonly used in monitoring programs and metapopulation ecology (Moilanen 2002, Joseph et al. 2006, Kéry & Schmidt 2008) because it is easy to collect these data relative to other metrics (e.g., abundance data [MacKenzie and Nichols 2004]). Trends in patch occupancy are often quantified using so-
called revisitation studies (Drost & Fellers 1996, Fischer & Stöcklin 1997, Kéry et al. 2006). Researchers first select sites where the species was recorded in the past from biodiversity databases. Resurveys at these sites are then undertaken to detect whether the species is currently present or absent. Declines can then be estimated as

\[ D = 1 - \frac{R}{H}, \]

(1)

where \( R \) is the number of occupied sites in the resurvey and \( H \) is the number of sites selected where the species was known to exist in the past (Kéry et al. 2006). Unfortunately, Eq. 1 cannot be used directly to estimate decline because both \( R \) and \( H \) are usually measured with error. The most common error is imperfect detection (i.e., false negatives or error of omission) because detection probabilities are usually <1 (Preston 1979, Pollock et al. 2002, Kéry & Schmidt 2008). Even though detection error is the rule rather than the exception (Kellner & Swihart 2014), there is still debate as to whether consideration of this bias is necessary or even desirable in population monitoring and conservation decision making (Banks-Leite et al 2014, Guillera-Arroita et al 2014).

We used data collected for an update of the Swiss Amphibian Red List (Schmidt & Zumbach 2005) to demonstrate problems associated with the estimation of population trends. We examined variation in detection probabilities among 14 Swiss amphibian species in order to assess the bias induced by ignoring imperfect detection when estimating population trends. We also examined how these biases can be avoided using occupancy models (MacKenzie et al. 2002, Tingley & Beissinger 2006) to adjust for imperfect detection and provide more reliable estimates of decline. Furthermore, we highlight how issues relating to imperfect detection can readily influence conservation decision-making through the assigning of inappropriate extinction threat (i.e., Red List category) to species. Finally, we considered the inherent problem that historical records typically contain presence-only data and why such
data sets can only be used to calculate a relative, rather than absolute magnitude of decline. We argue that this fundamental problem can be avoided in the future with a shift from the collection of presence-only biodiversity data to databases that also routinely record species non-detections.

**Methods**

**DATA COLLECTION**

Guidelines for the IUCN Red List permit the categorization of extinction risk based on the magnitude of population declines over 10 years or 3 generations (Mace et al. 2008, IUCN Standards and Petitions Subcommittee 2014). We quantified population decline (i.e. IUCN criterion A) as a change in the number of occupied sites throughout Switzerland, measured at the scale of individual amphibian breeding sites (typically a wetland or pond). We therefore assigned red-list categories to species on the basis of changes in the number of occupied ponds, which can be used as an index of abundance (Buckland et al 2005, IUCN Standards and Petitions Subcommittee 2014).

The distribution of all pond-breeding amphibian species was thoroughly surveyed in Switzerland in the 1970s and 1980s, when experienced herpetologists mapped all known amphibian breeding sites and recorded which species occurred at those sites (Grossenbacher 1988). The resulting database contains data on all amphibian species native to Switzerland and is maintained and updated by KARCH (the Swiss Amphibian and Reptile Conservation Programme, part of the Centre Suisse de Cartographie de la Faune CSCF). The database contains over 12,000 amphibian breeding sites and over 160,000 records (Schmidt & Zumbach 2016).
Sites from this database were selected for resurvey as follows. For each species, the number of the sites was randomly selected for resurvey on the basis of the species’ rarity and range. Twenty sites were selected for 9 species with >400 known breeding sites, 25 sites for 3 species (*Triturus cristatus*, *Lissotriton vulgaris*, *Rana dalmatina*) with <400 known breeding sites, and 12 sites for 2 species that occur only in the southern region of Switzerland, Canton Ticino (*Triturus carnifex*, *Hyla intermedia*). This resulted in 289 resurveyed sites (Fig.1), for which the historical records dated back on average to 1993 (SD 9).

Although individual sites were selected for inclusion based on records of an individual species, sites were commonly occupied by multiple species. Thus, for every species, we had more presence records in the sample than the number of sites selected specifically for that species. For each species, the data set analysed included all information from all sites that were located within the biogeographic regions (Gonseth et al. 2001) in which the species was known to occur and that were within the known elevational range of the species in Switzerland (Grossenbacher 1988). Thus, all sites where a species could potentially have been present were included; individual sites were assigned a binary covariate to describe the presence or absence of historical observations of species presence (Table 1).

For the resurvey, each site was visited four times from March to June in either 2003 or 2004 in order to account for differences in breeding phenology between species. One-hour visits were conducted in which the surveyor used multiple methods (visual encounter surveys, call surveys, dip netting) to collect detection and nondetection data for all pond-breeding amphibians. Data for all life stages (eggs, tadpoles, juveniles, adults) were pooled for analysis. Some of the sites scheduled for resurvey had been destroyed, predominantly as a consequence of agricultural intensification and urban development. In such cases the site was recorded as destroyed and a replacement site was surveyed (selected again using the above criteria). The number of destroyed sites is shown in Table 1.
DATA ANALYSES

Two estimates of decline were calculated: unadjusted declines, which ignored imperfect detection, and adjusted declines, which were calculated by estimating and adjusting for species detection probabilities. Unadjusted declines were calculated using a version of Eq. 1 modified to incorporate the effects of the destruction of some sites (and thus loss of those populations):

\[ D_{\text{unadjusted}} = 1 - \frac{N_{\text{obs}}}{H(1+L)} \]

where \( L \) is the proportion of historically occupied sites that were destroyed and \( N_{\text{obs}} \) is sites where the species was observed both during the surveys for the red-list update and in the historical records.

To estimate detection and site-occupancy probabilities, we fitted site-occupancy models (MacKenzie et al. 2002, Royle & Kéry 2007, Kéry & Schaub 2012) to each species data set. The data \( y_{ij} \) consisted of binary detection and non-detection indicators at each of \( i \) sites and \( j \) visits. The model was written as

\[ z_i \sim \text{Bernoulli}(\Psi_i), \]  
\[ y_{ij} | z_i \sim \text{Bernoulli}(z_i p), \text{ and} \]  
\[ \text{logit}(\Psi_i) = \alpha + \beta X_i. \]

Equation 3 defines the latent (i.e. true) state of occurrence of the species in site \( i \) as a Bernoulli trial with success parameter \( \Psi_i \) (occupancy probability). Equation 4 defines the observation data as a Bernoulli trial, where the success parameter is a product of the latent occurrence state and detection probability \( p \). Although we fixed \( p \) as a species-specific constant for simplicity and clarity of interpretation, this parameterisation could also be
expanded to incorporate site- and visit-specific covariates. We used a logit link function to model the relationship between current occupancy and a binary covariate $X_i$, which describes the presence or absence of a historical record of species presence at the site (Eq. 5). The $\alpha$ and $\beta$ are regression coefficients. Given the data and the model, $\alpha$ is the proportion (on the logit scale) of sites where the species was not recorded in the past but was estimated to occur now, which we refer to as an apparent colonization (see Discussion). $\alpha + \beta$ is the proportion (on the logit scale) of sites where the species was recorded in the past and is estimated to still occur at the site. It is an estimate of the probability of persistence at a site (hereafter, psi.persist). Declines adjusted for imperfect detection and site destruction were calculated using the measure of site persistence, psi.persist. This measure therefore accounted for both site destruction and imperfect detection as follows:

$$D_{\text{adjusted}} = 1 - \frac{\text{psi.persist}}{1+L}.$$  

(6)

To meet the closure assumption of site-occupancy models, species must be available for sampling during each site visit (MacKenzie et al. 2002). For each species we truncated the data set to consider only the site visits carried out between the first and last observation (inclusive) for that species across all sites. This data truncation reduced the number of site visits in a species-specific manner but ensured that only survey data that occurred during the active period of each species was used. This data truncation reduced our data set to a mean across species of 3.23 site visits, except for Hyla arborea, Hyla intermedia, and Triturus carnifex for which the mean (across the three species) was 1.76 site visits.

We used the equation of McArdle (1990) to estimate per-visit detection probability $\hat{p}$ and then calculated the cumulative probability of detecting a species $p^*$ after 1-4 visits:

$$p^* = 1 - (1 - \hat{p})^n,$$  

(7)

where $n$ is the number of site visits. This equation assumes that the species was present at the site (see Wintle et al. [2012] for the more general case that does not condition on species...
Calculating adjusted decline and $p^*$ explicitly as part of model fitting allows direct calculation of the uncertainty in parameter estimation.

Modeling was carried out in WinBUGS through the R package R2WinBUGS (Kéry & Schaub 2012). We used vague uniform priors for all model parameters, detection probability $p \sim \text{dunif}(0,1)$, and the coefficients $\alpha$ and $\beta \sim \text{dunif}(-10,10)$. Due to convergence problems, wider priors ($\text{dunif}(-20,20)$) were necessary for *Hyla intermedia*. Three Markov chains of 10,000 iterations were run for each model. The first 1,000 iterations were discarded as burn-in and the remaining thinned by 1 in 10. We assessed convergence with the Brooks-Gelman-Rubin statistic (Gelman et al. 2004).

**Results**

Per-visit detection probabilities were well below 1 and varied among species (range 0.50 (95% credible interval [CI] 0.39-0.61) (*Lissotriton vulgaris*) to 0.85 (95% CI 0.73-0.93) (*Hyla arborea*) (Fig. 2a). Cumulative detection probabilities after multiple visits to the same site (analogous to the proportion of occupied sites detected) approached 1 by the fourth site visit (Table 1, Fig. 2b). For most species, three visits were required for 95% confidence of detecting a species if it was present. For the two tree frog species (*H. arborea* and *H. intermedia*), only two visits were necessary, whereas for *L. vulgaris* even four visits were not sufficient to reach this level of confidence (95% credible interval for *L. vulgaris* after 4 surveys: 0.86-0.98 [Fig. 2b]). With each consecutive visit, 95% CI shrank; thus, for most species after four visits it was possible to be highly confident that the species was detected if present.

All species exhibited some losses from sites where they had been present in the past because such declines were recorded for all species irrespective of the method used to calculate the trend (Fig. 3). Declines did not appear to show any spatial patterns, except for
Alytes obstetricans. In this species, declines were more common in eastern Switzerland, which is at the species’ range edge. Unadjusted declines, whereby sites were considered occupied if the species was observed in one of the four surveys, ranged from 17.6% (Rana temporaria) to 66.1% (Epidalea calamita) (Table 1). When mapped to red-list criteria, these measurements resulted in 10 of 14 species being listed as threatened, 3 as vulnerable, and 7 as endangered (Fig. 3).

However, declines adjusted for detection probability were of a consistently lower magnitude than those not accounting for imperfect detection (Fig. 3, Table 1) (range 14.4% [Rana temporaria] to 59.9% [Epidalea calamita]). The difference between declines adjusted and not adjusted for imperfect detection was mostly small, however. Nevertheless, adjusting for detection probability resulted in changes to the ranking of species declines. For five species, the two measures of decline were sufficiently large that under IUCN Red List guidelines the different estimates would result in classification of the species under different threat categories (Fig. 3). These species were typically those with the lowest probabilities of detection; however, H. arborea, the species with the highest detection probability, was also one of those species for which the extinction risk was overestimated when detection probability was unaccounted for. Credible intervals for adjusted declines may encompass decline values higher than those observed. This is because the estimate of decline is a probability that relates not only to the sample (i.e., the sites that were surveyed) but to all populations from which the sample was drawn. Finite sample inference, as described by Royle and Kéry (2007), would lead to credible intervals that do not exceed observed decline values.

For all species, a number of observations were recorded in the resurveys at sites where the species was previously not known. From these data, the occupancy model estimated an occurrence probability (\( \alpha \) in equation 5) that was an apparent colonization
probability (i.e., the probability that a site that was previously recorded as unoccupied in the past transitioned to an occupied state). These apparent colonization probabilities were generally higher for common species than for rare and more strongly declining species (Table 1). Strong negative relationships were seen between apparent colonisation probability and both measures of decline ($r$ -0.78 and -0.81 for unadjusted and adjusted declines respectively, both $p<0.01$).

**Discussion**

The methods that we used to calculate species trends and the assumptions, both implicit and explicit, that we make when estimating changes over time have an unsurprising but often dramatic effect on the outputs of species monitoring. We focused specifically on one form of bias common to most wildlife monitoring, that of imperfect detection, and demonstrated that failing to consider such bias can easily lead to assignment of the wrong red-list category. Such inappropriate assignment may lead to management practices that fail to have the intended effect.

Our method can be extended to other taxa as well as to multiple time periods. Extending the approach to multiple periods with dynamic occupancy models (MacKenzie et al. 2003) would be a way test for a reduction or change in the rate of biodiversity loss (as for example required by the Convention on Biological Diversity). Furthermore, one could use covariates describing land use or management to understand the variation in the magnitude of trends and the factors causing the population declines (e.g., Miller et al. 2012). In Switzerland one of the main reasons for the large population declines (Fig. 3) was the lack of temporary ponds (Schmidt and Zumbach 2005). As a consequence, pond creation has been implemented and has had promising results (Schmidt et al. 2015).
We found that detection probabilities were variable among species that were surveyed simultaneously and that detection probabilities for most amphibians tended to be substantially <1. Given the large number of studies that have estimated detection probabilities of amphibians and other animals and plants (e.g., Kéry & Schmidt 2008, Sewell et al. 2012, Chen et al 2013), these results were not unexpected. Highly vocal tree frogs had the highest detection probabilities and cryptic newts the lowest; otherwise, species traits had no apparent effect on patterns of variation in detection among species (Garrard et al. 2013). Furthermore, very similar surveys (i.e., no obvious differences in the methods sections of the papers) can result in substantially different detection probabilities. *Epidalea calamita* had a detection probability of 0.62 (95% CI 0.48 - 0.74), whereas in other studies of this species with similar survey methods, Schmidt (2005) and Pellet and Schmidt (2005) calculated the detection probability as 0.27 and 0.44 respectively (no standard errors were provided in these studies).

It therefore appears that detection probabilities are not simply species or method specific. This suggests that one cannot assume a fixed value of detection probability but that one has to estimate detection probability in every survey.

Although cumulative detection probability for some species can be very high (> 0.95) after multiple visits to a site (Fig. 2b), there can still be a difference between estimates of decline adjusted and not adjusted for imperfect detection. This difference can lead to an overestimation of decline and therefore species may be assigned to the wrong red-list category (e.g., the species *Hyla arborea*, *Bufo bufo*, *Rana dalmatina*, *Lissotriton vulgaris* and *Triturus cristatus*) (Fig. 3). Because red lists are used for conservation priority setting, conservation effort (e.g., the list of species of national priority in Switzerland [BAFU 2011]) may be allocated suboptimally and focus on the wrong species. Thus, ignoring imperfect detection can directly impact conservation management. We therefore recommend adjusting for imperfect detection whenever possible. There may be financial or other constraints that
prevent the collection of the most reliable data, but we believe one should always strive to obtain the best data (The Rolling Stones 1969). Some concerns over adjusting for imperfect detection do not seem justified because it is not always necessary to visit all sites multiple times and space-for-time substitutions may lower survey costs (MacKenzie et al. 2002, Kendall & White 2009). There are also methods that allow the joint analysis of different types of survey data (Dorazio 2014), which could also act to reduce the burden of collecting information to estimate detection.

Our estimations of population declines are based on presence records of species. That is, we know that the species was present in the recent past, and we asked whether the species was still there at the time of a resurvey or whether a local extirpation occurred. Such revisitation studies are commonly used for estimating trends, but this method is flawed because it can only measure declines. Local extirpations may be part of a turnover process in a metapopulation (Hanski 1991, Hecnar & M’Closkey 1996); thus, the losses we describe may have been compensated for by colonizations elsewhere. We included sites in our survey where the species were not recorded in the past so that we could measure colonizations (i.e., the proportion of those sites where the species was present in the resurvey) (Table 1). Colonization probabilities were negatively correlated with the magnitude of declines, suggesting that for the declining species, colonization of new sites was not sufficient to compensate for declines and thus declines are real rather than a methodological artefact. (There is evidence for this interpretation from later resurveys [Lupi 2016]). Importantly, colonizations are not necessarily true colonizations of previously unoccupied sites. Although the historic status of sites where observations were recorded is certain, there may be uncertainty associated with those sites where historic presence was not recorded. It may be that the species was already present in the past but was never observed and recorded in a database; thus, the apparent colonization is instead the discovery of a previously unnoticed
population at a site. The true status of sites where a species was not recorded in the past is therefore uncertain.

If a distribution database holds only presence records, then one can in most cases only estimate a relative decline. Conceptually, this can be shown by rewriting Eq. 1 and acknowledging that we do not know $R$ and $H$. We only know the sites where the species was detected and reported: $C_R = R \times p_R$ and $C_H = H \times p_H$, where $C_i$ is the observed number of occupied sites and $p_i$ is detection probability for the historical data and the resurvey. This leads to a new equation:

$$\text{decline} = 1 - \frac{C_R}{C_H} = 1 - \frac{R \times p_R}{H \times p_H}. \quad (7)$$

Typically, only $C_R$ and $C_H$ are available for the estimation of decline. Using the $C_i$ for decline estimation is problematic because one has to assume $p_R = p_H$. If $p_R \neq p_H$, then the estimate of decline is biased (Pollock et al. 2002). In a resurvey, one can estimate detection probabilities such that one obtains $\hat{R}$, an estimate of $R$. The equation changes to

$$\text{decline} = 1 - \frac{\hat{R}}{H \times p_H}. \quad (8)$$

This is an improvement, but because $p_H$ is unknown and cannot be known, one can only estimate a relative decline. The expression $H \times p_H$ implies there are sites where the species did occur in the past but was not recorded. Thus, some putative absences are in fact presences (this is related to the problem of apparent colonizations discussed above). Certainly, an estimate of decline can be based on $C_H$ but with such presence-only data one can only measure a relative decline. In most cases, a decline will be overestimated. Furthermore, without ways of estimating historical detection, the sites selected for resurvey in revisitation studies may be affected by selection bias because larger populations are more likely to be detected (Tanadini & Schmidt 2011) and less likely to be extirpated (Alpizar-Jara et al. 2004). Trends derived from databases biased in this way could therefore suggest that declines are of a lower magnitude than the true trend based on all sites that were occupied in the past.
because the local extirpation of small populations may not be noticed. The problem outlined here applies equally to estimates of historical abundance (estimates are often not adjusted for imperfect detection [Nichols 1992]).

Uncertainty about historical absences and abundances may be the reason many indices of biodiversity decline start at an arbitrary value of 1 (e.g., the Living Planet Index [Loh et al. 2005] or estimates of global amphibian population declines [Houlihan et al. 2000]). There is a similar problem with presence-only data in species distribution modeling. With presence-only data, one can estimate only relative occurrence not absolute probability of occurrence (or species prevalence [Hastie & Fithian 2013]). Put simply, if \( y = a + b \times x \) describes the relationship between species occurrence, \( y \), and a habitat characteristic, \( x \), then one can estimate only the coefficient \( b \) while \( a \) cannot be estimated. For some applications, relative habitat suitability may be sufficient, but for others this is unlikely to be the case (Guillera-Arroita et al. 2015). What all this illustrates is that one often cannot learn from presence-only data what one would like to learn about patterns of biodiversity and changes therein.

We showed how estimation of detection probabilities can improve the estimation of declines and lead to better extinction risk assessments for conservation. If estimates of extinction risk are based on records that show where the species was known in the past, then estimates of extinction risk and decline remain relative. Similar problems exist for other indices of trends and species-distribution models. Sometimes it is possible to combine data sets from multiple species or surveys to arrive at unbiased estimates (Kéry et al. 2010, Sadoti et al. 2013). The better solution would be to complement observations of where species were observed with data on where species were not observed. One approach may be that observers should complete species lists rather than observations of a single species (Isaac & Pocock 2015). Such nonobservations are not evidence for the absence of species but when analyzed
using appropriate statistical models (MacKenzie et al. 2002), such data would nevertheless allow the unbiased estimation of absolute population decline, extinction risk, and species distributions. Ultimately, the lack of accurate historical baselines hinder current efforts to accurately monitor trends; a change toward the routine recording of nonobservations and absence data is required to stop these problems hindering future monitoring of biodiversity trends.

Acknowledgments

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Table 1. Rates of persistence and apparent colonization estimated from the occupancy model and two measures of decline for 14 species of amphibian found in Switzerland.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sites surveyed</th>
<th>Sites destroyed</th>
<th>Persistence probability (95% CI)</th>
<th>Apparent colonization probability (95% CI)</th>
<th>Unadjusted decline</th>
<th>Adjusted decline (95% CI)</th>
<th>Bias induced by ignoring detection (%)</th>
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</thead>
<tbody>
<tr>
<td>Alytes obstetricans</td>
<td>212</td>
<td>7</td>
<td>0.526 (0.412-0.641)</td>
<td>0.040 (0.017-0.080)</td>
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<td>0.625</td>
<td>0.561 (0.457-0.661)</td>
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<td>15</td>
<td>0.807 (0.728-0.876)</td>
<td>0.420 (0.323-0.521)</td>
<td>0.324</td>
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<td>0.040 (0.012-0.082)</td>
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<td>0.492 (0.356-0.628)</td>
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<td>0.742</td>
<td>0.233</td>
<td>0.367</td>
<td>0.319</td>
<td>15.0</td>
</tr>
<tr>
<td>Lissotriton vulgaris (L.vulg)</td>
<td>253</td>
<td>1</td>
<td>0.547</td>
<td>0.030</td>
<td>0.536</td>
<td>0.463</td>
<td>15.8</td>
</tr>
<tr>
<td>Pelophylax esculentus complex (P.escu)</td>
<td>253</td>
<td>1</td>
<td>0.834</td>
<td>0.254</td>
<td>0.224</td>
<td>0.171</td>
<td>31.0</td>
</tr>
<tr>
<td>Rana dalmatina (R.dalm)</td>
<td>228</td>
<td>1</td>
<td>0.742</td>
<td>0.026</td>
<td>0.344</td>
<td>0.270</td>
<td>27.4</td>
</tr>
<tr>
<td>Rana temporaria (R.temp)</td>
<td>277</td>
<td>15</td>
<td>0.918</td>
<td>0.685</td>
<td>0.176</td>
<td>0.144</td>
<td>22.2</td>
</tr>
<tr>
<td>Triturus carnifex (T.carn)</td>
<td>51</td>
<td>3</td>
<td>0.695</td>
<td>0.061</td>
<td>0.556</td>
<td>0.330</td>
<td>68.5</td>
</tr>
<tr>
<td>Triturus cristatus (T.cris)</td>
<td>211</td>
<td>3</td>
<td>0.449</td>
<td>0.007</td>
<td>0.617</td>
<td>0.573</td>
<td>7.7</td>
</tr>
<tr>
<td>-----------------------------</td>
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<td>------</td>
<td>------</td>
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<td>----</td>
</tr>
</tbody>
</table>

- **Number of sites used to calculate population declines.**
- **Number of sites destroyed before the resurvey and replaced in the analysis with equivalent sites.**
- **Probability of population survival at a site between historic observations and the red-list resurvey.**
- **Probability that a site with no historic observations of the species was estimated to be occupied during the resurvey.**
- **Population decline ignoring the influence of imperfect detection.**
- **Estimated population decline following incorporation of imperfect detection in the contemporary resurvey.**
- **Degree to which population declines were overestimated when imperfect detection ignored.**
Figure 1. Location of the 289 sites in Switzerland included in the resurvey for the Swiss Red List update. Map shading shows the major biogeographic regions within the country.

Figure 2. (a) Per-visit detection probabilities and 95% credible intervals for 14 amphibian species at sites throughout Switzerland. *P.escu* represents the *Pelophylax esculentus* species complex. Species abbreviations as shown in Table.1 (b) Cumulative detection curves and 95% CI for 4 amphibian species over 4 survey occasions (solid horizontal line, point at which one could have 95% confidence of detecting the species at a given site if it was present). *H. arborea* and *L. vulgaris* had the highest and lowest detection probabilities respectively.

Figure 3. Declines in site occupancy as estimated between the time of collection of historical records and the contemporary resurvey in 2003 and 2004 (bars, unadjusted estimates of decline based on whether the species was observed at the site at any of the 4 survey occasions; points, declines adjusted for the detection probability of each species as estimated from the occupancy model; solid lines, 95% credible intervals); horizontal dashed lines, levels of decline required to warrant an International Union for Conservation of Nature classification of critically endangered [CR] [decline >80%], endangered [EN] [decline of 50-80%], or vulnerable [VU] [decline of 30-50%]). Shading represents whether declines accounting for imperfect detection result in classification of a species into a different threat category to declines calculated assuming perfect detection. Species abbreviations as shown in Table.1 *P.escu* represents the *Pelophylax esculentus* species complex.