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Conservation of a threatened European tree frog (*Hyla arborea*) metapopulation

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Conservation of a threatened European tree frog (Hyla arborea) metapopulation

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pour Le Doyen de la Faculté de Biologie et de Médecine V ~ ~ Prof. Daniel Cherix

The ethical principle of reverence for life demands that human beings should protect their fellow-creatures, the animals, which, no less than themselves, are sentient beings. It also implies an obligation to respect their dignity and the right of each species to thrive and flourish in its natural manner

Swiss Academy of Sciences (1995)

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SUMMARY

Amphibians are among the most vulnerable animals of the world. One third of all species are currently threatened with extinction. Habitat loss is the major menace to pond- and stream-breeding species in the old world. In highly urbanized landscape like the Swiss Plateau, most species suffer from habitat reduction and fragmentation. Among all indigenous species, the European tree frog (*Hyla arborea* L., 1758) is one of the most endangered. It experienced an alarming decline during the last century and its regional long-term persistence is not guaranteed.

We developed a monitoring framework based on calling male counts which included multiple visits to each wetland during the reproduction period in order to precisely determine its distribution on the Lemanic coast. Our results indicate that visiting populations 3 times under suitable climatic conditions (temperature >20°C) provides reliable presence/absence data.

Based on our monitoring data, we analyzed the species requirements regarding its breeding habitat. It appeared that anthropogenic activities had paradoxical effects on the species. On one traffic hand, urbanization, and intensive agriculture had a strong detrimental effect on tree frog distribution. On the other hand, large tree frog populations were frequently associated with gravel pits and military training grounds. Our results allowed us to create a habitat suitability map taking into account detrimental landscape elements around ponds (>1'100m away from urban areas and >500m away from first class roads).

In parallel, we developed a metapopulation model of the European tree frog in order to identify the critical threats to the long term persistence of the species. Our results indicated that suitable pond density is at the low end of the species requirements. Pond creation must therefore be considered an essential complementary approach to pond conservation and restoration. Our model also provided a mapping solution permitting the location of the most suitable area for pond creation from a metapopulation perspective.

As many other amphibians, the European tree frog is not only exposed to an aquatic habitat (breeding and larval period), but also to a terrestrial stage (summer and overwintering Unfortunately, animals in habitats). their terrestrial phase are less conspicuous and, as a consequence, their terrestrial needs are relatively unknown. Using a recent tracking method (the Harmonic Direction Finder), we followed postbreeding frogs and identified favored terrestrial habitats, thus providing another practical conservation tool.

We conclude that only the combination of multiple spatially explicit approaches (landscapescale habitat suitability, metapopulation dynamics and terrestrial needs) is likely to provide wildlife managers with effective tools for the conservation of highly endangered amphibians.

Résumé

Les amphibiens font partie des animaux les plus vulnérables du monde. Un tiers des espèces est actuellement menacé d'extinction. Dans l'ancien monde, la disparition des habitats constitue la principale menace pour les grenouilles, crapauds, tritons et salamandres. Dans les paysages fortement urbanisés comme le Plateau Suisse, la plupart des espèces souffrent d'une réduction et d'une fragmentation de leurs habitats. Parmi toutes les espèces indigènes, la rainette verte (*Hyla arborea* L., 1758) est l'une des plus menacée. Sa distribution a régressé de manière alarmante durant le siècle passé et sa survie régionale à long terme n'est pas assurée.

Nous avons développé une méthode de suivi des populations se basant sur le comptage des mâles chanteurs durant la période de reproduction. Cette méthode requiert plusieurs visites à chaque plan d'eau de manière à déterminer précisément la distribution de l'espèce. Nos résultats démontrent que 3 visites par population dans des conditions climatiques favorable (température >20°C) permettent d'obtenir des données de présence/absence valables.

Sur la base de nos comptages sur la Côte lémanique, nous avons analysé les exigences de l'espèce concernant ses sites de reproduction. Il est apparu que les activités humaines avaient un effet paradoxal sur l'espèce. D'une part, l'urbanisation, le trafic routier et l'intensification de l'agriculture ont un effet fortement préjudiciable, tandis que d'autre part les plus grandes populations sont souvent associées à des gravières et autres places d'armes. Nos résultats ont permis de créer une carte de qualité d'habitat prenant en compte les éléments paysagers préjudiciables à la rainette (situé à plus de 1'100m de zones urbaines et à plus de 500m de routes de première classe).

En parallèle, nous avons développé un modèle métapopulationnel (incluant l'ensemble des populations) de manière à identifier les menaces prépondérantes sur la survie à long terme de l'espèce. Nos résultats ont permis de déterminer que la densité actuelle de plans d'eau adéquats est à la limite inférieure des exigences de l'espèce. La création d'étangs doit donc être considérée comme une approche indispensable et complémentaire à la protection et à la restauration des sites existants. Notre modèle a également fourni des résultats cartographiables permettant l'identification des sites les plus appropriés dans une perspective métapopulationnelle.

Comme de nombreux autres amphibiens, la rainette verte est exposée à une habitat aquatique (reproduction et développement larvaire) ainsi qu'à un habitat terrestre (été et hiver). Les animaux étant particulièrement cryptiques dans cette seconde phase, leurs besoins terrestres sont relativement mal connus. Nous avons donc développé une nouvelle méthode de télémétrie basée sur le goniomètre harmonique. Cette méthode nous a permis de suivre des rainettes dans leurs migrations jusqu'à leurs habitats d'été et d'établir ainsi des recommandations pratiques pour la conservation de la rainette.

Nous concluons que la combinaison de multiples approches spatialement explicites (qualité d'habitat, dynamique de métapopulation et habitats terrestres) est seule à même de produire des outils efficaces pour la conservation des espèces menacées d'amphibiens.

INTRODUCTION

AMPHIBIAN DECLINE

Nearly one-third of known amphibian species are currently threatened by extinction (Stuart et al. 2004), putting them among the most vulnerable of all living creatures. By comparison, slightly over 12% of all birds and about 23% of all mammals are similarly threatened. Amphibian declines and extirpations were only sporadically reported during the last few decades, but evidences of a global threat were recently presented, triggering large-scale concern about amphibian conservation (Alford & Richards 1999, Houlahan et al. 2000, Stuart et al. 2004).

Reasons for this decline are diverse, and most of them originate from the extreme sensitivity of amphibians to environmental variations due to their permeable skin and their dual life-cycle (aquatic and terrestrial). Principal threats are due to breeding habitat loss (filling and draining of wetlands) and terrestrial land modification (Delis et al. 1996, Alford & Richards 1999, Semlitsch 1998, Semlitsch & Bodie 1998, Knutson et al. 1999, Pope et al. 2000, Joly et al. 2001, Dodd & Smith 2003). Other causes, such as non-indigenous species introduction leading to extra competition and/or predation with local species have been shown to have a profound impact on amphibian assemblages (Bradford et al. 1993, Fisher & Schaffer 1996, Hecnar & M'Closkey 1997, Gillespie 2001, Kiesecker 2003). Climate changes, forcing individuals to shift their habitat use (Pounds et al. 1999, Blaustein et al. 2001, Carey & Alexander 2003), as well as seasonal increase in UV-B radiation, reducing egg hatching and survival (Blaustein et al. 1995, Blaustein et al. 2003), have also been shown to represent threats to many species. The emergence of infectious diseases (e.g. Carey 1993, Blaustein et al. 1994, Bosh et al. 2001, Carey et al. 2003, Daszak et al. 2003) and chemical contaminations (e.g. Hayes et al. 2002) are also commonly cited examples. Furthermore, it has been demonstrated that interactions of natural and anthropogenic factors are synergistically at work (Kiesecker & Blaustein 1995, Lips 1998, Kiesecker et al. 2001, Blaustein et al. 2003).

WETLAND UMBRELLA SPECIES

Human-associated factors remain the primary cause of amphibian declines and extinctions (Petranka et al. 1993, Hecnar & M'Closkey 1996, Davidson et al. 2002, Dodd & Smith 2003, Collins & Storfer 2003, Semlitsch 2003, Stuart et al. 2004). Amphibian assemblages can however respond very differently to such changes in habitat quality: some species will remain relatively unaffected by severe alterations of the vegetation and structure of their habitat (Winter & Alford 1999) while others will decline rapidly due to changes in community structure (Beebee 1977) and/or overall suitability of the habitat for the completion of their life cycle (Dodd and Smith 2003). Species of the latter group may be candidate as environmental sentinels by rapidly translating diminishing habitat quality into reduced abundance and distribution (Vitt et al. 1990, Welsch & Ollivier 1998, Carignan & Villars 2002).

The prevention of wetland loss and alteration is a high priority conservation target since they support a diverse abundance of amphibian and non-amphibian life. Reliable indicators of wetland habitat quality are therefore considered crucial. Being highly philopatric and long-lived (Smith & Green 2005), amphibians are believed to have the suitable attributes to be good indicators of local species richness (Welsh & Ollivier 1998, Welsh & Droege 2001). As such, their populations are often monitored in order to determine trends in habitat quality or to evaluate conservation actions (e.g., Heyer et al. 1994, Mossman et al. 1998, Dodd 2003, Buckley & Beebee 2004, **Chapter 1**).

Because of its sensitivity to the quality of breeding wetlands, the European tree frog (*Hyla arborea* L., 1758) is often associated with ponds rich in amphibians, as illustrated in Figure 1.



Figure 1: Amphibian species richness in 111 ponds in western Switzerland. European tree frog presence is associated with a higher amphibian diversity (t-test, P<0.001).

Ponds where tree frogs occur are usually shallow, fish-free, sunny, oligo- to mesotroph, and dynamic in nature (Stumpel & Hanekamp 1986, Fog 1988, Pavignano et al. 1990, Tester 1990, Brönmark & Edenhamn 1994, Edenhamn 1996, Vos 1999). They thus constitute secondary habitat for many pioneer species including Red-Listed plants, dragonflies and other amphibians. As ponds mature and natural succession occurs (or when anthropogenic changes take place) presence and/or abundance of *H. arborea* will vary, reflecting the state of the system for a large variety of species. The threatened European tree frog is therefore considered both a good umbrella species and a sentinel of wetland quality. The conservation of such species is fundamental for the protection of wildlife associated with temporary wetlands.

DUAL HABITATS REQUIREMENTS

As with many other pond- and streambreeding amphibians, the European tree frog is exposed to both an aquatic (breeding and larval period) and a terrestrial stage (summer and overwintering habitats). A set of complementary resources is therefore necessary for most species in order to prosper regionally (Lehtinen et al. 1999, Pope et al. 2000, Semlitsch & Jensen 2001, Pilliod et al. 2002). Conservation strategies as well as autecological investigations must therefore focus on both habitats.

THE AQUATIC AND TERRESTRIAL HABITATS

The quality of breeding sites has long been the focus of herpetological research. Ensuring a suitable habitat for both breeding and larval development is certainly crucial for the preservation of local populations. Nevertheless, restricting habitat selection studies to local-scale factors is very likely to be of limited value since there is evidence that medium- and large-scale factors can influence the distribution of amphibian species (Knutson et al. 1999, Joly et al. 2001, Findlay & Houlahan 1997, Green 1997, Johnson et al. 2002, Welsh & Lind 2002), including the European tree frog (Grosse & Nöllert 1993, Edenhamn 1996, Vos 1999, **Chapter 2**).

Evaluating the effect of landscape structures (e.g. hedgerows, forest borders) within accessible range of breeding ponds and/or the impact of anthropogenic land uses (e.g. roads) on amphibians can help broaden (both conceptually and geographically) the classical view of pond-associated species. Understanding the role of land uses in determining patterns of abundance is fundamental to achieve efficient conservation strategies (Bulger et al. 2003, **Chapter 3**).

Although advances have been made in identifying amphibian distribution correlates, our understanding of the terrestrial autecology of most species, including the European tree frog (Stumpel 1993) remains lacunar. The duality of many amphibians' life cycle has been somewhat neglected simply because breeding sites are the most convenient places to sample individuals. There is however a growing concern that conservation strategies restricted to the aquatic habitat are of limited use if the adjacent terrestrial habitats are destroyed or become unreachable following human activities (Semlitsch 1998). Unfortunately, it is difficult to identify the location of these terrestrial habitats since most amphibians are relatively cryptic outside their breeding season (Stumpel 1990). As a consequence, the tracking of marked individuals on their post-breeding migrations can prove extremely informative to both researchers and wildlife managers (Gibbons 2003, Schabetsberger et al. 2004, **Chapter 4**).

POPULATION DYNAMICS

Most amphibian populations experience wide fluctuations in number. They may therefore be extremely sensitive to stochastic events (Berven & Grudzien 1990, Pechmann et al. 1991, Marsh 2001, Green 2003) because naturally fluctuating populations are more likely to go extinct (Leigh 1981, Inchausti & Halley 2003).

Understanding the population-level mechanisms of such dynamics can provide insights into what factors (either extrinsic or intrinsic) are governing population fluctuations. Unpredictable external influences, such as climate and hydroperiod, are thought to influence demographic parameters (e.g. fecundity, survival) and to generate stochastic dynamics in many species. On the other hand, intrinsic factors, such as density dependent growth rates, are believed to act as general buffers against such variation in population sizes by allowing small populations to rapidly recover from declines.

The examination of long term time series of population dynamics is one of the possible ways to determine what variables or combination of variables drive population size variations (Dennis & Otten 2000, **Chapter 5**). In addition, they may improve the development of population viability analyses, which are classically used to assess management scenarios and risks of extinction in metapopulations (McCullough 1996, Akçakaya & Sjögren-Gulve 2000, Beissinger & McCullough 2002).

METAPOPULATION STRUCTURE

Assuming that population dynamics are the results of processes occurring in the aquatic habitat and that regular dispersal events occur between patches (Smith & Green 2005), amphibians suitable for are models metapopulation studies because they lend themselves particularly well to a pond-as-patch based framework (Gill 1978, Sinsch 1992, Sjögren-Gulve 1994, Skelly et al. 1999, Marsh & Trenham 2001).

The European tree frog, for example, has been shown to be structured in metapopulation with regular local extinctions and recolonization events taking place at breeding sites (Borgula 1993, Carlson & Edenhamn 2000, Vos et al. 2000, Schmidt and Pellet in press). A metapopulationbased approach to population dynamics is therefore likely to provide useful insights for wildlife managers (Driscoll 1997, Marsh & Trenham 2001, Storfer 2003, **Chapter 6**). Understanding the role of dispersal and the contribution of individual patches to the overall persistence of tree frog metapopulations provides clear indications for their conservation (**Chapter 6**).

Amphibian decline is "a global problem with complex local causes" (Alford & Richards 1999). This certainly holds true for the European tree frog in Switzerland. Research, as well as conservation managers, must therefore look for multiple answers to the alarming loss of our indigenous herpetofauna.

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CHAPTER 1



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Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence

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Abstract

Monitoring programs serve to track changes in the distribution and abundance of species. A major problem with most monitoring programs is that species detection is imperfect and some populations are inevitably missed. Therefore, in most monitoring programs the true distribution of a species will be underestimated. Here, we report a field test of the reliability and performance of a commonly used method to monitor the distribution of amphibians (anuran call surveys). We surveyed the distribution of four anuran species in western Switzerland, and estimated detection probabilities to account for imperfect species detection and used these estimates to adjust our estimate of site occupancy (i.e., distribution). Next, we assessed how detection probabilities were affected by weather and how site occupancy was affected by site specific covariates. For one species (*Hyla arborea*), call surveys proved efficient in determining the regional distribution with only few site visits because detection probabilities were relatively high. The call surveys apparently missed many populations of another common species (*Bufo calamita*) because detection probabilities were lower. Two other species (*Bombina variegata* and *Alytes obstetricans*) were uncommon and strong inference from the analysis is not possible. Thus, multispecies surveys may be inefficient for rare species. Estimates of detection probabilities were used to calculate how many site visits are necessary to infer the absence of a species with some predetermined statistical certainty. The implications of "false absences" are important in ecology as they are known to bias usual habitat suitability models and overestimate extinction/colonization events in metapopulations. Large-scale monitoring programs would benefit from the application of an estimation-based approach to monitoring the distribution of species.

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1. Introduction

Monitoring programs increasingly are used to assess trends in species abundance, distribution, and biodiversity (Gibbs et al., 1998; Hintermann et al., 2000; Yoccoz et al., 2001). Monitoring data are essential to identify key issues for policy and management goals, such as assessing priorities for conservation and land use, for environmental impact assessment, and for informing managers, policy-makers, and the general public about the state of nature (Stork and Samways, 1995). Two elements of a monitoring program are crucial to ensure that the goals can be achieved: clear specification of objectives and the collection of data

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from which reliable inference can be made (Thompson et al., 1998; Yoccoz et al., 2001; Pollock et al., 2002; Karanth et al., 2003).

It is often very difficult, if not impossible, to detect all individuals, populations, or species during a monitoring program (Preston, 1979; Nichols and Conroy, 1996; Yoccoz et al., 2001; Pollock et al., 2002; Williams et al., 2002). Hence, inference from such data will bias estimates of population and community parameters, wildlife-habitat models and metapopulation models (Yoccoz et al., 2001; Pollock et al., 2002; Karanth et al., 2003; Schmidt, 2003; Tyre et al., 2003; Gu and Swihart, 2004; Kéry and Schmid, 2004). The problem can be stated simply using the formula

$$E(C) = Np, \tag{1}$$

where E(C) is the expected value of a count (e.g., the number of ponds where a species was heard), N is the true value of the population parameter of interest (e.g., the number of sites occupied by a species) and p is a detection probability (Nichols, 1992). Because p is generally smaller than one and often variable, analysis of trends based upon these data is difficult at best (Yoccoz et al., 2001). In a trend analysis based on counts C, one assumes tacitly that detection probabilities p are constant. Although most monitoring uses standard methods, detection probabilities are never constant (MacKenzie and Kendall, 2002). A related problem is that one can detect the presence of individuals, populations, or species, but one can never be certain that individuals, populations, or species are truly absent rather than simply undetected (McArdle, 1990; Solow, 1993; Reed, 1996; MacKenzie et al., 2002; Kéry, 2002). The perfect monitoring program would identify sites where a species is present and those where it is truly absent. The estimation of detection probabilities can improve monitoring programs (Yoccoz et al., 2001; Pollock et al., 2002). Here, we address these issues using an example from an anuran call survey.

Amphibians are often considered reliable indicators of ecosystem health (Welsh and Droege, 2001). Moreover, a large number of amphibian species are declining or at risk of extinction because of human activity (Cooke, 1972; Blaustein and Wake, 1990; Alford and Richards, 1999; Houlahan et al., 2000; Collins and Storfer, 2003). This has lead to the creation of monitoring to determine the status of species and to improve conservation and management (e.g., Mossman et al., 1998; Dodd, 2003; Buckley and Beebee, 2004). Monitoring the distribution and abundance of anuran amphibians often involves registering the calling activity during the breeding season. Such call surveys are used to monitor both distribution and abundance (e.g., Lepage et al., 1997; Mossman et al., 1998; Hemesath, 1998; Stevens et al., 2002; Buckley and Beebee, 2004). Although calling facilitates detection of anurans, the frequency and intensity of calls may be influenced by date and time of day, survey length, observer experience, and other factors (e.g., Shirose et al., 1997; Bridges and Dorcas, 2000; Crouch and Paton, 2002; Genet and Sargent, 2003). The typical protocol of a study to assess the reliability of an anuran call survey is to visit a site many times or for much longer time period than is typical for a standard anuran call survey. Subsequently, the time until all species present at a site are detected is measured. Such information can be used to estimate the optimal allocation of survey effort (monitoring of birds is often also based on vocalizations and the same problems apply, e.g., Bart and Schoultz, 1984; Thompson et al., 1998; Nebel and McCaffery, 2003). Ideally, surveys should aim for high detection probabilities at peak calling periods. However, some uncertainty in the proportion of species that have been detected, and in the timing of peak calling, inevitably will remain (Mac-Kenzie et al., 2002).

Here, we present the results of a survey to determine the regional distribution of four anuran species. We estimated detection probabilities from repeated site visits and adjusted estimates of species' distributions accordingly (MacKenzie et al., 2002, 2003; Royle and Nichols, 2003; Tyre et al., 2003; Wintle et al., 2004). We then used the detection probabilities to determine the number of visits for adequate statistical power to reliably determine site absences. Taken together, these two elements of information are essential to design a monitoring program from which reliable inference is possible. Moreover, the method for inferring absence could be used in environmental impact assessment to shift the burden of proof. One may demand that a developer provides evidence that a species is absent from a site rather than providing evidence that a species is present.

The four anuran species we studied are prolonged breeders that differ strongly in their calls (Nöllert and Nöllert, 1992). Two species, the natterjack toad Bufo calamita and the tree frog Hyla arborea, have very loud calls that can be heard more than a kilometre away in good conditions. The calls of the other two species, the yellow-bellied toad Bombina variegata and the midwife toad Alytes obstetricans, are rather soft and have a low (Bombina) or high (Alytes) pitch. The four species often occur together in the same sites (Grossenbacher, 1988) and thus are suitable for comparative analysis. Here, we apply a rigorous statistical approach to estimate detection probabilities and site occupancy based on mark-recapture theory (MacKenzie et al., 2002) that proved to be very useful for the analysis of monitoring data.

2. Methods

2.1. Study area and field work

During spring, 2002, we surveyed 27 ponds in western Switzerland, between the villages of Allaman and Bière (Lat. N46°30'; Long. E6°25'). The study area covers a total of 396 km² (see Pellet and Neet (2001) and Pellet et al. (in press) for further information). Surveys were conducted for 15 min, beginning at sundown, on 32 nights from March 27 to June 18. Each site was visited on average 3.7 times (range 1–17) during the breeding season. Pond shores were walked systematically, and calling activity of all four species was recorded as present (1) or absent (0). Weather data were provided by Meteo-Swiss from the Changins weather station, 16 km from the centre of the study area. RAIN was computed as the sum of rainfall (in mm) during the day of the survey while TEMP was calculated as the mean temperature (in °C) from 3 measurements taken during the day of the survey (morning, noon and evening). During the days that preceded nights of fieldwork, average rainfall was 10.3 mm (median 0.05 mm, range 0-90.8 mm). Temperature during field work was on average 13.1 °C (median 12.8 °C, range 4.8-26.8 °C). RAIN and TEMP were weakly correlated ($R^2 = 0.093$, P = 0.045). Conditions during field work were not the same for the four species because of variation in breeding phenology (Table 1).

2.2. Data analysis

We used the mark-recapture-like approach of Mac-Kenzie et al. (2002) as implemented in program PRES-ENCE (available for download from http:// www.proteus.co.nz/) to estimate the proportion of sites occupied by each species. These models assume that a distribution is "closed" within a season, i.e., there are neither colonisations nor extinctions. Thus, for each species, we restricted analyses to the time span during which that species was active and calling in at least one site (MacKenzie et al., 2002). For Hyla and Alytes, all 32 survey nights were retained while only 28 and 14 nights were included in the analyses for *Bufo* and *Bombina*, respectively.

We defined a small set of a priori models we believed might explain site occupancy of the four species. First, we used the continuous covariates "distance to nearest road" (DIST2ROAD). Previous analysis showed this variable was strongly correlated with tree frog presence and absence (Pellet et al., in press). Second, we used the categorical variable NATURAL, which describes whether a site was man-made (e.g., gravel pits), or natural or originally man-made, but left undisturbed for many years. Some species are almost completely restricted to man-made habitat (Grossenbacher, 1988). The third model assumed no effect of DIST2ROAD or NATURAL. Mean DIST2ROAD was 0.111 km (SE 0.070; n = 14) for natural habitats and 0.084 km (SE 0.054; n = 13) for gravel pits (two-sample *t*-test, P = 0.277).

To model detection probability, we developed three models. In the first model, we assumed that detection probability was constant (p). In the second and third, we assumed that detection probabilities were affected by temperature during the day (TEMP) or by the amount of rainfall (RAIN), respectively. Both temperature and rainfall affect anuran calling and hence detection probabilities (e.g., Blankenhorn, 1972). The three models for occurrence and detection were combined to yield a total of nine candidate models.

Since the data set was small, we kept the candidate models simple (Anderson and Burnham, 2002). The pattern of species distribution is probably best described by models with multiple covariates and some relationships may be non-linear (e.g., Austin, 2002; Knapp et al., 2003), but such complex models require larger data sets (i.e., more sites surveyed).

We used Akaike's Information Criterion (AIC) to rank models and to calculate Akaike weights (Burnham and Anderson, 2002). Akaike weights are equivalent to Bayesian posterior model probabilities and indicate the relative support of a model (Burnham and Anderson, 2002; Wintle et al., 2003). The sum of the Akaike weights across all candidate models is one. Akaike weights were then used to calculate model-averaged parameter estimates (proportion of sites occupied, detection probabilities) and confidence intervals. Model-averaged confidence intervals take model selection uncertainty into account (Burnham and Anderson, 2002; Wintle et al., 2003).

Estimates of detection probabilities can be used to estimate, with a specified degree of confidence, the number of visits necessary to assert that a species is truly absent from a site (McArdle, 1990; Reed, 1996; Kéry,

Γa	ıble	1		

Weather conditions during field work

Species	Temperature (°C)				Rainfall (mm)			
	Mean	Median	Minimum	Maximum	Mean	Median	Minimum	Maximum
Hyla arboreal Alytes obstetricans	13.2	12.9	4.8	26.8	10.4	0.1	0.0	90.8
Bufo calamita	13.8	13.9	5.7	26.8	11.9	0.5	0.0	90.8
Bombina variegata	16.6	16.0	12.0	26.8	18.8	2.8	0.0	90.8

Conditions were the same for H. arborea and A. obstetricans.

2002). Assuming that visits are comparable and independent, the probability F of not seeing a species after N visits with detection probability p is

$$F = (1-p)^N.$$

If we want to be 95% confident that a species is absent, then F = 0.05. The above equation can be solved for the N_{\min} , the minimum number of visits necessary to be 95% certain that a species is absent,

$$N_{\min} = \frac{\log(0.05)}{\log(1-p)}$$

3. Results

The difference between the naïve proportion of ponds occupied (naïve in the sense that detection probability is assumed to be 1; i.e., the number of ponds where the species was detected), and the estimated proportion of ponds occupied varied considerably among species after accounting for imperfect detection (Table 2). Also, the models that explained the data best varied among species, but the estimated proportion of ponds occupied was consistent among models (Table 2).

3.1. Hyla arborea

This species was heard at 18 of 27 sites. Thus, the naïve proportion of sites used by this species is 18/ 27 = 0.67. During the period when *Hyla* was active, the sites were visited an average of 3.7 times (median 2, range 1–17). Tree frogs, if present, were detected an average of 3.3 times (median 2, range 1–15). Detection probability varied strongly with temperature (Fig. 1). The sum of Akaike weights of all three models including TEMP as a covariate for detection probability is 0.961. Hyla was detected more often on during warm nights (Fig. 1). In contrast, none of the factors thought to explain the proportion of ponds occupied was strongly supported by our data. All ψ (the estimated proportion of sites occupied) were within the range of less than 1 SE. The model averaged estimated proportion of ponds was slightly higher than the naïve proportion, but within the range of the standard error. With the small number of visits to each site, ψ tends to be positively biased (MacKenzie et al., 2002). Moreover, because we visited 27 ponds, naïve proportions can only take values which are a manifold of 1/27 (e.g., 0.666, 0.703, 0.740,...). Thus, some difference between the naïve and estimated proportion of sites occupied is expected. Therefore, we believe that we found all sites where *Hyla* breeds. This result is not surprising given the weather conditions under which field work was done and the high average detection probability ($\hat{p} = 0.743$).

Three visits at an average temperature of 13 °C were required to be 95% certain that a species was absent. However, since detection probability varied strongly with temperature (Fig. 1), the minimum number of visits declined with increasing temperature (Fig. 2).

3.2. Bufo calamita

This species was heard in 10 of 27 sites. Thus, the naïve proportion of sites used by this species is 0.37. During the period when Bufo was active, the sites were visited an average of 3.3 times (median 2, range 1-14) and Bufo, if present, detected an average of 2.0 times (median 1.5, range 1-5). Model selection was dominated by the effect of DIST2ROAD. Models including DIST2-ROAD had a joint Akaike weight of 0.628, indicating the species was more likely to occur further from roads. In contrast to tree frogs, there were no clear predictors of detection probabilities. All $\hat{\psi}$ were within the range of less than 1 SE. The model averaged estimated proportion of ponds occupied was much higher than the naïve proportion, suggesting that in many sites (23%) where the species occurs it was not detected. The estimated mean detection probability was 0.442. Thus, a minimum of 6 visits were required to be 95% certain the species was absent.

3.3. Bombina variegata

This species was heard in 3 of 27 sites. Thus, the naïve proportion of sites used by this species is 0.11. During the activity period of Bombina, the sites were visited an average of 1.2 times (median 1, range 1-4); the activity period of this species started in May whereas all other species were already active in late March or April, thus reducing the dataset to only 14 survey nights. Bombina, if present, was detected an average of 1.7 times (median 1, range 1-3). The model selection yielded no clear pattern because the models did not converge to good parameter estimates and the variance-covariance matrix could not be calculated in PRESENCE. We present the results of the PRESENCE analysis in Table 2, but refrain from an interpretation. For example, some estimates of detection probabilities were 0, which suggests that the entire analysis is probably of questionable value.

3.4. Alytes obstetricans

This species was heard in 3 of 27 sites. Thus, the naïve proportion of sites used by this species is 0.11. During the activity period of *Alytes*, the sites were visited an average of 3.7 time (median 2, range 1–17) and *Alytes*, if present, detected an average of 4.33 times (median 6, range 1–6). Model selection suggests that *Alytes* occurs more often in anthropogenic habitats (gravel pits and

 Table 2

 Model selection and parameter estimation of site occupancy

Model	ΔΑΙC	W	$\hat{\psi}$	$SE(\psi)$	Difference		\hat{p}
					Absolute	Proportional	
<i>Hyla arborea</i> (naïve $\psi = 0.667$)							
$\psi(.)$ p(TEMP)	0.000	0.476	0.730	0.100	0.06	-0.09	0.742
ψ (NATURAL)p(TEMP)	0.913	0.302	0.717	0.097	0.05	-0.07	0.745
ψ (DIST2ROAD)p(TEMP)	1.913	0.183	0.732	0.100	0.06	-0.09	0.741
ψ(.)p(.)	7.181	0.013	0.740	0.101	0.07	-0.10	0.713
ψ (NATURAL)p(.)	7.940	0.009	0.729	0.098	0.06	-0.09	0.715
$\psi(.)p(RAIN)$	8.913	0.006	0.740	0.102	0.07	-0.10	0.716
ψ (DIST2ROAD)p(.)	9.088	0.005	0.742	0.102	0.08	-0.10	0.712
ψ (NATURAL)p(RAIN)	9.679	0.004	0.729	0.099	0.06	-0.08	0.719
ψ (DIST2ROAD)p(RAIN)	10.811	0.002	0.742	0.102	0.08	-0.10	0.716
Model averaged			0.726	0.099			0.742
Bufo calamita (naïve $\psi = 0.370$)							
ψ (DIST2ROAD)p(.)	0.000	0.224	0.482	0.116	0.11	-0.23	0.439
ψ (DIST2ROAD)p(TEMP)	0.078	0.215	0.478	0.114	0.11	-0.23	0.464
ψ (DIST2ROAD)p(RAIN)	0.340	0.189	0.484	0.115	0.11	-0.24	0.425
$\psi(.)$ p(.)	1.768	0.093	0.501	0.133	0.13	-0.26	0.425
$\psi(.)p(RAIN)$	1.931	0.085	0.501	0.129	0.13	-0.26	0.413
$\psi(.)$ p(TEMP)	1.951	0.084	0.491	0.128	0.12	-0.25	0.452
ψ (NATURAL)p(.)	3.474	0.039	0.516	0.141	0.15	-0.28	0.419
ψ (NATURAL)p(TEMP)	3.684	0.035	0.503	0.135	0.13	-0.26	0.447
ψ (NATURAL)p(RAIN)	3.722	0.035	0.511	0.135	0.14	-0.28	0.409
Model averaged			0.489	0.122			0.438
Bombina variegata (naïve $\psi = 0$.	.111)						
ψ (DIST2ROAD)p(TEMP)	0.000	0.146	0.248	0.134	0.14	-0.55	0.000
ψ (NATURAL)p(TEMP)	0.041	0.143	0.265	0.159	0.15	-0.58	0.000
ψ (DIST2ROAD)p(.)	0.249	0.129	0.241	0.130	0.13	-0.54	0.421
ψ (NATURAL)p(.)	0.284	0.127	0.263	0.171	0.15	-0.58	0.384
ψ (NATURAL)p(RAIN)	0.386	0.121	0.234	0.122	0.12	-0.53	0.001
ψ (DIST2ROAD)p(RAIN)	0.406	0.119	0.224	0.109	0.11	-0.50	0.840
$\psi(.)$ p(TEMP)	1.134	0.083	0.335	0.220	0.22	-0.67	0.000
ψ(.)p(.)	1.449	0.071	0.320	0.217	0.21	-0.65	0.382
$\psi(.)$ p(RAIN)	1.747	0.061	0.264	0.143	0.15	-0.58	0.943
Model averaged			0.260	0.154			0.288
Alytes obstetricans (naïve $\psi = 0$.111)						
ψ (NATURAL)p(TEMP)	0.000	0.281	0.130	0.067	0.02	-0.14	0.574
ψ (NATURAL)p(RAIN)	0.744	0.194	0.132	0.068	0.02	-0.16	0.566
ψ (NATURAL)p(.)	0.950	0.175	0.127	0.066	0.02	-0.13	0.569
$\psi(.)$ p(TEMP)	1.790	0.115	0.142	0.078	0.03	-0.22	0.566
$\psi(.)p(RAIN)$	2.752	0.071	0.139	0.077	0.03	-0.20	0.561
ψ(.)p(.)	2.769	0.070	0.138	0.076	0.03	-0.20	0.562
ψ (DIST2ROAD)p(TEMP)	3.789	0.042	0.142	0.079	0.03	-0.22	0.566
ψ (DIST2ROAD)p(RAIN)	4.747	0.026	0.139	0.077	0.03	-0.20	0.561
ψ (DIST2ROAD)p(.)	4.769	0.026	0.138	0.077	0.03	-0.20	0.562
Model averaged			0.133	0.071			0.568

 ΔAIC is the difference between the model with the lowest AIC and the given model, w is the Akaike weight, ψ is the estimated proportion of sites occupied and the SE(ψ) the standard error thereof, absolute difference is ($\hat{\psi} - na\ddot{v}e\psi$) and relative difference (1 – $(na\ddot{v}e\psi/\hat{\psi})$), and \hat{p} is the estimated detection probability.

alike), but this results is based on only three sites where the species is present.

There was no clear pattern which covariates would best predict detection probabilities. Again, we cannot make any conclusive statement regarding the importance of the covariates. The $\hat{\psi}$ were within the narrowest range of all four species. The model averaged estimated proportion of ponds is slightly higher than the naïve proportion, but within the range of the standard error. As with Hyla, we believe that we found all the sites where *Alytes* occurs. Given the conditions under which field work was done, the estimated mean detection probability was 0.570. Thus, a minimum of four visits were required to be 95% certain the species was absent.

Most information on detection probabilities is obtained from sites where the species is detected at least



Fig. 1. The relationship between temperature and detection probability for the treefrog (± 1 SE), *H. arborea.* Estimation of the detection probability is based on model ($\psi(.)$, p(TEMP)) which has an Akaike weight w = 0.645.



Fig. 2. The relationship between temperature during the survey and the probability that treefrogs, *H. arborea*, have not yet been detected during the current and previous visits to a site. The probabilities of non-detection were calculated using the relationship between temperature and detection probability shown in Fig. 1.

once (B.A. Wintle, personal communication). Because *Alytes* was detected at only three sites, a careful interpretation of detection probabilities and the minimum number of visits to infer absence is warranted.

4. Discussion

4.1. The utility of anuran call surveys

The probability of detection varied strongly among species. The good news is that it is possible to detect all the sites where a species is present using call surveys with relatively few visits (e.g., *Hyla*, *Alytes*). The bad news is that in the same survey many populations of other species were overlooked (*Bufo*, *Bombina*). The statistical analysis revealed that many sites with *Bufo* were apparently missed. This may not be surprising, since six visits were necessary to infer absence of this species with 95% certainty, and sites were visited an average of only

3.3 times. Thus, even when using standardized methods, simple unadjusted counts alone cannot reliably be used to determine species distributions, but estimates of detection probabilities are needed. While we could model the covariates of site occupancy for three species (*Hyla*, *Bufo*, *Alytes*), the analysis is only reliable for two species (*Hyla* and *Bufo*). *Alytes* was detected at only three sites and more sites are needed to model the relationship between the distribution and habitat variables reliably (Harrell, 2001).

We expected that species detection would be correlated with call volume. This was not the case. Instead, overall calling behaviour, not the call per se, was most important. Both Alytes and Hyla call relatively constantly during the breeding season whereas Bufo calls infrequently. This is most obvious at the most frequently visited site, where both Hyla and Bufo occur. This site was visited 13 times during the breeding season of Bufo. Hyla was heard calling 13 times while Bufo was heard only five times. Large Bufo choruses only occur after heavy rains have filled temporary pools. Nonetheless, candidate models that included rain were not well supported by the data, probably because of the intrinsic temporal structure of breeding activity in this species (Sinsch, 1988). Additionally, only a subset of the males call during a night (Arak, 1988) and the duration of calling activity in a given night may vary from 20-500 min (Blankenhorn, 1972). Knowledge of the factors that affect detection probabilities can help to design efficient surveys. For example, the relationship between temperature and detection probability displayed (Fig. 1), may be used to determine ideal conditions for anuran call surveys. However, the explanatory power of covariates varied among species. Temperature clearly predicted detection probability of tree frogs (Fig. 1) whereas no environmental variable significantly predicted detection probability for other species. This implies that optimal survey conditions may vary among species.

4.2. Estimating the proportion of sites occupied by a species and inferring absence

We used the models of MacKenzie et al. (2002) to estimate site occupancy and reliably infer species absence. For three species (*Hyla*, *Bufo*, and *Alytes*) the analysis worked well. For the fourth species, *Bombina*, the analysis was not satisfactory, because of sample size limitations. This shows that when multiple species are surveyed in parallel, reliable inference may only be possible for the commoner species which are present at a sufficiently large number of sites. Rare species may require surveys that are designed specifically for these species.

With relatively few visits to the sites, standard errors were quite narrow and in the range expected from the simulation study of MacKenzie et al. (2002). Coefficients of variation depended strongly on $\hat{\psi}$: CV was lowest for *Hyla* (13%), intermediate for *Bufo* (25%), and highest for *Alytes* (54%). The simulations of MacKenzie et al. (2002) lead us to expect that adding more visits to sites would not reduce standard errors (and hence, CV).

The statistical methods we used assume that there are no false positives, i.e., species should not be recorded as present when they are in fact absent. Given our experience with the species, we believe that this assumption was met in our analyses. However, Genet and Sargent (2003) found that volunteers falsely recorded species at sites where they were not present. The mark-recapture approach that we have used can deal with false negatives (i.e., species present but not detected) but not with false positives. Future site occupancy models should allow for false positives.

Because detection probabilities were relatively high (Table 2), it is possible to infer species absence with relatively few site visits. If detection probabilities are much lower, then financial constraints on the monitoring program may preclude a sufficient number of site visits to infer species absence. However, if a development project threatens a site where an endangered species occurs, it would still be possible to reverse the burden of proof and demand that the development company provide evidence that a species is absent from a particular site with a statistical certainty (Dayton, 1998; Kéry, 2002).

The detection probabilities we estimated are based on a single season of field work. Before they are used to design a monitoring program, variation in detection probabilities among years should be assessed. MacKenzie et al. (2003) found that detection probabilities of the salamander *Ambystoma tigrinum* varied strongly between two years ($\hat{p} = 0.27$ and 0.65, respectively). Consequently, the number of visits necessary to be 95% certain that *Ambystoma tigrinum* was absent from a site was 10 and 3, respectively.

4.3. The importance of an estimation-based approach to monitoring

With multiple visits to the ponds, it was possible to detect all populations (or rather choruses) of two out of four species, namely *Hyla* and *Alytes*. If conditions for field work are selected appropriately (e.g., temperature >20 °C), the entire regional distribution of *Hyla* might be determined with >95% confidence using a single visit to each site (Fig. 2) without a need for statistical analysis. Nevertheless, we believe that an estimation-based approach, such as MacKenzie et al. (2002) models that we used, is superior to other approaches, for several reasons. First, the same survey may yield good data for some species whereas populations of other species remain undetected (*Bufo, Bombina*; see also Heimbucher, 1986). Here, it is important to estimate detection probabilities and adjust the counts accordingly. Second, an

estimation-based approach also gives a standard error or confidence interval. This allows gauging of how much confidence is warranted in the results of the survey. Third, the estimate and confidence interval of site occupancy are independent of the method used. Thus, in a long-term monitoring program, different methods could be used in different years. It is also possible to use slightly different protocols (e.g., time spent at a site) or even different methods at different sites and incorporate such differences as covariates in the analysis. Whereas the counts are likely to differ, the estimates should not.

A statistical approach to the analysis of monitoring and survey data is important. However, it cannot replace a thorough knowledge of the natural history, calling behaviour, and phenology of the species (e.g., Shirose et al., 1997; Bridges and Dorcas, 2000; Crouch and Paton, 2002). Such knowledge and statistical analysis should go hand-in-hand as they can strengthen each other.

4.4. Implications for large-scale monitoring programs

Large-scale monitoring programs are often expensive. They should provide good quality data and allow the inference they were designed for (Yoccoz et al., 2001; Pollock et al., 2002; Kéry and Schmid, 2004). Estimating population sizes at multiple locations using mark-recapture methods is often prohibitively expensive (but see Royle, 2004; Dodd and Dorazio, 2004). Monitoring presence-absence of species is easier and cheaper and a commonly used approach to monitoring (Thompson et al., 1998; Campbell et al., 2002). If costs of multiple visits are high, then detection probabilities may only be estimated at a subset of the sites (Pollock et al., 2002). However, during most monitoring programs and surveys, sites are often visited multiple times during a season anyway, so basing inference on estimation methods (e.g., MacKenzie et al., 2002; Royle and Nichols, 2003; Tyre et al., 2003) comes at no great cost. Estimation approaches also provide a means of involving volunteers (Lepage et al., 1997; Mossman et al., 1998; Genet and Sargent, 2003; Kéry and Schmid, 2004) without suffering substantial bias in inference.

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Chapter 2
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Multiscale determinants of tree frog (*Hyla arborea* L.) calling ponds in western Switzerland

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Abstract. A tree frog (*Hyla arborea* L., 1758) metapopulation in western Switzerland was studied during spring 2001. All potential calling ponds in an area of 350 km^2 were searched for tree frog calling males. Twenty-nine out of 111 ponds sheltered between 1 and 250 callers. Most ponds were occupied by less than 12 males. Pond parameters were measured at three different levels using field analysis and a Geographical Information System (GIS). The first level was water chemistry and pond-associated measures. The second level was the surrounding land use in a 30 m buffer around the pond. The third level consisted of landscape indices on a broader scale (up to 2 km). Logistic regression was applied to identify parameters that can predict the presence of calling males in a pond. Response variable was the presence or absence of the observed occupational pattern. Urbanization around the pond had a highly negative impact on the probability of presence of calling males. Hours of direct sunlight on the pond was positively correlated with callers. Higher water conductivity was associated with a lesser probability of species presence. Finally, the further the closest two-lane road, the higher the probability of callers presence. Our results show that presence of callers is influenced by factors acting at various geographical scales.

Introduction

Highly endangered in Switzerland (Duelli 1994), the European tree frog (*Hyla arborea*) has been disappearing from its distribution range over the last decades (Berthoud and Perret-Gentil 1976; Grossenbacher 1988). What once was a continuum from eastern to western Switzerland is now a series of more or less isolated metapopulations. The western-most of these metapopulations is now limited to a 350 km^2 area (Pellet and Neet 2001). Figure 1 shows the current distribution of tree frogs in Switzerland and the study area.

Tree frog population decline has been studied by many authors (reviewed by Borgula 1993) and has proved to be occurring at different geographic scales. Factors that influence tree frog populations at the pond level are, among others, predation (Tester 1990; Brönmark and Edenhamm 1994), competition (Fog 1988; Pavignano et al. 1990; Tester 1990), water pollution (Stumpel and Hanekamp 1986; Tester 1990), eutrophication (Fog 1988),



Figure 1. Black dots indicate tree frog observations in Switzerland from 1998 to 2002. The study area is the western-most metapopulation. Data source: Swiss Amphibian and Reptile Conservation Program.

natural succession (Tester 1990; Grosse 1994; Geiger 1995) or simply destruction. It has also been proposed that terrestrial determinants at a local scale around the pond affect tree frog populations. Food availability (Borgula 1990), traffic (Borgula 1993), disturbances and reduction of suitable terrestrial habitat are the most cited causes (Borgula 1990; Tester 1990; Stumpel 1993). At an even broader scale, factors such as pond isolation (Borgula 1990; Tester 1990; Edenhamm 1996; Vos 1999) proved to be of influence. The loss of landscape dynamics (Borgula 1990) and/or disappearance of particular structuring elements such as hedgerows or forest borders have been proposed as potentially influencing factors for many other amphibians (Knutson et al. 1999; Pope et al. 2000; Joly et al. 2001). Most probably a combination of all these factors, including some unknown, is leading populations toward extinction.

On the Swiss plateau, the intensification of agriculture has direct influence on most water bodies. Whether water quality or general landscape changes are responsible for the observed population decline is not clear. Exploring parameters at different scales should allow us to identify relevant features and the scale at which they are acting.

Here we investigate ponds and their immediate surroundings to establish a statistical model that can predict the presence or absence of tree frog calling males with a limited number of predictors readily available from field evaluation. The adequacy of the model to evaluate ponds is discussed.

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Methods

Ponds identification and survey

Ponds were identified using various national and regional databases; national 1:25,000 maps, aerial photos, and field knowledge. All ponds were searched for calling males at least three times during the spring. Tape-recorded mating calls were used to stimulate isolated males (Tester 1990). All ponds where at least one calling male was heard were defined as occupied. Reproductive success or failure was not taken into account. All ponds were included in the analyses.

Ponds characterization

Three levels of pond characterization were used. The first level considers only the water itself and the pond vegetation. At this level, water conductivity and pH were measured using a HACH conductimeter (model 44600) and a ME-TROHM pH-meter (model 691). For both, the final value is the mean of three measurements taken around the pond. Percentage of vegetation cover on the pond was estimated visually. Mean hours of direct sunlight on the pond was estimated with the help of a solar compass (calibrated for latitude 47° N) positioned at the southern-most end of the pond. This procedure allows to visually estimate for any given month the hours of the day when the sun is obscured by tree, building or hills. The shore development index was calculated as:

$$\text{SHOREDEV} = \frac{\text{PERIMETER}}{2 \cdot \sqrt{\text{AREA} \cdot \pi}}$$

A shore development index equal to 1 indicates a circular pond. A higher development indicates that the pond shores are longer than expected for a circular pond with the same area as the one measured.

The second level describes the surroundings of the pond in a 30 m buffer, corresponding to the potential daytime refuge of individuals (Fog 1993) during the calling season. This set of parameters was computed via ground-proofed aerial photos interpretation. The third level is used to measure parameters on a broader scale of 2 km. This last set of measures describes the part of the landscape that is potentially reachable by migrating tree frogs (Fog 1993; Vos 1999). Geographical data originated from vector translation of national 1:25,000 maps (VECTOR25) for which precision is estimated to 4 m (Office Fédéral de la Topographie 2000). Levels of description and predictors are described in Table 1. In total, 35 predictors were measured on the field or using a GIS (Geographical Information System: MapInfo 6.0 and Idrisi32).

Table 1. Parameters measured and associated level of description.

Parameter	Description	Scale
AGRIC	Percent of agricultural landuse in a 30 m buffer	2
ALTITUDE	Altitude	1
BUSHES	Percent of bushes in 30 m buffer	2
BUSHVEG	Bushes overhanging the pond	1
CONDUCTIVITY	Mean water conductivity (μ S/cm)	1
COUNTPOND	Number of ponds in 2 km buffer	3
COUNTSAT	Number of satellite ponds in 30 m buffer	2
DEPTH	Depth	1
DIST2FOREST	Distance from the nearest forest	3
DIST2POND	Distance from the nearest pond	3
DIST2RIVERS	Distance from the nearest river	3
DIST2ROAD	Distance from the nearest two-lane road	3
DISTURBAN	Distance from the nearest village	3
DISTURBEDLANDUSE	Percent of disturbed landuse in 30 m buffer	2
DIVSAT	Typological diversity of satellite ponds	2
ERECTEDVEG	Erected vegetation cover over the pond	1
FISH	Fish presence (yes/no)	1
FLOATINGVEG	Floating vegetation cover	1
FOREST	Percent of forest in 30 m buffer	2
GRAVELPITS	Percent of gravel pits landuse in 30 m buffer	2
HYDRIC	Water source (categorical)	1
LAKE	Percent of lake in 30 m buffer	2
LENGTHROAD	Total length of two-lane roads in 2 km buffer	3
MARSH	Percent marshes in 30 m buffer	2
MEADOWS	Percent of meadows in 30 m buffer	2
PERIMETER	Perimeter of the pond	1
РН	pH	1
QUANTRUBUS	Categorical quantity of <i>Rubus</i> sp.	2
SHOREDEV	Shore development index	1
SUN	Hours of sunlight during mating season	1
SURFACE	Surface	1
TREECOVER	Tree cover over the pond	1
TYPEPOND	Type of pond (categorical)	1
URBAN	Density of urban landuse in a buffer of 30 m around the pond	2
WINTERDRYING	Drying of the pond in winter 2000-2001 (yes/no)	1

Statistical analysis

The presence (1) or absence (0) of calling males in a pond was analyzed using stepwise logistic regression (Sokal and Rohlf 1995). We first tested all predictors individually in an univariate logistic regression and retained for further analysis only those whose *p*-value was lower than 0.25 (Hosmer and Lemeshow 1989). We entered all remaining predictors in the model (in a decreasing explained deviance order) and removed in a backwards stepwise fashion all those whose *p*-value was higher than 0.05. The significance of the explained

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Table 2. Results of logistic regression for calling sites selection by males of *H. arborea* in western Switzerland.

Variable name	Regr. coef.	SE	Expl. dev. (%)	p(expl. dev.)	Wald χ^2	p(Wald)
URBAN	-0.229	± 0.108	21	< 0.001	4.483	0.037
SUN	0.382	± 0.123	12	< 0.001	9.666	0.002
CONDUCTIVITY	-5.201	± 1.723	8	0.005	9.115	0.003
DIST2ROAD	0.012	±0.005	8	0.006	7.187	0.009

Null deviance = 127.51, residual deviance = 78.58, $D^2 = 0.38$.

Variables are density of urban landcover in a buffer of 30 m around the pond (URBAN), hours of direct sunlight during mating season (SUN), conductivity (mS/cm) of the water (CONDUCTIVITY) and distance (m) from the nearest two-lane road (DIST2ROAD). p(Wald) values test the linear component of the regression.

deviance of each of the predictors was tested in a 1000 permutations on the response variable (Guisan and Zimmermann 2000; Jaberg and Guisan 2001).

Evaluation of the model was made using a resubstitution of the dataset following methods described by Mondserund and Leemans (1992), Fielding and Bell (1997) and Pierce and Ferrier (2000). This method includes the computation of an occupational probability for each pond. This probability is converted to a presence/absence value using a threshold calculated via the kappa-statistic (Mondserund and Leemans 1992). It is then possible to compare predicted values versus observed ones in a confusion matrix. Misclassification indices can finally be calculated to evaluate the goodness-of-fit of the statistical model.

Correlation analysis was made using a Spearman rank correlation (Sokal and Rohlf 1995) at a 5% confidence level.

Results

A hundred and eleven ponds were identified in a 350 km^2 area. A little more than a quarter (28) of these sheltered at least one calling male during spring 2001. Most choruses were composed of less than 12 callers. One exceptional pond was used by more than 200 callers.

Logistic regression allowed us to identify four significant predictors (Table 2) for calling site selection. A fairly large proportion (38%) of the total deviance is explained by these parameters. The most important predictor is the density of urbanized surfaces in the immediate surroundings of the pond (URBAN). The exposure of the pond to sunlight (SUN) explains more than 10% of the deviance. Measured electrical conductivity (CONDUCTIVITY) seems to have a negative impact on caller presence. Finally, the probability of calling males being present increases with distance from roads (DIST2ROAD).

The kappa-statistic allowed us to compute a threshold value that optimizes the reclassification of the ponds in the right categories (presence or absence) based on the predicted occupation probabilities. With a 0.7 threshold ($\kappa_{\text{max}} = 0.524$), the false positive rate (unoccupied ponds with a predicted value higher than 0.7) is as low as 1.2% while the total misreclassification rate is 15.2%.

Discussion

The presence of urbanized (waterproofed) surfaces around the pond seems to have a negative impact on tree frog calling males. Although it seems trivial that artificialized areas are unsuitable for tree frog, there can be two reasons for this. First, callers face the absence of suitable terrestrial habitat (the quality of which is unknown here). Second, it could be possible that the human presence accompanying urbanized areas has a direct impact on populations in a way that is not yet known. Either way, creating private ponds in urban areas may not necessarily be an effective way of establishing new tree frog choruses.

The total hours of sunlight on the pond during the reproductive season positively influences the presence of callers. This feature has already been highlighted by many authors using different measurement techniques (Stumpel and Hanekamp 1986; Fog 1988; Tester 1990; Grosse and Nöllert 1993; Zysset 1995). It can be explained by the warming of the water and the potentially faster development of the tadpoles (Moravec 1993). Metamorphosing earlier, the larvae are less subjected to predation and reproductive success is higher.

A negative impact of conductivity in Zealand Flanders populations was also highlighted by Vos and Stumpel (1996). In their case, conductivity was highly correlated with chloride ions resulting from seawater flooding and seepage. In our study area, conductivity indirectly measures dissolved organic and mineral ions of another type. In gravel pits and quarries on limestone bedrocks, conductivity is mainly due to dissolved Ca^{++} , HCO_3^{-} and CO_3^{2-} . In agricultural landscapes, high conductivity usually indicates a high nitrates (NO₃) load resulting from agricultural runoffs (Tchobanoglous and Schroeder 1985). This hypothesis is supported by the observed correlation between agriculture intensivity around the pond (AGRICULTURE) and measured conductivity (CONDUCTIVITY). A Spearman rank correlation between these two parameters showed significance with a correlation coefficient of $r_s = 0.303$ (p < 0.05). This tends to support the hypothesis that organic pollution via agricultural effluent can be high in such landscapes. The presence of effluents in water is potentially troublesome, as it indicates that pesticides and herbicides are probably being washed from fields in the same way. The lethal effects of some of these organic chemicals on tree frog larvae have been studied by Tester (1990) and could explain these results. Conductivity is also generally considered a measure for eutrophication. The proliferation of algae can cause acute anoxia in the morning due to oxygen consumption by algae and could be responsible for a lower larvae surviving rate.

The proximity to roads showed a negative impact on the caller probability of presence. Whether this is because of direct mortality due to traffic (Fahrig et al.

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1995; Findlay and Bourdages 2000), although no casualties have been observed on potentially dangerous roads, or because of some unknown indirect effect is unclear. The creation of an index measuring traffic load around each pond would probably allow us to gain insights into the specific role played by vehicles.

The statistical model obtained is altogether satisfying, as it is able to correctly reclassify about 85% of the ponds with only four parameters that are pretty easily acquired in the field. One should also be aware that resubstitution methods tend to give relatively optimistic evaluation of models because of overfitting and loss of generality (Fielding and Bell 1997). However, this method permitted the identification of potentially suitable ponds for callers (not necessarily successful reproduction). This ability was validated by a colonization event in spring 2002 in a pond for which the model predicted a false presence in 2001. This clearly shows that such a model can be a tool for conservation in that it can help identify potentially suitable ponds for tree frogs. The best validation of the model would be to compute occupational probabilities for ponds situated in another metapopulation in Europe (included in a similar agricultural landscape). Comparing predicted and observed presence/absence patterns in another region would allow us to have an independent evaluation to validate the model. One should nevertheless be aware that such a model is developed at a regional scale (the Swiss plateau) and so cannot be simply applied to another type of landscape to calculate pond quality for tree frogs. It is more than likely that other limiting factors than those described here are affecting frog populations in other places.

This method and the obtained model show that determinants in calling sites selection can be found at various scales in the landscape. Here, parameters related to the water body (CONDUCTIVITY, SUN), its surroundings (URBAN) and adjacent landscape (DIST2ROAD) proved significant. It suggests that many mechanisms affect the calling sites selection by males of tree frogs.

Exploring landscape elements densities systematically at scales varying from pond to the potential dispersal distance of tree frog will certainly allow us to identify determinant structures and, even more important, the range at which they influence tree frog populations. Further analyses should also take into account the size of the choruses as well as (and even especially) the reproductive success, as the latter has the greatest importance in conservation policies.

Acknowledgements

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CHAPTER 3

A Concentric Analysis of the Impact of Urbanization on the Threatened European Tree Frog in an Agricultural Landscape

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Abstract: Pond-breeding amphibians are affected by site-specific factors and regional and landscape-scale patterns of land use. Recent antbropogenic landscape modifications (drainage, agriculture intensification, larger road networks, and increased traffic) affect species by reducing the suitable babitat area and fragmenting remaining populations. Using a robust concentric approach based on permutation tests, we evaluated the impact of recent landscape changes on the presence of the endangered European tree frog (Hyla arborea) in wetlands. We analyzed the frequency of 1 traffic and 14 land-use indices at 20 circular ranges (from 100-m up to 2-km radii) around 76 ponds identified in western Switzerland. Urban areas and road surfaces bad a strong adverse effect on tree frog presence even at relatively great distances (from 100 m up to 1 km). When traffic measurements were considered instead of road surfaces, the effect increased, suggesting a negative impact due to a vebicle-induced effect. Altogether, our results indicate that urbanization and traffic must be taken into account when pond creation is an option in conservation management plans, as is the case for the European tree frog in western Switzerland. We conclude that our easy-to-use and robust concentric method of analysis can successfully assist managers in identifying potential sites for pond creation, where probability of the presence of tree frogs is maximized.

Key Words: amphibian conservation, calling males, circular buffers, Hyla arborea, traffic density, urban areas

Un Análisis Concéntrico del Impacto de la Urbanización sobre la Rana Arborícola Europea Amenazada en un Paisaje Agrícola

Resumen: Los anfibios que se reproducen en charcas son afectados por factores específicos del sitio y por patrones a nivel región y paisaje. Modificaciones antropogénicas recientes del paisaje (drenaje, intensificación agrícola, redes carreteras más extensas e incremento de tráfico) afectan a las especies al reducir el área de bábitat adecuado y fragmentar a las poblaciones. Evaluamos el impacto de cambios recientes en el paisaje sobre la presencia de la rana arborícola Europea (Hyla arborea) en bumedales mediante un método concéntrico robusto basado en pruebas de permutación. Analizamos la frecuencia de 1 índice de tráfico y 14 índices de uso de suelo en 20 parcelas circulares (de 100 m basta 2 km de radio) alrededor de 76 charcas identificadas en el oeste de Suiza. Las áreas urbanas y las superficies de carreteras tuvieron fuertes efectos adversos sobre la presencia de tráfico en lugar de las superficies de carreteras, el efecto aumentó, sugiriendo un impacto negativo debido a un efecto inducido por vebículos. En general, nuestros resultados indican que la urbanización y el tráfico deben ser considerados cuando la creación de charcas es una opción en los planes de gestión de conservación, como es el caso para la rana arborícola Europea en el oeste de Suiza. Concluimos que nuestro

*email jerome.pellet@ie-zea.unil.cb Paper submitted September 16, 2003; revised manuscript accepted March 25, 2004. método concéntrico de análisis, fácil de usar y robusto, puede ayudar a que gestores identifiquen exitosamente sitios potenciales para la creación de charcas, donde se maximice la probabilidad de presencia de ranas arborícolas.

Palabras Clave: amortiguamientos circulares, áreas urbanas, conservación de anfibios, densidad de tráfico, *Hyla arborea*, machos llamadores

Introduction

Decline in local and regional amphibian fauna has been documented by herpetologists and conservation biologists worldwide (Blaustein et al. 1994; Alford & Richards 1999; Houlahan et al. 2000; Blaustein et al. 2002; Green 2003). In densely populated landscapes, such as the Swiss agricultural plateau, most amphibian species show a clear geographical range contraction (Grossenbacher 1988). Uniformly distributed throughout Switzerland at the beginning of the twentieth century, the European tree frog (Hyla arborea) is now restricted to a few metapopulations completely isolated from one another (Pellet & Neet 2001), with local populations undergoing regular extinctions and recolonization events (J.P. & N.P., unpublished data). The tree frog is therefore considered a highly endangered species in Switzerland (Duelli 1994) and has been protected since 1968.

Habitat loss or deterioration and landscape fragmentation are the leading factors in local population extinction (Dellis et al. 1996; Alford & Richards 1999; Semlitsch 1998; Semlitsch & Bodie 1998). As for the tree frog, many causes of decline have been identified at the pond scale, such as fish introduction (Brönmark & Edenhamn 1994), competition (Fog 1988; Pavignano et al. 1990; Tester 1990), water pollution (Stumpel & Hanekamp 1986; Tester 1990), eutrophication (Fog 1988), and natural succession (Tester 1990; Grosse 1994; Geiger 1995). At larger scales, factors such as the reduction of terrestrial habitat (Tester 1990; Borgula 1993; Stumpel 1993) and pond isolation (Edenhamn 1996; Vos 1999) are influencing tree frog distribution. It is also clear that landscapelevel changes in land use have direct and indirect effects on amphibian populations (Findlay & Houlahan 1997; Green 1997; Lehtinen et al. 1999; Pope et al. 2000; Johnson et al. 2002; Welsh et al. 2002; Pellet et al. 2004).

Recent anthropogenic modifications of the agricultural landscape in western Switzerland include transitions from grazed pastures and natural meadows to peri-urban developments or intensive crop plantations, drainage of marshes and wetlands, and road construction. Distribution of European tree frogs should reflect anthropogenic changes such as reduced terrestrial habitat (Vos 1999), impeded migration between ponds (Sjögren-Gulve & Ray 1996; Vos 1999), modified pond hydrology, and increased human disturbance.

We developed a concentric approach to evaluate the impact of land use on the presence or absence of tree

frogs in ponds. This method allows one to identify critical elements in the landscape to estimate the range at which they influence species distribution. Our goal was to evaluate to what extent these landscape modifications affect the European tree frog. Evaluating the effects of land uses on the presence of focal species should then allow us to determine how landscape management and amphibian conservation in a densely populated agricultural landscape could be improved.

Methods

Species

The European tree frog is one of the smallest terrestrial anurans (4-6 cm snout-to-vent length) of Western Europe. Breeding, oviposition, and tadpole development take place in a wide range of wetlands, from gravel pits to lake shores (Grosse & Nöllert 1993). During the breeding period, males call conspicuously to attract gravid females (Schneider 1993). Counts of calling males are used to evaluate the size of breeding populations (Edenhamn 1996; Carlson & Edenhamn 2000). The terrestrial habitat consists of perennial herbs, shrubs, and hedgerows, almost always characterized by a high sun exposure, allowing individuals to bask during daytime (Stumpel 1993). Migrations to ponds occur during early April in Switzerland, and dispersal of breeders from the site usually happens 2 months later (Fog 1993). Metamorphs leave the water between July and August and can be found in the shore vegetation until the end of September. Dispersal of froglets to terrestrial hibernation sites usually occurs before the first night frosts.

Study Area and Census

Our study area was located in western Switzerland between the villages of Allaman and Bière ($46^{\circ}30'N$, $6^{\circ}25'E$) and covered 396 km², of which only 0.5% constituted amphibian breeding ponds. We identified ponds based on various national databases and field knowledge (Pellet et al. 2002).

The landscape is typical of the Swiss Plateau and is mainly agricultural, with medium-sized villages (200-2500 inhabitants) connected by a relatively dense communication network, including highways, primary roads, secondary roads, and railroads.

Tree frog censuses took place during the spring of 2001 and 2002. Each potential calling pond in the area was surveyed for tree frogs at least three times during the breeding season (mid-April to late June). Because a previous study estimated the detection probability to be as high as 0.94 for each visit (J. P. & B. Schmidt, unpublished data), this method ensured that tree frog presence was unlikely to go undetected (Edenhamn 1996). Ponds were defined as occupied (1) when at least one calling male was heard during one of the two field seasons. All other ponds were defined as empty (0). The presence of calling males is an indicator of reproductive activity that can be easily compared between ponds with variable shore accessibility. The presence or absence of calling male tree frogs was thus used as the binary response variable in further analyses.

Landscape and Traffic Data

Landscape data originated from the Vector25 database, which is the vector format of the 1:25,000 topographical maps of Switzerland. The database is provided by the Office Fédéral de la Topographie, and the precision of the data can be estimated at approximately 3-8 m in flat areas (SWISSTOPO 2003). We used a subset of the complete coverage containing only "primary surfaces," which includes basic land uses such as urban areas, forests, marshes, and arable lands. We aggregated these geographical data into 14 categories to reflect major changes in substratum (e.g., urban vs. agriculture) and potential human disturbance sources (e.g., road1class and railroads) (Table 1).

Traffic data were provided by the Service des Routes du canton de Vaud for all primary roads in the study area. For each first-class road segment in the geographic information system (GIS), the traffic load was expressed as a mean number of vehicles per hour (mvh).

Concentric Analyses

For our concentric method we created 20 circular buffers (from a 100-m radius up to a 2000-m radius, in 100-m increments) around each of our 76 study ponds. Radii up to 2 km are justified because this tree frog travels great distances (Fog 1993; Vos 1999). In each buffer, we calculated the frequency of all 14 land-use categories as the sum of the surface for a given land use divided by the surface of the buffer, and we repeated this operation for each of the 20×76 buffers. We also calculated a traffic impact index (traffic) inside each buffer as the sum of all road segments (in meters) multiplied by the mvh of each segment, the total being divided by the buffer area and by 10^6 for clarity (Table 1). Fourteen land-use frequencies and one traffic index calculated in 20 nested concentric buffers yielded a total of 300 predictors tested against tree frog presence or absence. We named predictors after the land use they described and the radius at which they were

lable 1.	The 15 lands	cape and land-use	e predictors	of tree frog
oresence	or absence.*			

Predictor abbreviation	Description
Ponds	number of ponds included in the buffer
Occupied ponds	number of ponds included in the buffer where tree frogs were detected at least once during the survey
Lake	frequency of lakes
Urban	frequency of urban areas (isolated houses or farms not included)
Vine	frequency of vineyards
Orchard	frequency of orchards
Road1class	total length of first-class roads divided by buffer area
Road2class	total length of second-class roads divided by buffer area
Marsh	frequency of marshes
Bush	frequency of bushes and hedgerows
River	total length of rivers divided by buffer area
Mineral	frequency of bare soil (gravel pits or military training grounds)
Highway	total length of highways divided by buffer area
Railroad	total length of railroads divided by buffer area
Traffic	sum of each first-class road segment multiplied by its traffic load, measured as mean number of vehicles per hour (mvh), the total being divided by buffer area

*Predictors are composed of the name of the land use they describe and the radius of the buffer at which they have been computed. Frequencies are calculated as the sum of the land use contained in the buffer, divided by the total buffer area.

calculated (e.g., forest 1700 represents the frequency of forests closer than 1700 m from a given pond).

To ensure that ponds were independently distributed over our landscape and not located in clusters of occupied and empty ponds (i.e., no spatial autocorrelation), we analyzed our data set to check whether the response variable could be predicted with pond-based variables. If this was not the case, the ponds could appropriately be considered independent of one another and the speciesenvironment statistical tests considered valid. To test that, we created two sets of predictors reflecting the density of both ponds and tree frogs (Table 1). The density of ponds was simply expressed by the number of ponds (empty and occupied) in each buffer (ponds), whereas tree frog density was expressed as the number of occupied ponds in each buffer (occupied ponds). We computed these predictors at each radius in the same fashion as the landscape predictors and analyzed them statistically in the same way. Ponds can be considered independent units (which validates our statistical inferences) if none of these two sets of predictors affect tree frog presence.

Statistical Methods

To determine the influence of land use on tree frog presence or absence, we used binary logistic regressions (Sokal & Rohlf 1995). All predictors whose univariateexplained deviance (D^2) and regression coefficient were both significant at the 5% level were kept as relevant models (Hosmer & Lemeshow 1989). Because the number of predictors used was relatively high in relation to our sample size, we then validated the remaining significant models with the permutation methods described by Jaberg and Guisan (2001). The permutation method recalculates the explained deviance of each fitted model with 1000 random permutations of the response variable (in our case, the presence or absence of callers). When explained deviances higher than the one measured occur in more than 5% of the permutations, the model cannot be considered robust because the observed deviance can be statistically observed by chance alone. Such an empirical randomization test allows the selection of only the most robust models because it is more restrictive than traditional statistical inferences.

Results

Tree frog choruses were heard in 27 of the 76 study ponds (prevalence of 36%). None of the first set of predictors (ponds and occupied ponds) were significantly correlated with presence or absence of tree frogs at any radius when the spatial distribution of ponds was analyzed. Of the 15 land uses and traffic indices we chose (Table 1), 4 (marsh, urban, road1class, and traffic) were significantly correlated with tree frog presence, at radii varying from 100 m to 1000 m (Table 2).

The frequency of marshes (marsh) had a significant positive effect on the presence of tree frogs when situated close to ponds. The amplitude of the effect was relatively low ($D^2 = 5\%$), and the two models based on marshes (marshes200 and marshes300) did not withstand the validation step, with probabilities of obtaining a higher explained deviance by chance alone being 6% and 10%, respectively.

The frequency of urban areas (urban) had a strong negative effect on the occurrence of tree frog presence. This effect was measured from a close range (100 m) up to 1000 m. The explained deviance of models based on urban areas was as high as 14% at 400 m. All models based on urban areas resisted the permutation step, emphasizing the amplitude of the observed effect, even at extreme radii (100 m and 1 km). The explained deviance of urban models increased up to 300 m and then decreased until becoming nonsignificant at the 1000-m threshold (Fig. 2). Models based on urban areas were not significant over the 1000-m threshold.

The density of first-class roads also showed a negative effect on chorus presence, but only at a range of 200 m.

 Table 2. Land use and traffic indices (concentric variable and radius)

 significantly correlated with presence of tree frogs.

Sign of the coefficient	Explained deviance (%)	Permutation resistance (p)*		
+	5	ns		
+	5	ns		
_	7	< 0.05		
_	9	< 0.05		
_	14	< 0.001		
_	14	< 0.001		
_	11	< 0.001		
_	9	< 0.001		
_	8	< 0.001		
_	8	< 0.01		
_	7	< 0.01		
_	5	< 0.01		
_	6	< 0.01		
_	5	< 0.05		
_	8	< 0.05		
_	6	< 0.01		
_	8	< 0.01		
	Sign of the coefficient + + - - - - - - - - - - - - - - - - -	Sign of the coefficient Explained deviance deviance (%) + 5 - 7 - 9 - 14 - 14 - 9 - 8 - 8 - 5 - 8 - 5 - 8 - 5 - 6 - 8 - 8 - 6 - 8		

*Abbreviation: ns, not significant.

The effect was low (only 6%) but resistant to permutation. When traffic data were used instead of surface density on first-class roads, the effect, still negative, rose up to 8%, and its range of influence widened from 100 m up to 400 m (Fig. 1). The geographical data used for both figures (road1class and traffic) were the same but were balanced by traffic indices in the traffic predictor. There were increasing differences of traffic load around empty and occupied ponds at the four significant radii (100-400 m) (Fig. 2).

By removing from the landscape all surfaces less suitable for tree frogs, we were able to geographically visualize the area with the maximum probability of tree frog presence. We adopted a conservative approach when drawing such maps by using buffer distances 100 m larger than the largest significant one (e.g., using 500 m when the largest significant traffic buffer was 400 m). Based on our models, we mapped all surfaces that were farther than 1100 m from urban areas and 500 m from first-class roads. Forests were also excluded from these surfaces because the European tree frog never reproduces in forest ponds (Grosse 1994). With this map we located potential sites for pond creation, where landscape-scale factors would not adversely affect tree frog populations (Fig. 3).

The lake shores, being densely populated, present too dense a network of roads and urban areas to optimally suit tree frogs. Only the northwestern part, less developed, contains suitable surfaces. The remaining suitable portions of the landscape are relatively small and usually located near forest borders. These surfaces are mostly arable lands and pastures. Only a few occupied ponds are located in the potentially suitable surfaces, so pond localization in our study area was not optimal.



Figure 1. Explained deviance of models based on urban areas, first-class roads, and traffic at 20 radii. Filled circles indicate significant models at 5% threshold; open circles indicate nonsignificant models.

Discussion

Our results obtained from the first set of predictors, which reflect pond and tree frog densities, emphasize that in our study area tree frogs are distributed regardless of pond density and conspecific individual local abundance. Hence, ponds can be regarded as independent of one another.



Figure 2. Traffic indices measured at four significant radii (100-400 m) around empty and occupied ponds (\pm 95% confidence interval). Traffic indices are calculated as the sum of all lengths of first-class road segment multiplied by their traffic load (mean vehicles per bour), the total being divided by the buffer area and 10⁶ for clarity.

By using one traffic and 14 land-use predictors readily available in most GIS, we were able to highlight the strong negative effect of anthropogenic land uses on tree frog presence in ponds. We also evaluated the range of influence of each land use with statistical models based on systematic concentric buffers.

Models based on the frequency of marshes explained only a relatively small part of the deviance and did not withstand the validation procedure with permutations. Edenhamn (1996) found a positive effect of marsh frequency on the regularity of reproduction of the European tree frog in southern Sweden. In our landscape, marshes are more scattered than in Sweden, usually located in less densely populated areas and in extensively exploited agricultural surfaces. It is probable that the low occurrence of marshes (zero values in the marshes predictors) in western Switzerland explains the fact that models based on this land use were not resistant to the permutation step.

The influence of urban areas had by far the strongest effect on tree frog presence. Our landscape is more densely populated than the landscapes in previous studies of tree frogs (Zealand Flanders, Netherlands: Vos 1999; southern Sweden: Edenhamn 1996), which thus increases the probability of finding a human-induced effect. The impact was significant up to 1 km (Fig. 1), a seemingly large distance for one of the smallest amphibians in Europe. This probably indirectly reflects changes in the landscape that affect tree frogs at a smaller, local scale (roadkill, pollution, noise disturbances).

Replacing first-class road densities with traffic data corresponding to the same roads increased the observed deviance from 6% to 8% and widened the range of influence from 200 m to 400 m. This result alone emphasizes the fact that not only do impermeable roads represent inhospitable habitat for tree frogs, but that vehicles are furthermore responsible for low densities of tree frogs. Whether direct mortality on roads (Fahrig et al. 1995; Hels & Buchwald 2001) or indirect impacts such as pollution and/or disturbance are responsible for this pattern is unknown, although in some road segments of our study area massive tree frog casualties have been observed. Vehicular traffic can have a highly variable impact on amphibians, depending on the vagility of the species (Carr & Fahrig 2001). Because the European tree frog is one of the most vagile species in Europe (Fog 1993), it might be more sensitive to traffic loads. Similarly, a negative effect of road proximity to breeding ponds on the probability of tree frog presence has been found (Pellet et al. 2004). Together, theses two studies show clear adverse effects of traffic abundance on tree frog populations.

The use of circular buffers assumes that the landscape has an isotropic effect on the tree frog, so that the species is affected by landscape elements equally in every direction from a given pond. It is probable that frictions in the landscape—such as barriers or inhospitable surfaces reduce movement patterns and reshape the ideal circular surface we used in this study into a noncircular form reflecting the actual use of the landscape matrix by tree frogs. These kinds of shapes could be modeled with friction algorithms based on the permeability of land uses to frog movements. Unfortunately, parameterization of such a home range is usually time- and cost-constraining because it requires intensive field work and expensive radiotracking materials (for the only published experiment with radiotracking of tree frogs, see Vos 1999).

Because our study was strictly correlational, the mechanisms of causality between predictors used and tree frog presence are mostly unknown and can only be hypothesized. The use of more proximal predictors more tightly related to the physiology of the species and/or including terrestrial habitats should give us stronger insights into the observed phenomena.

Because it is potentially applicable to any species functioning on a geographically defined patch basis, the concentric method proposed here should find many applications for identifying critical land-use units in highly heterogeneous landscapes, evaluating the range of influence of specific landscape elements, and, finally, mapping suitable areas for focal species. Although other studies have made use of buffers to study landscape patterns around amphibian breeding ponds (e.g., Vos & Stumpel 1995; Findlay & Houlahan 1997; Vos & Chardon 1998; Edenhamn 1996; Johnson et al. 2002), the use of systematic buffers at regular radii permits the evaluation of landscape effects and their range of influence on pond-breeding amphibians. It also allowed the mapping of potential areas for amphibian breeding sites, which is of great importance in conservation management. This is especially true for the European tree frog in western Switzerland, where the lack of breeding ponds seems to be an important



Figure 3. The study area in western Switzerland, distribution of studied ponds, illustration of the concentric design on one of the 76 ponds, and suitable locations for tree frog breeding ponds (distance of more than 1100 m from urban areas and 500 m from first-class roads).

cause of decline (Pellet & Neet 2001; Pellet et al. 2002). This lack of breeding ponds is emphasized by the low occurrence of ponds in the potentially suitable surfaces we mapped. The mapping method could be improved by the introduction of geographically defined probabilities of occurrence instead of the binary suitable-or-unsuitablesurfaces approach. This would facilitate fine-scale identification of areas less affected by adverse landscape parameters. Restricting the wetland creation effort to these areas would enable conservation managers to focus on a limited surface, maximizing the probability of tree frog presence. Combined with pond-level characterization and identification of dispersal corridors, the concentric method shows great potential in conservation plans that create new ponds suitable for breeding of *Hyla arborea* and possibly other species.

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CHAPTER 4

USE OF THE HARMONIC DIRECTION FINDER TO STUDY THE TERRESTRIAL HABITATS OF THE EUROPEAN TREE FROG (*Hyla arborea*)

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Although most amphibians spend a substantial part of their life in terrestrial habitats (Dodd and Cade, 1998; Semlitsch, 1998; Semlitsch and Jensen, 2001), herpetological research has mostly focused on breeding aggregations in wetlands (Duellman and Trueb 1986, Alford and Richards 1999). Consequently, very little data are available on the terrestrial ecology of most species (Gibbons 2003). This lack of information hinders the development and application of efficient amphibian conservation policies. Without proper conservation of terrestrial habitats, even the most common amphibian species are susceptible to decline (Johnson 2003). The need for extensive and scientific knowledge on amphibians' terrestrial habitats is extremely important in a context of evidence-based conservation (Pullin et al. 2004, Sutherland et al. 2004). Data on the use of terrestrial habitat by amphibians is unfortunately very hard to obtain without using labor- and cost-intensive methods such as telemetry (Heyer et al. 1994). Since the 1960s, authors have tried to address this issue by equipping amphibians with different tracking systems, which facilitate the location of cryptic animals. Thread bobbin trailing devices (Dole 1965), Co⁶⁰ radioactive tags (Karlstrom 1957, Barbour et al. 1969, Ashton 1975), fluorescent pigments (Eggert 2002), and radio emitter (Sinsch 1989, Vos 1999, Eggert 2002, Bulger et al. 2003, Schabetsberger et al. 2004) have been applied to a wide range of species. These methods have proven efficient in answering many ecological and behavioural questions but are limited by either the weight of the attached equipment (10% of individual's body mass, Richards et al. 1994) or its longevity (Dole 1965, Kenward 1987, White and Garrot 1990). More recently, experiments on insects (Lovei et al. 1997, Capaldi et al. 2000, Riley et al. 1996), reptiles (Engelstoft et al. 1998), frogs (Langkilde and Richards 2002) and toads

(Leskovar and Sinsch, in press) have used harmonic direction finders (HDF). Since this method is based on microwaves reflection and the attached transponder does not require batteries, the latter has a potentially endless life. Moreover, these devices are relatively lightweight making them potentially suitable for many small species, including amphibians. Here we present details of the development of a miniature harmonic transponder and describe its effectiveness in studying the terrestrial movements of the European tree frog (*Hyla arborea*).

The HDF is a portable scanning device originally developed for the rescue of avalanche victims which includes both an emitter and receiver (sold for \$6,660 by RECCO AB, Box 4028, SE-181 04 Lidingö, Sweden). The HDF sends a directional and polarized microwave at a precise frequency (870 MHz), which is doubled (1740 MHz) on hitting a reflector (or harmonic transponder). The reflected microwave is detected by the receiver which translates it into an acoustic signal. The user evaluates the amplitude of the reflected microwave beam to determine directionality. The transponder consists of a schottky diode (model R2 RECCO AB) soldered between a base plate and a perpendicular wire antenna, the whole system creating an electrical dipole costing ~\$2. The wire antenna is mounted vertically to obtain optimum detection range and is wound at its base to form a small helix which acts as a small spring, giving more flexibility to the antenna. Beryllium bronze (BzBe) is used for both the base plate and for the radiating wire, because of its high conductivity and mechanical elasticity. This latter property guarantees that the antenna recovers its original shape after being bent during animal's movements through dense vegetation. The length of the antenna and the small size of tree frogs (~4 cm snout-to-vent, and weight ~6 g) prohibit

implantation of transponders. Cyanoacrylate glues cause skin damage to Ranidae and Hylidae (U. Sinsch, pers. com.). Thus, we used waistbands to attach transponders, which have proven useful for similar studies (Fukuyama et al. 1988, Hodgkison and Hero 2001). Waistbands are made of gauze from which the cotton linings are removed. The advantage of this material is its elasticity and the fact that it degrades over a few weeks freeing the animals of their equipment if not recaptured after some time.



Figure 1: The elements of a waistband-fixed anuran harmonic transponder.

We tested two aspects of field operation: detection range vs. antenna length and waistband retention time. We first ran systematic trials in which we measured transponder detection range vs. wire antenna length. Second, waistband retention time was tested in terrariums after field experiments started, because we observed an increasing number of detached waistbands in the field. To evaluate the efficiency of the waistband attachment method, 18 tree frogs were captured and kept in a terrarium in which vegetation cover mimicks the field in which they had been captured. Frogs were marked with transponders and waistbands and were checked daily for 3 weeks to document the rate of waistband loss.

To study capabilities of HDF use in the field we captured and monitored movements of frogs during the breeding season and during post-breeding migration. Our study took place in 2004 in one of Switzerland's federally protected amphibian spawning ponds. Located east of the village of Lavigny (46°30' N; 6°25' E, see Pellet and Neet, 2001) this breeding pond is a natural meadow depression where ground water emerges temporally from winter to early summer. The surrounding landscape is agricultural, mostly with fields of wheat and corn. Some patches of natural meadow and hedgerow are present in low density, along with two riparian forests. Frogs were captured at dusk on the shore of

the pond. Because of the cryptic behaviour of females during the breeding season, only males were marked with transponders. Frogs were manipulated and released at their capture locations after 5 minutes. Date, time and GPS location of the capture/release point were recorded on a Trimble GeoExplorer GPS system with a precision of ~1 m. During the rest of the breeding season (mid-April to the end of May in western Switzerland) the pond shores and the surrounding landscape were systematically scanned for frogs concealed in the vegetation three times a week during at least 4 hours of daylight. Once a signal was detected, and given the directional signal of the HDF, it was possible to locate transponders by regularly reducing the transmitted power and homing on the target in a centripetal fashion until the animal was discovered and identified with the number tag glued on the post-breeding transponder. То study migration, 15 frogs were detained until 4 weeks after the end of the breeding season (last caller heard) and then one marked frog was released each night on the shore of the pond. We surveyed the movements of the released frogs every 5 minutes from dusk to dawn. At dawn, the observed path and last location of the animal were recorded.

The harmonic transponder and waistband we constructed (Figure 1) weighed ~0.11 g and represented ~1.8% of an average tree frog's body mass (6 g). Detection ranges

increased according to antenna length. When placed on the ground, detection range reached 10 m with a 3 cm antenna and increased linearly up to 30 m with a 10 cm antenna. Detection range was generally tripled when the transponder was placed at a 0.8 m height. We decided to opt for a 5.2 cm antenna, an empirical optimum between equipment dimension and tree frog size and weight. With this configuration, detection range was 12 m when the transponder was on the ground and 34 m when the transponder was 0.8 m high, which is concordant with the results obtained by Leskovar and Sinsch (in press) with similar equipment. Waistband retention time as observed in the terrarium proved sufficient to track frogs for several days at the most (mean retention time \pm SD = 7.6 \pm 3.6 days, range: 1-14 days). At the end of the two weeks trial, only two out of 18 frogs still had a functional waistband. The loss of transponders was a result of development of swollen legs and subsequent removal of waistbands (n=12), selfremoved waistbands (n=2), and turned-over waistbands (n=2). This loss rate is somewhat better than Leskovar and Sinsch (in press) achieved with cyanoacrylate glues on juveniles of Bufo calamita and B. viridis.

During the breeding period, 29 frogs were marked, of which 26 were recaptured at least once in the following 6 weeks (mean recapture occasions \pm SD = 2.5 \pm 1.4, range: 1-7 recaptures). Four animals were found dead. We thus gathered 79 locations of daytime localities. Most of the recaptured animals had moved <40 m from the release point. In general, tree frogs males did not move far from their spawning site during the breeding season. Fog (1993) compiled data on observed breeding tree frogs <22 m from the pond in nearly 20 incidental daytime observations. Our results from systematic monitoring confirm this range (we found 90% of our marked frogs within this area) and also indicate that very few animals move >30 m away from the pond at this time of the year.

During the first night following their release, the 15 frogs that we marked to study post-breeding migration moved between 18 and 440 m. Ten frogs were lost by dawn of the following day. Of the 5 frogs remaining, 3 were found up to 48 hours after they were released, either in natural meadows (n=2) or corn crops (n=1), but never >50 m from their release points. The last two frogs moved 860 and 660 m in less than 14 and 40 hours, respectively. Movements were southwest to the vicinity of a riparian woodland where frogs stayed for >3 days and were thus considered to have reached their post-breeding habitat (Figure 2).



Figure 2: Diurnal locations of breeding tree frogs (small white dots) around the pond (hatched area). Path taken by animal during post-breeding dispersal to summer habitats (white rhombus indicate release point, small black circles are post-breeding locations of frogs lost during migrations, large black circles are locations of frogs on summer ranges).

Because our sample size of marked male frogs that arrived at post-breeding habitats was low (n=2), we cannot generalize the terrestrial habitat needs of the European tree frog. Both marked frogs moved to the same riparian woodland, but this could have been due to chance. Nevertheless, our observations of migrating frogs in spring corroborate these results. We observed >20 frogs in 2001-2004 migrating to the ponds across the access road exactly where they would be expected had they come in a straight line from the same woodland (Pellet et al. unpubl. data). Tree frogs also have been heard calling from the canopy of ash trees (Fraxinus excelsior) (Pellet et al. unpubl. data), which is consistent with observations of Schmidt et al. (2003), who discovered tree frogs 30 m up in the tree canopy. These observations are also consistent with Stumpel (1993) who indicates high air humidity, high intensity of sunlight and complex vegetation structure as determinants of tree frog terrestrial habitats. Although females have also been incidentally observed in this riparian wood, there are no indications so far about sex differences in use of these terrestrial habitats (Stumpel 1993).

We believe it is important that every potential means to help identify amphibian terrestrial habitat be evaluated. Because telemetric studies are time-consuming, but can provide unbiased and quality movement information, they should be justified only after assessing the effort-knowledge ratio. In this context, the HDF technology and transponders attachment method for anurans needs to be improved in order to achieve larger detection range and longer equipment retention time. Even though limited in lifespan, we believe that small-sized (less than 0.3 g) radio-emitters still constitute our best tool to uncover terrestrial habitats of small anurans, given a reliable attachment method. Only when such tracking tools are available will we be able to identify the terrestrial habitats cryptic and vagile species such as the European tree frog. The development of efficient and evidencebased amphibian conservation strategies depends on it.

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CHAPTER 5

DENSITY, CLIMATE AND VARYING RETURN POINTS: AN ANALYSIS OF LONG-TERM POPULATION FLUCTUATIONS IN THE THREATENED EUROPEAN TREE FROG

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Abstract

Causes of decline in amphibian populations around the world have been a major field of research in recent decades. The complex and highly fluctuating nature of amphibian populations have long hindered the understanding of underlying population-level regulation mechanisms. The scarce availability of long time series limits the possibilities of statistically powerful and biologically meaningful analysis. Here we analyzed a 22 year-long time series of calling males counts of the European tree frog (*Hyla arborea*) in order to detect density-dependence patterns, while allowing for climatic covariates. Using Dennis and Taper's method (1994) combined with an information-theoretic approach, we were able to identify a combination of extrinsic (amount of rainfall) and intrinsic (loglinear density-dependence) factors accounting for >70% of the variance in population dynamics. Hence, population size fluctuates around a return point which varies through time. Such a varying return point might explain the seemingly erratic fluctuations in many amphibian populations.

Key-words

Density dependence, amphibian, model selection, population viability analysis, weather, population regulation, population fluctuations

INTRODUCTION

Declines in amphibian natural populations have extensively been documented over different parts of the globe (Blaustein and Wake 1990, Houlahan et al. 2000, Stuart et al. 2004). Although possible causes for decline have been suggested (Collins and Storfer 2003, Semlitsch 2003, Stuart et al. 2004), inference is based largely on experimental studies of the effects of natural and anthropogenic stressors on single vital stages (eggs or larvae). It is unknown whether individual effects detected under experimental conditions translate into effects in natural populations. While population models and mark-recapture analyses of long-term data help understand the relative contributions of different demographic parameters to population growth (Biek et al. 2002, Vonesh and De la Cruz 2002, Hels and Nachman 2002, Conroy and Brook 2003, Grafe et al. 2004,

Halpern et al. 2005, Schmidt et al. in press), time series analyses of amphibian populations are still rare. Time series analyses can provide information on whether and how intrinsic (i.e., density) and extrinsic factors (i.e., weather, anthropogenic stressors) affect population dynamics. Understanding the relative importance of intrinsic and extrinsic processes is important because the interplay between factors determines whether a population goes extinct or remains stationary (Dennis and Otten 2000, Bjørnstad and Grenfell 2001, Blaustein and Kiesecker 2002, Lande et al. 2003). Intrinsic factors, such as density dependence, may buffer against negative impacts of anthropogenic stressors (Anderson and Burnham 1976, Forbes and Calow 2002, Vonesh and De la Cruz 2002).

In striking contrast to many other groups of organisms where the analysis of time series of natural populations has been a major source of information on the relative

importance of the mechanisms underlying population dynamics (Bjørnstad and Grenfell 2001), the effects of intrinsic and extrinsic factors on amphibian population dynamics have rarely been assessed at the population level using time series analysis based on longterm data sets (Jaeger 1980, Semlitsch et al. 1996, Meyer et al. 1998). Combinations of factors have only rarely been the focus of a long-term amphibian population data analysis (Blaustein et al. 1994). This is especially unfortunate, because it is well known that single-factor analysis can be misleading (Hilborn and Stearns 1982). Such analyses are also of importance to conservation biology by providing the foundations upon which realistic population models, necessary to simulate population dynamics and estimate extinction risks, can be built (Akçakaya and Sjögren-Gulve Gärdenfors 2000, 2000. Beissinger 2002, Lande et al. 2003, Henle et al. 2004).

Here, we present an analysis of a longterm time series (22 years) of a population of the European tree frog (Hyla arborea L., 1758). Using recently developed statistical tools for short time series (Dennis and Taper 1994, Dennis and Otten 2000), we compare models that represent hypotheses about the action of different extrinsic and intrinsic factors and how they affect population dynamics. Namely we test whether (and how) density dependence and climatic variables affect the dynamics of this population, either alone or in combination.

METHODS

Tree frog monitoring

The European tree frog is listed as "near threatened" in the global IUCN Red List, and can be considered highly vulnerable in most of distribution (IUCN, 2004) including its Switzerland (Grossenbacher 1988) where the status on the Swiss Red List is "endangered" (Schmidt and Zumbach 2005). H. arborea first breeds at 2 years of age and has a life expectancy of 5-6 years (Friedl and Klump 1997). Tadpole growth and juvenile metamorphose usually take place between early June and late September. Juveniles disperse before the first night frosts to their terrestrial overwintering habitats (Stumpel 1993), where they will remain until late March. As with most frogs and toads, males of the European tree frog exhibit a conspicuous breeding behavior by calling from pond shores to attract gravid females (Giacoma et al. 1993). Counts of calling males is considered an appropriate technique for evaluations of tree population density (Carlson frog and Edenhamn 2000, Tester 1993) and is actually one of the most widely used methods to assess population size in anuran populations (Heyer et al. 1994). Visiting ponds regularly during the breeding season (mid-March to late May in Switzerland: Pellet et al. 2004) provides several counts of calling males, from which the highest value for a given year is generally used as an index of breeding population size (Tester 1993, Edenhamn 1996, Carlson and Edenhamn 2000, Schmidt and Pellet 2005).

We studied an isolated population in western Switzerland (Lerchenfeld near Thun, 46°45' N, 7°35' E) from 1979 until 2004. Calling males were counted multiple times (range 1-4, mean=1.52) during the season by the same observer (KG) in all years. The maximum count was used for analysis, as described above. In our population, breeding choruses were small, making it easy to individually count calling males accurately. The proportion of satellite males, the mean time spent at the pond, and the overall probability of breeding are assumed to have remained roughly constant through years. Because new breeding ponds were created in the area in the winter of 2000, the dataset was restricted to the time frame where carrying capacity of the habitat was expected to have remained stable (1979-2000 thus reducing it to a 22 year-long time series, Figure 1).

Statistical analysis and candidate models

We used models of the general form (Dennis and Taper 1994, Dennis and Otten 2000): $ln(N_{t+1} / N_t) = a + bN_t + cW_t + \sigma Z_t$, where N_t is population size at time t, W_t is a climatic covariate, Z_t is a normal (N~0,1) random noise variable, and a, b, c and σ are the coefficients to be estimated.

We built a set of candidate models and used information-theoretic model selection to determine which model describes the data best (Burnham and Anderson 2002). We first built a density independent null model which assumes stochastic exponential growth or decline, where slopes of N_t (*b*) and W_t (*c*) in equation 1 were constrained to be zero (model H0; Dennis and Taper 1994). We then tested for linear and loglinear density dependence (Saitoh et al. 1997). The linear function between growth rate $(ln(N_{t+1}/N_t))$ and N_t corresponds to Ricker's (1954) density dependence model (model H1), while the loglinear model is obtained by replacing N_t in the right-hand part of equation 1 with the logabundance index transformed $X_t = ln(N_t)$ (Gompertz 1825, Saitoh et al. 1997, model H2). The third group of candidate models tested the effect of climatic variables. The first climatic model (model H3) represents the hypothesis that population growth rate is affected by rainfall during the larval period in year t-2. Rainfall is considered a general proxy for weather conditions which may affect tadpole performances and survival (Semlitsch 1985, Reading & Clarke 1995, Reading & Clarke 1999, Friedl and Klump 1997, Donnelly and Crump 1998, Tryjanowski et al. 2003). We expect a negative effect of the total amount of summer rainfall (from April to July) on future adult population size with a 2-year lag. Our second climatic model tested the influence of the pond water level during the period of tadpoles' development (H4) on population growth rate. Here, the underlying hypothesis is that water level reflects pond volume which in turn is supposed to reflect the carrying capacity of the pond for tadpoles. Since the pond under study is located close to the river Aar (<50 m) and share its water table, we used the mean river water level from April to July (again with a two-year lag). Both rainfall and water level are weakly correlated by 13%, suggesting that pond water level is not influenced by atmospheric precipitations. The third climatic model (model H5) tested the effect of winter temperature on population growth rate. Cold winters are known to negatively affect the survival of adult frogs (Anholt et al. 2003). We used mean daily temperature from October to March, obtained from the Payerne weather station (46°49' N, 6°56' E) provided by MeteoSwiss. Mean temperatures (°C) during winter months (October through March) and total amount of rainfall (mm) during spring and summer (April through July) were calculated for each year. The fourth group of models represented the hypotheses that both intrinsic (density) and extrinsic (weather) variables affect population growth (model H6-H11). These candidate models combined density and weather variables as shown in Table 1.

We used the second-order Akaike information criterion (AICc; Hurvich and Tsai 1989) and Akaike weights (a posterior model probability; Burnham and Anderson 2002) for ranking candidate models, and R² to estimate the proportion of variance explained. Testing for the significance of a regression slope between growth rates and population size (Equation 1) has been shown to be statistically flawed because of autocorrelation, producing an excess of type I errors (Dennis and Taper 1994). Thus, the statistical significance of the density-dependence slope b was estimated by the parametric bootstrap likelihood ratio test (PBLR, 10,000 bootstraps) described in Dennis and Taper (1994) and Dennis and Otten (2000). The analysis as well as the computer-intensive PBLR procedure was implemented in the statistical package R (R Development Core Team 2004).

RESULTS

All 9 candidate models, parameter estimates (Equation 1), model selection criteria and R² are presented in Table 1, in increasing AIC_c order. Models that include both density (Ricker or Gompertz type) and rainfall effect perform best among our candidate models with a cumulated weight of 0.981. Gompertztype density dependence was far better supported by the data than Ricker-type density dependence (evidence ratio = 57; Burnham and Anderson 2002: p. 77). With an R^2 of 73%, the best model indicates that a large part of the variance is explained. Models that included density only or environmental covariates only had virtually no support from the data (all Akaike weights < 0.003).

Parametric bootstrap likelihood ratio tests indicate that the coefficient of b (density) in H6, H9 and H11 is statistically significant with estimated P-values of 0.0041, 0.0001 and 0.0031 respectively. Density dependence was not significant in our simple density dependence model H1 (Ricker type) with P=0.0713 while the simple Gompertz model (H2) showed statistically significant density dependence with P=0.0086.

As expected under the hypothesis of density dependence, the effect of density on population growth rate was negative (Table 1); the stronger support for the Gompertz model suggests that density dependence in tree frogs is loglinear. Rainfall negatively influenced population growth rate (Table 1).

Table 1: Model selection and parameter estimates of all candidate models. Models are ranked in an increasing AIC_c order. w is the Akaike weight of the model. "Type" refers to the form of density dependence.

	Predictors	Туре	Intercept	Density slope	Rain slope	Temperature slope	Water level slope	σ	R ²	AIC _c	ΔAIC_{c}	w
H9	Density and rainfall	Gompertz	4.653	-0.913	-0.01	-	-	0.213	73%	37.588	-	0.974
H6	Density and rainfall	Ricker	3.327	-0.058	-0.01	-	-	0.313	60%	45.708	8.120	0.017
H11	Density and water level	Gompertz	872.236	-1.188	-	-	-1.582	0.390	50%	47.801	10.214	0.006
H2	Density only	Gompertz	2.416	-0.863	-	-	-	0.441	43%	49.817	12.230	0.002
H10	Density and temperature	Gompertz	2.432	-0.868	-	-0.012	-	0.441	43%	52.900	15.313	0.000
H8	Density and water level	Ricker	858.718	-0.069	-	-	-1.562	0.505	35%	53.266	15.679	0.000
H1	Density only	Ricker	0.997	-0.051	-	-	-	0.561	28%	54.856	17.268	0.000
H3	Rainfall only	-	1.898	-	-0.01	-	-	0.583	25%	55.682	18.095	0.000
H7	Density and temperature	Ricker	0.953	-0.050	-	0.059	-	0.558	28%	57.841	20.254	0.000
H0	Random walk	-	-0.013	-	-	-	-	0.774	0%	58.878	21.290	0.000
H4	Water level	-	-177.84	-	-	-	0.324	0.770	0%	60.118	22.531	0.000
H5	Temperature only	-	-0.068	-	-	0.157	-	0.754	3%	61.073	23.485	0.000

If there is a negative relationship between density and population growth rate, the population is expected to fluctuate intrinsically around a return point (Dennis and Taper 1994) which can be viewed as the population's carrying capacity: R = -a/b. In the population under study, the return point is dependent on rainfall, an extrinsic factor. The expected return point for model H9 can be computed as $R_i = \exp\left[-(\hat{a} + \hat{c}W_i)/\hat{b}\right]$ with W_t being the total amount of rainfall two years

before surveys; \hat{a} , \hat{b} , \hat{c} being the estimated intercept and coefficients. Moreover, the return point, R_t , fluctuates between 3 and 42 callers depending on the amount of rainfall two years before (rounded to the nearest integers; Figure 1). The mean return point $\hat{R}_t = \exp\left[-(\hat{a} + \hat{c}\hat{W}_t)/\hat{b}\right]$ (where \hat{W}_t is the mean amount of rainfall during the study interval) is 17 (to the nearest integer).



Figure 1: Tree frog calling males counts in Lerchenfeld from 1979 to 2000 (bars) and expected return point (lines and dots). The return points are based on model H9 which has an AIC_c weight of 0.974 (Table 1). The arrow on the y-axis indicates the position of the mean return point (based on model H9).

DISCUSSION

Our results suggest that the magnitude of population fluctuation in the European tree frog is affected by a combination of intrinsic and extrinsic factors, which cause variation in the return points around which the population will fluctuate. While there is abundant evidence that density and/or extrinsic factors affect single vital rates or life cycle stages (e.g., Smith 1983, Petranka 1989, Berven 1990, Van Buskirk and Smith 1991, Beebee et al. 1996, Anholt et al. 2003, Altwegg 2003, Reading 2003, Grafe et al. 2004), our study is one of the few to show that these factors also affect population growth rate (e.g., Jaeger 1980, Semlitsch et al. 1996, Meyer et al. 1998).

We expected and observed a negative relationship between the amount of rainfall during the larval period and future population growth (e.g. Semlitsch et al. 1996). Our explanation is that pond water temperature will be colder during rainy springs and perhaps coupled with lower productivity. This would lead to a delayed metamorphosis of tadpoles (Moravec 1993, Reading & Clarke 1995, Reading 2003) and hence a lower weight before winter, which could in turn lead to a lower juvenile survival (Smith 1987, Altwegg and Reyer 2003).

Our best model explains alone 73% of the total variance of the population dynamic, leaving only 27% of unexplained variance for other environmental variables and demographic stochasticity. These results have very important implications when modeling demographic amphibian structured (meta)populations. So far, most models deal rather simply with density dependence. Conroy and Brook (2003), Griffiths (2004) and Hatfield et al. (2004) included ceiling type dependence density when modeling population and metapopulation dynamics. Other modeling approaches have simply ignored density (Biek et al. 2002). Since the results of population viability analyses may critically depend on the way density dependence is modeled (Henle et al. 2004), we believe that incorporating loglinear density dependence is a key to improve these population models.

Here we show that not only does density affect growth rate at the population level, but also that it acts in combination with lagged climatic variables. This is relatively good news for this threatened species since density dependence is known to buffer small populations against extinction (Henle et al. 2004). However, Gompertz type density dependence will also lead to a lognormal distribution of population size (Halley and Inchausti 2002) which in turn leads to a higher extinction risk (Halley and Inchausti 2002, Lande et al. 2003). This is even truer when the amplitude of population fluctuation is wide (Leigh 1981, Schoener and Spiller 1992, Inchausti and Halley 2003). Populations are likely to show very large amplitude of fluctuations when the return point around which they fluctuate is fluctuating itself. In the case of the tree frog population we analyzed, the return point was not fixed ($\hat{R} = 17$) but

varying through time ($R \subset [3; 42]$, Figure 1). It is therefore no surprise that populations of the tree frog are very likely to go extinct, especially when small (Carlson and Edenhamn 2000, Schmidt and Pellet 2005). Moreover, if the dynamics of a natural population are driven by both intrinsic and extrinsic factors, then the likely effect of a novel anthropogenic stressor is not easy to predict. The population may or may not be able to compensate for additional mortality; potential compensation is determined by the strength of density dependence. An extrinsic factor could lead to a population decline if it causes the return point to decline or it may lead to stronger fluctuations. Under either scenario, demographic or environmental stochasticity may then cause the population to collapse and go extinct.

The fact that we found evidence for density-dependence contrasts with other studies on the population dynamics of amphibians breeding in temporary ponds. Pechmann and Wilbur (1994) and Alford and Richards (1999) argued that the dynamics of anurans breeding in temporary ponds is largely driven by stochastic variation in recruitment. There is empirical support for the mechanisms leading to such a pattern (e.g., Berven 1990, Semlitsch et al. 1996, Alford and Richards 1999). Green (2003), however, argued that this model for amphibian population dynamics is unlikely to be general. He found that positive and negative population growth were equally common. Such a rates distribution of population growth rates could result from fluctuations around a return point. Population fluctuations driven by stochastic factors, such as under the models of Pechmann and Wilbur (1994) and Alford and Richards (1999), would not show such a pattern (Houlahan et al. 2001, Green 2003).

The interplay of extrinsic and intrinsic factors that affect population dynamics of the tree frog and that cause fluctuations in the return point may be a general explanation for the often erratic fluctuations of amphibian populations. This fact has two consequences. First, the effect may be that population

fluctuations appear erratic and determined by stochastic extrinsic factors. Nevertheless, intrinsic factors have a much stronger effect on population fluctuations than hitherto thought. Second, varying return points cause population fluctuations that go beyond the fluctuations caused by density dependence alone. Hence, the regional persistence of amphibians may be fundamentally dependent on a metapopulation structure where rescue effects allow the species to persist at a regional scale (Marsh and Trenham 2001, Smith and Green 2005). This would suggest that dispersal is of fundamental importance for amphibian conservation. Indeed, Green (2003) found that small anuran populations fluctuate widely in size, such that they should go extinct often (Leigh 1981, Schoener and Spiller 1992, Inchausti and Halley 2003) unless dispersal is much higher than commonly thought (Smith and Green 2005). However, a rescue-effect metapopulation structure is only likely if the environmental covariate does not lead to a synchronization of population dynamics across large scales (Bjørnstad et al. 1999).

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CHAPTER 6

THE CONTRIBUTION OF PATCH TOPOLOGY AND DEMO-GRAPHIC PARAMETERS TO PVA PREDICTIONS: THE CASE OF THE THREATENED EUROPEAN TREE FROG.

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Abstract

Population viability analyses (PVA) are increasingly used in metapopulation conservation plans. Two major types of models are commonly used to assess vulnerability and to rank management options: population based stochastic simulation models (PSM such as RAMAS or VORTEX) and stochastic patch occupancy models (SPOM). While the first set of models relies on explicit intrapatch dynamics and interpatch dispersal to predict population levels in space and time, the latter is based on spatially explicit metapopulation theory where the probability of patch occupation is predicted given patch area and isolation (patch topology). We applied both approaches to a European tree frog (*Hyla arborea*) metapopulation in western Switzerland in order to evaluate the concordances of both models and their applications to conservation. Although based on different paradigms and input data, the two approaches were largely concordant regarding ranking of equilibrium patch occupancy, population sizes and sensitivity to input parameters. We conclude that explicit intrapatch demographic modeling is only necessary when the relative contributions of demographic rates are to be determined. Global metapopulation dynamics are more robustly and easily assessed with lightly parameterized models such as the SPOM, which, in addition, provide a rapid evaluation of the potential contribution of any new patch to the stability of the metapopulation.

KEYWORDS

PVA, RAMAS, SPOM, extinction, colonization, dispersal distance, *Hyla arborea*, patch occupancy, population size, Switzerland

INTRODUCTION

Metapopulation modeling is being increasingly used for the development of wildlife conservation strategies (McCullough 1996, Akçakaya and Sjögren-Gulve 2000, Beissinger and McCullough 2002). The understanding of the mechanisms underlying extinction, dispersal and colonization in metapopulations is a key issue that needs to be addressed in order to estimate wild populations' vulnerability. To address this issue, two major types of population viability analyses (PVA) are being used: population based stochastic simulation models (PSM) and stochastic patch occupancy models (SPOM) (Akçakaya and Sjögren-Gulve 2000).

PVA based on species-specific data have been intensively exploited in metapopulation frameworks during the last decade, mainly because user-friendly softwares were made available (e.g. VORTEX and RAMAS: Lindenmayer et al. 1995, Akçakaya 2002). Quantitative methods such as PSM present many advantages, including the ability to encapsulate all data and knowledge available for a given species and explicitly modeling intra- and inter-patch dynamics. It also allows identifying, through sensitivity analysis, specific demographic parameters on which conservation action are most likely to be effective in order to prevent species extinctions. However, PSM suffer the drawback of requiring large amount of population-level demographic data (e.g. fecundity, survival), information on population dynamics (e.g. stage structure, density dependence, dispersal, environmental and demographic stochasticity...) in order to provide meaningful results. In PSM, the focus is mostly set on population and demographic processes rather than on habitat patches. Local populations can be structured in age classes, and demographic rates are assumed to be identical among all individuals of a given age class. Corresponding year-to-year transition matrices can be formulated in order to reflect the life history of the focal species, assuming discrete time steps. Environmental and demographic stochasticity is also implemented in those models (Akçakaya 2000, Akçakaya 2002). Such models aim at describing global population dynamics by modeling both local population dynamics and dispersal. This kind of PVA has been applied to a wide range of species among which birds, butterflies and mammals share an important part (Akçakaya et al. 2004). Because in most cases estimates of vital rates and/or original population sizes were inaccurate, uncertain or lacunar, the application of such models was mostly done through sensitivity analyses in order to assess vulnerability, rank management options or plan data collection (Akçakaya and Sjögren-Gulve 2000).

Along with the development of spatially realistic metapopulation theory (Hanski 2001, Hanski and Ovaskainen 2003) emerged stochastic patch occupancy models (Etienne et al. 2004). These models are also based on a spatially explicit patch network but do not, contrarily to PSM, explicitly describe local population dynamics. SPOM have the ability to predict the probability of a patch being occupied at any time in the future given patch extinction and colonization probabilities. Contrarily to the PSM, this second set of metapopulation models, while requiring monitoring data on patch occupancy and/or turnover events, require less information on the focal species vital rates, since it does not explicitly model intrapatch dynamics (Hanski 1994, Sjögren-Gulve 1994, Sjögren-Gulve and Ray 1996, Vos et al. 2000). This modeling approach thus usually requires less parameter to be collected on a metapopulation level. Occupancy models such as SPOM aim at estimating the equilibrium proportion of patches occupied by a focal species; they do not keep track of local population dynamics (Sjögren-Gulve and Hanski 2000). They assume that patches are either occupied or empty, with local extinctions and colonization probabilities being dependent on the size and spatial configuration of all patches.

The first set of metapopulation models (PSM) is widely used in conservation planning (Kindvall 2000, Hels and Nachman 2002,

Akçakaya et al. 2004, Schtickzelle and Baguette 2004) while the second set (SPOM) is somewhat restricted to a more theoretical field (although applied examples exist: Hanski and Ovaskainen 2000, Thomas et al. 2001, Moilanen and Cabeza 2002, Drechsler et al 2003).

Although both approaches are being intensively discussed and criticized (Baguette 2004, Hanski 2004), only a few attempts have been made to evaluate their convergences and/or divergences in a real metapopulation (Kindvall 2000, Lopez and Pfister 2001) and their potential applications to conservation management. Here, we present the development of both a demographically explicit model (using RAMAS Metapop 3.0) and a SPOM for a metapopulation of the European tree frog (Hyla arborea L., 1758). It has been previously demonstrated that European tree frog populations undergo regular extinction and recolonization events (Carlson & Edenhamn 2000, Vos et al. 2000, Schmidt and Pellet in press), fulfilling the metapopulation definition (Hanski and Simberloff 1997, Smith and Green 2005). Using demographic and occupancy data, we aimed at answering the following two questions: (1) Are the two approaches concordant regarding indicators metapopulation various of persistence in time? (2) Do sensitivity analyses on model input parameters identify the relative importance of the same parameters? We finally discuss the conservation implications of both approaches.

METHODS

Species and study area

Widely distributed across the Swiss Plateau at the beginning of the 20th century, the European tree frog has regressed to the point where only a few metapopulations now remain in the country (Grossenbacher 1988, Pellet et al. 2004). It is thus considered highly threatened in Switzerland (Schmidt and Zumbach 2005). Breeding and oviposition take place in gravel pits, military training grounds and other temporary wetlands (Grosse & Nöllert 1993, Pellet et al. 2004, Pellet et al. 2005). During the breeding period, males call conspicuously from pond shores to attract gravid females (Schneider 1993). Counts of calling males are thus used to evaluate the size of breeding populations (Carlson & Edenhamn 2000). The maximum number of calling males heard in a single visit each year is thought to reflect annual breeding male population size (Edenhamn 1996, Pellet and Schmidt 2005). The remnant metapopulation that we modeled here has been described elsewhere (Pellet et al. 2004, Pellet et al. 2005). It consists of 16 local populations (breeding ponds) located in a 225 km² area in western Switzerland of which less than 0.5% consists of amphibian breeding ponds. Patches location is represented in Figure 1. Patch carrying capacity is estimated as the mean maximum number of calling males heard during 4 years of survey (2001-2004).



Figure 1: Tree frogs patch number and location. Patch surface is proportional to estimated carrying capacity. Scale is in kilometers based on the Swiss geographic reference system.

Population based stochastic simulation model (RAMAS)

We implemented a two-stage structured demographic model in RAMAS Metapop 3.0 in which only the sex that limits reproductive capacity (females) was included (assuming a 1:1 sex ratio). Population size assumes a prebreeding census where count of females is expected to equal the count of calling males. The first stage included all non-reproductive yearlings, while stage two is a complementary class including all reproductive individuals. Our model assumes that all individuals become reproductive on their second year (Friedl and Klump 1997). The corresponding year-to-year transition Leslie matrix is thus defined as:

$$L = \begin{pmatrix} 0 & f_a \\ s_a & s_a \end{pmatrix} (1)$$

where f_a is the effective adult fecundity (which includes sex ratio, probability of egg laying, clutch size and all pre-yearling survival rates: Vonesh and De la Cruz 2002), and s_a is the yearly adult survival rate. Adult survival rate was estimated from a 4-year long capturemark-recapture (CMR) experiment undertaken on 3 tree frog populations in Switzerland by Tester (1990). Eight year-to-year adults return rates provide us with a minimum estimate (and standard deviation) of tree frog adult survival. This mean return rate was estimated to s_a =0.303 (SD=0.097). This value is coherent with our own observations in similar CMR experiments in western Switzerland (Pellet et al. unpublished results).

To evaluate f_{a} , we used an indirect approach based on the relationship given by $det(L - \lambda I) = 0$ (Caswell 2001) which, assuming equilibrium population dynamics (λ =1), allowed us matching fecundities to growth rates using the following formula:

$$f_a = \frac{\lambda^2}{s_a} - \lambda \quad (2)$$

The numerical resolution of (2) gave f_a = 2.297. This approach unfortunately did not allow computing standard deviation of adult fecundity. All demographic rates were thus assumed to be affected by environmental stochasticity in a similar way (similar coefficient of variation CV). The CV on s_a being estimated by SD(s_a)/ s_a =32%, we were able to estimate SD(f_a) as f_a ·32%=0.735, leading to a full transition matrix *L*:

$$L = \begin{pmatrix} 0 & 2.297 \pm 0.735 \\ 0.303 \pm 0.097 & 0.303 \pm 0.097 \end{pmatrix} (3).$$

Demographic parameters at each time step of the simulations were randomly taken from lognormal distributions based on the above values. Given the above transition matrix *L* (3), we simulated the dynamic of a single population over 50 years. We then compared the resulting $SD(\lambda)$ with observed variations in growth rate over 20 years in an isolated population near Lerchenfeld (unpublished manuscript). Standard deviation on mean growth rate was estimated as $SD(\lambda_{RAMAS})= 0.860$ while the observed value was $SD(\lambda_{obs})=0.668$, thus suggesting that our transition matrix provided a reasonably good approximation of environmental stochasticity.

We also assumed that reproduction was undergoing catastrophic events (droughts) every 10 years, leading to total reproduction failure in every pond of the metapopulation (which was not the case in the Lerchenfeld population).

Evidences dependent of density regulation have been highlighted in an analysis of long-term tree frog population dynamics (unpublished manuscript). We thus included a Ricker-type (linear or scramble) density dependence function for each population, assuming that density dependence affected both fecundity and survival. The maximum growth rate of all populations (R_{max}) was estimated as the intercept of the regression of growth rates on population sizes. Populations' carrying capacities K_i were defined as the mean number of calling males heard in our set of 16 populations between 2001 and 2004 (assuming a stable age distribution). Because Allee effect was likely to occur in extremely small populations, we defined a local extinction threshold at 2 females.

The proportion of individual dispersing from patch *i* to *j* is defined as $m_{ii} = a \exp^{-\alpha d_{ij}}$ where *a* is the intercept value of the dispersal function (or dispersal rate), $1/\alpha$ is the mean dispersal distance and d_{ij} is the distance between patches *i* and *j*. Data on European tree frog dispersal were provided by a large-scale experiment (Stumpel & Hanekamp 1986, Vos et al. 2000) which provided unbiased dispersal data (Smith and Green 2005). On a total of 89 dispersal events, they evidenced a mean dispersal distance of $1/\alpha = 1.469$ km (max 12.570 km). We set yearlings' dispersal rate to a=0.2 (Sjögren-Gulve 1994) and adult dispersal rate was set to 10% of the yearlings' dispersal value (Fog 1993, Vos 1999).

The demographic model was applied to our set of 16 local populations in Western Switzerland (Figure 1) with initial population sizes set to values recorded in 2001 (counts of calling males, Pellet & Schmidt 2005). Yearlings' population was set assuming stable age structure, given the transition matrix *L*. The baseline model included 10,000 simulations over 50 years.

Stochastic patch occupancy model (SPOM)

Our second modeling approach was derived from Hanski and Ovaskainen (2000) and Ovaskainen and Hanski (2001). Their model is a spatially realistic version of the Levins metapopulation model in which patch size and location contribute to the dynamics of the system. The rate of change in the probability of patch *i* being occupied is:

$$p_{i,t+1} = c_i (1 - p_{i,t}) + (1 - e_i) p_{i,t}$$
(4)

where c_i and e_i are patch-specific colonization and extinction rates defined as:

$$c_{i} = c \sum_{i \neq j} e^{-\alpha d_{ij}} A_{j} p_{j} \quad (5)$$

and

$$e_i = e \frac{1}{A_i^{\varsigma}} \quad (6)$$

respectively. A_i is patch *i* size (or carrying capacity as defined previously), d_{ij} is the distance between patches *i* and *j*, and $1/\alpha$ is the mean species dispersal distance. In the previous equations, *c* and *e* are species-specific colonization and extinction rates, p_j is the probability of patch *j* being occupied and ζ is a scaling parameter defining the relationship between patch extinction rates e_i and patch size A_i . Expected equilibrium patch occupancy may then be computed and metapopulation size may be extrapolated from both patch occupancy and population carrying capacity.

Our application of this modeling approach used the same populations and carrying capacities as those used in the RAMAS model. Four parameters were needed to fully parameterize the model: e, c, α and ζ . These values were extracted from a study of frog metapopulation dynamics tree undertaken by Carlson and Edenhamn (2000). During a three year study period, they estimated extinction rates as a function of patch size (defined as the count of calling males) in a set of 378 patches. Using their published data, we estimated *e* and ζ from the intercept and slope of the following regression:

$$ln(e_{i}) = ln(e) - \zeta ln(A_{i})$$
(7)

 e_i being the observed extinction probability and A_i being local patch size. This approach led to $\zeta = 0.388$ and e = 0.725 with an explained variance of 87%. Species dispersal ability was again set to $1/\alpha$ =1.469 km, as in the PSM. As patch-specific colonization rate c_i was not available from Carlson and Edenhamn (2000), we estimated *c* by minimizing discrepancies (sum of squared residuals) between expected and observed patch occupancy in the metapopulation during 2001-2004. This numerical approach provided c=0.420 $(R^2=51\%).$

Average population size N_i was computed as $N_i = A_i \cdot p_i$, where A_i is patch *i* carrying capacity and p_i is the equilibrium probability of patch *i* being occupied.

Model output comparison

Both models provide estimates of patch occupancy (MPO or proportion of patches occupied) as well as the probability of any given patch being occupied. Similarly, they supply global metapopulation sizes (MFN) in addition to local patches population sizes.

Concordance between our two baseline models regarding probability of patch occupancy and mean local population size was evaluated using Spearman ranked correlation coefficient.

Sensitivity analysis

Sensitivity analyses were run for both approaches. Mean number of occupied patches (MPO) and mean final metapopulation size (MFN) were used as sensitivity indicators (Conroy & Brook 2003). Input parameters were changed one at a time (\pm 50%) from the baseline model and resulting indicator values were reported. The direction of the parameter change was always chosen such as to reduce metapopulation occupancy and final size. Parameters were ranked according to their impact on final indicators and a mean rank was computed in order to summarize information on input parameter sensitivity.

RESULTS

Comparison of baseline models

Both baseline models reach the conclusion that equilibrium patch occupancy

should be around 14-15 occupied patches with a total of approximately 200-300 callers distributed in the whole metapopulation.

Comparison of baseline models of both approaches at the patch level provides good concordance, both in terms of probability of patch occupancy and of population sizes (Figure 2). Spearman's rank correlation between patches' MPO is good (r_s =0.810, P<0.001) and very good regarding patches' MFN (r_s =0.968, P<0.001). The RAMAS model tends however to provide higher estimates of patch probability of occupation while the SPOM, on the other hand, shows slightly higher mean patch population sizes. Taken together, these results indicate that qualitative outputs of our two metapopulation modeling approaches are similar in various respects.

Sensitivity on the RAMAS model

Sensitivity analysis (Table 1) showed that maximum growth rate R_{max} has a preponderant effect on both MPO and MFN. The effect is however much stronger on final metapopulation size (-40% compared to baseline model) than on patch occupancy (-5%). With a mean third rank in our sensitivity analysis, the mean dispersal distance evidences the importance of dispersal on population size and persistence. The effect of this parameter is stronger on patch occupancy (-8%) than on final metapopulation size (-2%). Similarly, the other dispersal parameter (dispersal rate *a*) ranks on average third, but it appears that a relatively large modification in its baseline value (-50%) modifies final indicators MPO and MFN by less than 5%. Standard deviation on demographic rates also appears marginally important, not changing final indicators by more than 6%. Drought frequency and simulation duration both appear to have virtually no impact.

Sensitivity on the SPOM

Mean dispersal distance ranked first, again suggesting the importance of dispersal on patch occupancy (Table 2). Species specific colonization factor *c* comes second, which again appears logical in a recolonization perspective, while extinction-linked factors (e and ζ) appear both of lesser importance ranking third and last out of 4 parameters.



Figure 2: Concordance between the two modeling approaches regarding probability of local patch occupation probability and mean final population size. Patch number are indicated for outliers. Spearman's rank correlation coefficients are highly significant for both indicators: $r_s=0.810$ and $r_s=0.968$ for probability of occupation and population size respectively.

Table 1: Sensitivity of the RAMAS model regarding uncertainty in input parameters. Mean patch occupancy (MPO) and mean final metapopulation size (MFN) are used to rank parameters in a decreasing sensibility order.

Parameter	Baseline value	Parameter change	MPO (SD)	MFN (SD)	Mean rank
Baseline simulation	-	-	95% (6%)	217 (66)	-
Maximum growth rate (R_{max})	2.710	-50%	90% (9%)	130 (51)	1.5
Mean dispersal distance $(1/\alpha)$	1.469	-50%	88% (6%)	213 (63)	3
Dispersal rate (<i>a</i>)	0.2	-50%	93% (6%)	210 (62)	3
SD demographic rates	-	+50%	94% (6%)	204 (73)	3
Droughts frequency	0.1	+50%	95% (6%)	212 (71)	4.5
Simulation duration	50	+50%	96% (5%)	217 (61)	6

Table 2: Sensitivity of the stochastic patch occupancy model (SPOM) regarding uncertainty in input parameters. Mean patch occupancy (MPO) and mean final metapopulation size (MFN) are used to rank parameters in a decreasing sensibility order.

Parameter (abbreviation)	Baseline value	Parameter change	MPO	MFN	Mean rank
Baseline simulation	-	-	86%	312	-
Mean dispersal distance $(1/\alpha)$	1.469	-50%	66%	281	1
Colonization (c)	0.420	-50%	78%	300	2
Scaling factor (ζ)	0.388	-50%	79%	303	3
Extinction (e)	0.725	+50%	81%	305	4

DISCUSSION

Model comparison and sensitivity analyses

The two metapopulation indicators (MPO and MFN) rank populations similarly even though their computation follows very different pathways. The RAMAS model, on one hand, uses local population dynamics (including stage-structured densities) to

compute local population sizes and finally metapopulation patterns of occupancy in time. On the other hand, the SPOM uses patch topology and species-specific metapopulationlevel parameters to compute expected equilibrium occupancies. The latter is therefore more closely related (both conceptually and in terms of input data) to a metapopulation-level background while the RAMAS model scales up from the population to the metapopulation level. Nevertheless, qualitative concordance between the two approaches is impressive.

The quantitative differences between the two models arise largely from the fact that a patch will be considered occupied in the PSM even if it is occupied by a single individual. It thus indicates that populations in the PSM are frequently unsaturated. In the SPOM, on the other hand, a population will be considered either occupied with K_i individuals or empty.

Absolute predictions of PVA are known to be of limited values and since both approaches rely on uncertain parameters, sensitivity analysis must be run in both cases in order to interpret their predictions (Taylor 1995, Ruckelshaus et al. 1997, Reed et al. 2002, McCarthy et al. 2003, Lotts et al. 2004) and rank the relative importance of input parameters. Because both models rely on different input parameters, comparison of sensitivity analyses results is difficult. Nevertheless, it appears that the only parameter they share (mean dispersal distance) ranks most and second-most important in sensitivity analyses. It thus suggests that the preservation of patches density and landscape permeability is a critical conservation target for the European tree frog.

Growth rate (R_{max}) appears of great importance in the RAMAS sensitivity analysis. Given the large amount of change used (-50%), the growth rates slightly exceeded unity on most occasions, which increased population likeliness to go extinct from environmental and demographic stochasticity.

Similarly, the SD on demographic rates, which accounts for the major part of environmental stochasticity, appears to be determinant, ranking third out of 6 parameters.

Conclusively, it appears that although based on fundamentally different paradigms, both modeling approaches are largely concordant in terms of sensitivity to input terminal parameters and mean metapopulation size indices (MPO and MFN). Our results are concordant with Kindvall (2000) who found incidence function model, logistic regression and RAMAS to be similar regarding turnover rates and regional occupancy. It thus appears that SPOMs provide a lightly parameterized modeling framework which produces results very similar to those of highly-parameterized models such as RAMAS, at least in terms of

metapopulation persistence indicators and in the ranking of patch values.

This result suggests that the extensive demographic parameters and intrapatch demography may not be fundamental in order to model global metapopulation occupancy. Our results suggest that models' sophistication (the inclusion of intrapatch dynamics) does not necessarily translate into better metapopulation predictions, especially since it is almost impracticable to parameterize models with accurate data on the demography of most threatened species (Wennergren et al. 1995). Simple models, based on a sound theoretical framework are those more likely to provide applicable and meaningful results for wildlife managers in terms of metapopulation patterns of occupancy.

In both cases, model parameterization represents the major issue for conservation managers. The PSM implemented in RAMAS requires a minimum of 9 parameters including demographic rates while the SPOM only requires 4 parameters. On the other hand however, PSM make fewer assumptions about local extinction dynamics than do SPOM: they simply model local patch dynamics with environmental and demographic stochasticity in order to predict patch occupancy while the SPOM makes strong assumptions about extinction dynamics (Equation 6). In general, SPOM are lightly parameterized models with numerous assumptions while PSM required more parameters but fewer assumptions.

Limitations

The validation of metapopulation models can usually rely only on the partition of the dataset, the first partition being used for model parameterization and the second for model validation (Kindvall 2000). Our dataset being too small to be partitioned, this was an unrealistic option, as is often the case. In our SPOM, validation is also confronted with a circularity problem (the occupancy pattern being used to predict equilibrium occupancy) for which no realistic solution exists (Akçakaya and Sjögren-Gulve 2000, Coulson et al. 2001, Hels and Nachman 2002).

We assumed in both models that carrying capacities would remain constant (Hanski 2001, Hanski & Ovaskainen 2003, Etienne et al. 2004), which is unlikely to hold since natural succession changes habitat quality. There also are numerous evidences

that habitat quality is more important than patch topology in predicting metapopulation dynamics (Thomas et al. 2001, Fleishman et al. 2002, Baguette 2004). Furthermore, the SPOM is assumed to be parameterized from data on steady-state metapopulations. Again, our short term metapopulation monitoring (2001-2004) as well as the data provided by Carlson and Edenhamn (2000) are unlikely to fulfill this assumption. Furthermore, our models assume that both demographic rates and landscape structure (patch size, location, dispersing matrix) will remain stable in the future. Because both assumption are unlikely to hold in an urbanizing landscape (Pellet et al. 2004), the results of our models are weakened (Meir et al. 2004).

Conservation implications

These metapopulation approaches allow identifying the critical parameters for the persistence of a European tree frog metapopulation. Both models highlight the importance of dispersal distance. Since it is known that *H. arborea* is an excellent disperser (Stumpel & Hanekamp 1986, Edenhamn 1996), it indicates that the actual density of pond is at the low end of the species' requirements. Although patches are not extremely distant from one another (median=1.54, mean=2.17, SD=2.06), the mean dispersal distance of H. arborea (1.47 km) seems just enough to maintain exchanges between local populations and ensure recolonization. This suggests that patch density is a limiting factor for the European tree frog in our landscape. It is yet another example of the detrimental effects of habitat loss and fragmentation for amphibians (Semlitsch & Bodie 1998, Vos & Chardon 1998, Lehtinen et al 1999, Marsh & Trenham 2001) to which the European tree frog appears to be extremely sensitive (Edenhamn 1996, Vos et al. 2000). A conservation rule of thumbs deduced from our results would be to have a least one suitable pond per km², thus allowing frogs to maintain sufficient exchanges between patches given their actual mean dispersal distances in agricultural landscapes.

From a modeling perspective, our results also suggest that the solid theoretical framework associated with the SPOM (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001) allows a rapid evaluation of metapopulation processes without requiring extensive data on the demography of the focal species. Additionally, their method allows computing the contribution of any new patch to the metapopulation dynamics (Ovaskainen & Hanski 2003). This feature, although potentially available within classic PSM such as RAMAS or VORTEX (but requiring many manipulations and simulations) has direct conservation application because it allows managers mapping the contribution of any new patch in the landscape given its size and location (topology). The combination of such spatially explicit PVA with landscape-scale habitat suitability mapping can certainly help two fundamental us bridge and complementary approaches in threatened species management by identifying the best location for patch creation both from a landscape and a metapopulation perspective.

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CONSERVATION IMPLICATIONS

BREEDING AGGREGATIONS MONITORING

Many threatened amphibians (including the European tree frog) are associated with rapidly evolving pioneer wetlands. The quality of the aquatic habitat can undergo rapid changes and breeding populations may respond to these natural changes by leaving a climactic wetland to find a younger pond. Being able to anticipate the evolution of the population levels, grants onestep-ahead information to target conservation actions on the most threatened wetlands.

Because there is limited use in casual observations and anecdotal reports, designing a specific monitoring scheme for a species can help to keep track of distribution. Repeated caller counts can provide a sound and relatively cheap basis to this goal (**Chapter 1**). In order to obtain reliable data on tree frog distribution, we recommend a minimum of 3 visits at each potential site at the peak of the reproduction season (with sunset temperature above 18°C) associated with a rigorous estimation-based analysis of the field data (**Chapter 1**).

HABITAT CONSERVATION AND SURVEILLANCE

When a region is monitored for anuran species, the usual result is a distribution of calling male aggregations, which unfortunately does not necessarily translate into reproduction patches. For instance, in the Lemanic coast metapopulation only 11 of the 34 sites where H. arborea was calling showed evidence of regular reproductive success. These ponds represent source populations and their preservation guarantees mid-term survival of the European tree frog. The conservation of these breeding hotspots must therefore be considered a high priority conservation target. Among those source populations, six profit from some kind of legal protection status, which will hopefully ensure their long term preservation. Among these hotspots, four are directly dependent on ongoing human activities (military training grounds and gravel pits). In these cases, economic and ethical incentives must be initiated in order to protect and maintain pioneer conditions.

Because pioneer habitats are often at a transitory stage in natural succession, and/or because they are often dependent on unsteady human activities, all breeding patches are likely to experience habitat degradation. A surveillance of these habitats is therefore highly recommended, since most harmful factors for the European tree frog can be easily identified and prevented if detected on time (shadow due to tree growth, introduction of fishes, agricultural runoffs... see Chapter 2).

WETLAND CREATION/RESTORATION

As highlighted in **Chapter 6**, the actual density of ponds on the Lemanic coast is just about sufficient to maintain exchanges between remnant populations. Existing patches must therefore be conserved in order to secure the population network. Since most wetlands, highly dynamic in nature, will become unsuitable for tree frogs in the long term, a strict habitat protection strategy is insufficient. Habitat creation and/or restoration are thus a required complementary approach to pioneer amphibian conservation. In many cases, such efforts have proven useful in preventing population declines and it can be therefore considered a suitable conservation tool.

Recommendations for wetland creation can be derived from our findings on the preferences of the tree frog (**Chapter 2**). The main determinants are linked to water bodies themselves: they should be shallow, sunny, oligotrophic, fish-free and located outside agriculturally intensive catchment areas (**Chapter 2**).

Our results also demonstrated that landscape-scale factors (**Chapter 3**) are highly correlated with tree frog presence. The intensity of urbanization (measured on a land-use basis) severely reduces tree frog presence. This approach provides managers with a mapping solution, facilitating fine-scale identification of areas less affected by adverse landscape features (**Chapter 3**). Restricting the wetland creation effort to such optimal areas would allow us to focus on an optimal surface where the probability of tree frog occurrence is maximized.

METAPOPULATION STRUCTURE

Evidences of metapopulation functioning in the European tree frog highlight the need to extend our vision of landscape suitability by including the dynamics of local populations. Although single-year patch occupancy patterns can suggest pond statistical independence in space, individual movements between ponds oblige us to extend this view to a larger temporal frame where such independence is not guaranteed. The spatial location of ponds has a decisive importance in determining the overall persistence of tree frog metapopulations (Chapter 6). Thus, conservation strategies must now explicitly deal with metapopulation structure in order to maximize long-term persistence. The relative contribution of both existing and potential new patches to metapopulation persistence can be

estimated via spatially realistic approaches, thereby providing an efficient tool for resource managers. Classical metapopulation conservation practices, as well as our findings, indicate that a centrifugal network densification is more likely to produce successful conservation results than an opportunistic approach to wetland creation.

The combination of both the metapopulation and the landscape approaches provides the most likely promising conservation tool (Figure 1). It can potentially be applied to any species functioning on a geographically defined patch basis and for which evidences of metapopulation dynamic is present.



Figure 1: The process of population monitoring (top) is the basis for both the metapopulation (left) and the landscape suitability (right) approaches. The spatial combination of both paradigms (bottom) is most likely to produce successful results.

TERRESTRIAL HABITATS

Pond and stream-breeding amphibian conservation policies around the world usually focus not only on the preservation of the aquatic habitat but also on a terrestrial buffer zone. In Switzerland, a federal law defines two local protection perimeters around a selection of 701 particularly species-rich ponds in the country. The central perimeter contains "breeding ponds and adjoining natural biota" and the peripheral perimeter contains "other terrestrial habitats and migration corridors". Although this law certainly helped to conserve amphibian diversity in Switzerland, the protection perimeters are mostly based on presumptions and as such are not evidence-based. The location and extent of the upland surfaces used by most amphibians remains unknown. Few tracking experiments have allowed the identification of such terrestrial resources (**Chapter 4**) and the need for scientific knowledge on amphibians' terrestrial habitats is in this context extremely important.

The explicit addition of terrestrial habitats and migration pathways in conservation plans will greatly enhance the effectiveness of conservation practices that currently deal only with a small, but crucial, part of the life cycle of our native amphibians: wetlands.

GENERAL CONSERVATION STRATEGIES

Literature reports as well as our work on habitat suitability have emphasized the major importance of wetland protection for the European tree frog in agricultural landscapes. Conservation of existing source populations must therefore be a primary target. Since many of these ponds already benefit from legal protection status, the efforts should be concentrated on those ponds where less regulated human activities currently maintain adequate conditions for tree frogs (military training grounds and gravel pits).

Because we have demonstrated that pond density in the Lemanic coast is at the low end of the requirements of the European tree frog (**Chapter 6**), conservation efforts should secondarily be targeted at identifying all opportunity to create new ponds. Our work suggests guidelines on where and how to create suitable ponds for the European tree frog (**Chapters 2, 3 and 6**).

Finally, setting up conservation strategies as deliberate experiments from which lessons can be learned can prove an effective tool to improve conservation practices. In this context, monitoring the success of conservation actions is crucial. Such adaptive management however requires that a compromise must be found between the economic costs of habitat protection and/or creation vs. knowledge acquisition. Collaborative actions initiated both with wildlife managers and researchers will provide a solid and durable framework for this challenging task.

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APPENDIX

MONITORING DATA

Location	Coordinates		Count of calling males					
	(Swiss reference system)		2001	2002	2003	2004	2005	
ARBOREX (LAVIGNY)	521800	150600	209	149	170	165	130	
BORNERIE (BALLENS)	519240	157570	0	0	6	2	3	
CAMP ROMAIN (BIERE)	516770	152860	39	27	18	20	78	
CHAMPS CARROZ (YENS)	522760	152540	0	1	0	0	0	
CHANIVAZ (BUCHILLON)	519760	145960	3	0	0	0	0	
CHEMIN DE LA PLAGE (ALLAMAN)	519080	146520	7	10	17	10	7	
CORJON (SAUBRAZ)	514100	152520	3	0	0	0	4	
CORNAZ (ALLAMAN)	520290	146850	5	0	0	1	3	
CROISEE DE LA MURA (MOLLENS)	519350	158600	12	9	18	12	7	
EN CHAMPAGNE (BIERE)	515250	153100	17	5	5	15	23	
ETANG DE VIGNY (COSSONAY)	526950	162500	3	0	0	0	0	
ETANGS DE L'ARBORETUM (MONTHEROD)	517640	151610	12	9	4	6	4	
GRAVIERE DE BALLENS (BALLENS)	517960	155940	5	4	0	0	0	
LA CROIX (MONTRICHER)	519590	160970	5	2	1	0	0	
LA GINGINE (BOUGY-VILLARS)	515450	149310	0	0	0	3	5	
LA PERRAUSE (ACLENS)	528410	157760	0	1	9	0	13	
LE BIOLEY (PAMPIGNY)	521630	158390	1	2	0	1	0	
LE BON (GIMEL)	514700	150900	6	3	7	5	9	
L'EPINE (APPLES)	521690	155930	3	4	0	0	0	
LES BATIAUX (ALLAMAN)	519460	146330	2	0	1	4	2	
LES BIOLES (ST LIVRES)	519220	152330	5	0	0	1	1	
LES BONS (MOLLENS)	518000	158000	26	13	15	15	10	
LES MOSSIERES (SAINT-LIVRES)	517600	154200	19	25	15	20	17	
LONGE VERNE (PAMPIGNY)	522700	160840	0	0	1	2	2	
MONTOSSET (ST LIVRES)	519010	153573	4	5	5	10	10	
MOULIN MARTINET (YENS)	520660	152080	0	0	6	4	4	
PLANCHAMP (PAMPIGNY)	521900	159520	0	0	1	4	7	
PLOMMAPAU (APPLES)	521980	154220	3	0	0	0	0	
PREVONDAVAUX (GIMEL)	511890	150530	1	0	0	0	0	
SAVORET (ST LIVRES)	520110	151890	8	9	3	1	3	
SUR LE SIGNAL (ALLAMAN)	519280	147350	3	0	0	0	0	
VAUDALLE (LAVIGNY)	520150	150200	20	11	10	13	4	

Boldface type indicates reproduction success (not monitored in 2005).

All other data used in this thesis are available from the author or at www.unil.ch/dee