Assessing spatial and temporal population dynamics of cryptic species: an example with the European pond turtle

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Abstract. Within the current context of biodiversity loss a number of biodiversity indicators have been developed to help measure the state of nature and how it is changing. However, most indicators are derived from bird populations. Reptiles and amphibians could be useful ecosystem indicators, but this requires obtaining precise and unbiased population parameters. This is a particularly challenging task for these two groups of species, because individuals are extremely difficult to detect for various reasons. We illustrate the use of a sampling and analytical method that explicitly takes into account imperfect detection to assess the population dynamics of a reptile species and its temporal and spatial variation. European pond turtles (*Emys orbicularis*) were sampled at two different locations during a 10-year study. The two sites differed by their water management regimes and number of livestock. At each site and for each sex, the data were modeled using a robust design capture–mark–recapture framework to obtain and compare estimates of survival, temporary emigration, time-specific abundance, density, and population growth rate, while taking into account effects of individual heterogeneity, trap-response, and time on capture probabilities. Temporary emigration was higher in males (0.344 ± 0.046) (mean $\pm$ SE) than in females (0.228 ± 0.071), did not differ between sites for each sex, and was mainly Markovian. Apparent adult survival was higher in females (0.966 ± 0.031) than in males (0.864 ± 0.024), and was negatively related to the proportion of individuals with repaired shell fractures in the population. Average density was 63.7 ± 6.6 turtles/km^2 but was higher for females (39.2 ± 14.0 females/km^2) than for males (23.5 ± 5.7 males/km^2). The population sizes of males and females decreased where long periods of artificial drought and the highest density of livestock occurred. This research highlights differences in demographic parameters according to sex and site in a turtle species, and it provides evidence that significant human-induced disturbance represents a potential risk to European pond turtle populations. The sampling and analytical approaches illustrated in this study are applicable to many other species of reptiles and amphibians, and estimated population parameters could be combined to produce population indicators useful for conservation and management.

Key words: *Camargue; capture–recapture; cattle grazing; demographic parameters;* Emys orbicularis; *European pond turtle; population dynamics; robust design; survival probability; temporary emigration.*

Introduction

Reptiles and amphibians are receiving increasing attention as organisms for studying evolutionary and ecological questions. The two groups inhabit a wide variety of terrestrial and marine habitats and present a large variation in life history traits (Dunham and Miles 1985, Morrison and Hero 2003). Within the current context of an accelerating loss in species diversity, it is essential to understand population dynamics of reptile and amphibian species in order to assess their role and influence in ecological systems. Although organisms such as birds are commonly used as monitors of environmental change (Furness and Greenwood 1993, Gregory et al. 2005), reptiles and amphibians could potentially be used as status and trend indicators in ecosystem dynamics, since their populations might be affected by global changes (Gibbons et al. 2000). This necessitates acquiring appropriate and precise information on population demographics to infer the effects of environmental factors on populations, and to develop meaningful reptile and amphibian indicators. However, few populations of reptiles and amphibians have been monitored over long periods of time, making it difficult to test for explicit links between population declines or changes in demographic parameters and environmental drivers (Pechmann et al. 1991, Banks et al. 1994, Converse et al. 2005, Pounds et al. 2006). Strong inferences about population dynamics useful for guiding management plans are also scarce due to this lack of precise and unbiased demographic data available for

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many of these species. This is in part because of the extreme difficulty of detecting individuals of most amphibian and reptile species in their environment. Many of these species are relatively small, seasonally active under particular weather conditions, nocturnal, use underground cavities or turbid waters, and have cryptic color patterns. Because of their ectothermic nature, reptiles and amphibians often have reduced behavioral activities compared to endothermic organisms, which make them particularly elusive. Together, these characteristics pose considerable sampling and analytical challenges. The problem of imperfect detection is particularly acute when monitoring many species of reptiles and amphibians (Kéry 2002, Mazerolle et al. 2007), and causes biases in abundance and survival estimates (Yoccoz et al. 2001, Williams et al. 2002), but also in estimated magnitudes of regression coefficients reflecting association of occurrence with other factors (Tyre et al. 2003, Defos du Rau et al. 2005).

Relatively few studies have attempted to estimate spatial and temporal variability in vital rates and population size of reptiles and amphibians taking into account detectability (i.e., the probability of detecting individuals within the surveyed area). The recent development of relevant methods of population analysis (Pollock 1982, Seber 1982, Williams et al. 2002) has expanded the range of demographic parameters that can be estimated, while improving the robustness of estimators, and the biological hypotheses that can be tested. Recently, Mazerolle et al. (2007) reviewed the methods available for estimating detection probability and unbiased demographic parameters in populations of reptiles and amphibians. Of particular interest is the "robust-design" capture–mark–recapture (CMR) approach (Pollock 1982, Kendall et al. 1995, 1997). This CMR design includes several secondary sampling occasions within each primary period (each season or year). The capture histories obtained are used to estimate parameters such as time-specific abundance, annual survival, and temporary emigration probabilities, explicitly taking into account capture probability. However, this approach has rarely been used to help conservation planning in species of reptiles and amphibians.

In this study, we use a 10-year robust CMR design to estimate probabilities of temporary emigration, capture, recapture, effective capture, annual adult survival, and population size for two European pond turtle *Emys orbicularis* populations in southern France to test a priori hypotheses about spatial and temporal differences in demographic parameters (Appendix A). We use this turtle monitoring program to illustrate how sampling and analysis with the robust design permit the estimation of key demographic parameters and help in proposing management plans for reptiles and amphibians, which share several life history attributes with the European pond turtle that influence sampling and analysis. The European pond turtle (see Plate 1) is one

of the most threatened reptiles in Europe, with populations occurring patchily (Lenk et al. 1999), and few data are available on vital rates and their variability (Keller et al. 1998; C. Ayres and A. Cordero Rivera, *unpublished manuscript*). It is protected in the European Union, and the species has been placed in Annex II of the Habitat Directive (92/43/EEC) and of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention).

First, we anticipated relatively high temporary emigration for the following reasons: (1) individuals that aestivate (Naulleau 1992) and/or do not reproduce every year (Olivier 2002) would not be exposed to the capture effort each year, and (2) sampling was performed using stationary traps. Therefore, if a turtle chooses a path randomly each year, then this is absorbed into the capture probability. At the other extreme, if they are totally faithful to their paths, then trap locations simple cause heterogeneity, and some individuals have zero probability of capture. The behavior of turtles in nature probably lies between these two extremes. Second, the two study populations were spatially separated and experienced different environmental conditions. One population (Moncanard) had access to permanently flooded marshes during the entire study period, with relatively few livestock in the area (~0.33 individuals/ ha), whereas the other population (Esquineau) was living in temporary marshes with periods of desiccation during the summer and a higher density of cattle (~0.64 individuals/hectare). Cattle density increased during the study period at Esquineau, whereas it remained stable at Moncanard. Turtles may be heavily trampled when immersed in the mud during the dry season when cattle congregate in shallow areas on canal banks for drinking, or when these reptiles cross the grazed areas to reach the laying sites, and repaired shell fractures observed in adult specimens have this origin (Olivier 2002). We therefore suspected (1) a negative effect of cattle density on adult survival, (2) differences in temporary emigration, adult survival, and population size between the two populations due to local environmental differences, and (3) temporal variation of parameters among years. Finally, due to differences in activity patterns between males and females (Cadi et al. 2004) we expected differences between the sexes in temporary emigration and adult survival.

METHODS

Study area and field methods

We studied *E. orbicularis* in the Camargue (southern France), a vast wetland area comprising ~145 000 ha, where the species occurs at relatively high densities (Cheylan 1998). Details of the Camargue habitats can be found elsewhere (Tamisier and Grillas 1994). The studied populations occupy two restricted areas within the Tour du Valat estate (~43°30′ N, 4°40′ E), which are ~1.5 km apart (Fig. 1). At both sites turtles inhabit two kinds of habitats: permanent and semipermanent

marshes dominated by reed beds of *Phragmites australis*, and man-made irrigation and drainage canals. The Esquineau site is composed of 16 ha of temporarily flooded reed bed and 8 km of irrigation channels, and the total area studied is ~250 ha. The Moncanard site covers a surface area of 100 ha and includes 2 km of drainage channels and 3 ha of permanently flooded reed beds.

European pond turtles have occasionally been sampled in Tour du Valat since 1976 using CMR, but we only used the CMR data collected in 1997–2006, during which sampling was intensive. Dates of fieldwork varied from year to year, but generally included May to July and sometimes March, April, and August. Turtles were captured with baited funnel traps and by hand. The traps were placed in canals and marshes. The average distance between traps was 185 ± 80 m (mean ± SD). Traps were deployed in the field once a month during three to five consecutive days and were visited daily in the morning. Hand captures were also made during these daily visits. Date of capture, sex, and carapace length were recorded on each capture. Sex was identified by observing male secondary sexual characteristics (Zuffi and Gariboldi 1995). Turtles were classified as adults if they were >140 mm maximum carapace length for females and >110 mm for males, and/or had no visible growth rings (Castanet 1988, Olivier 2002). Each individual was marked with permanent notches cut into the carapace marginal scutes with a small hacksaw (Cagle 1939). Turtles were returned within 24 h to the place where they had been collected. A total sampling effort of 502 hours of capture by hand and of 7037 trap-days, which resulted in capture of 502 individual turtles, was made during the 10-year study (Appendix B). The data consisted of capture–recapture histories from 231 males and 271 females.

Analysis methods

Data collected yielded capture histories of individual turtles that followed the standard CMR format for the robust design (Pollock 1982, Kendall et al. 1995, 1997). Months were used as secondary samples, and the three to five days of capture were pooled into one secondary sampling period. The study consisted of 10 primary periods covering 10 years. The turtle populations were expected to be open to gains (immigration and recruitment) and losses (mortality and emigration) between these years. Within each primary period, there were multiple secondary sampling periods (from two to six), and the populations were assumed to be closed to gains and losses among these secondary periods, an assumption that we tested. Kendall et al. (1995, 1997) developed full likelihood approaches that combined open and closed population models and that permit estimating a number of parameters from data collected under a robust design. We suspect the robust design approach to be particularly relevant for estimating demographic parameters of turtles. Individuals of many
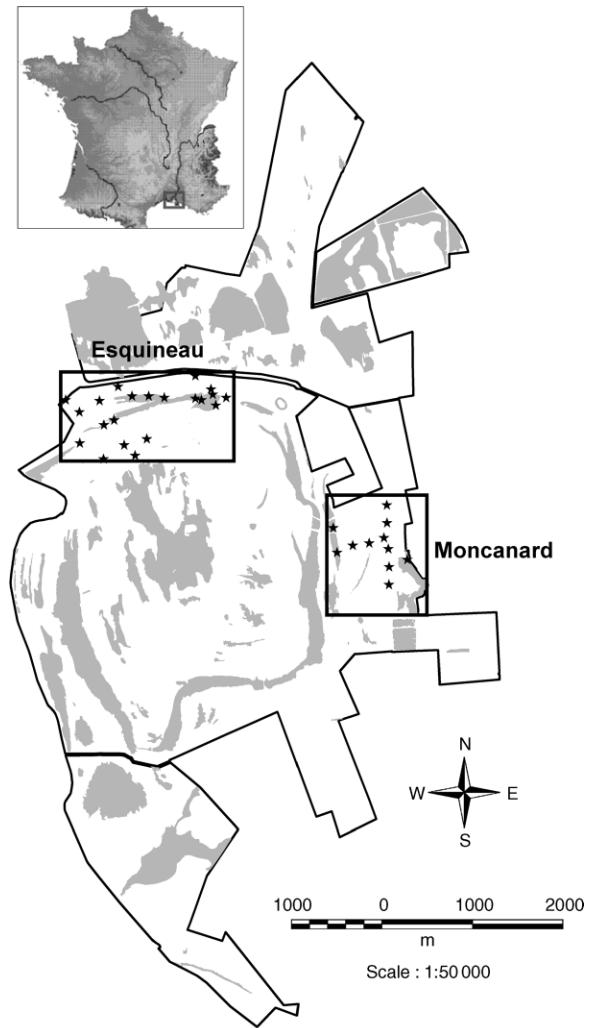

Fig. 1. A map of the areas where European pond turtles (*Emys orbicularis*) were sampled by baited funnel traps and by hand in the Tour du Valat estate, Camargue, France, during 1997–2006. The inset shows the location of the study site within France. Stars indicate the location of funnel traps. Gray areas indicate bodies of water.

terrestrial or freshwater species may spend some of their time hidden in the vegetation or under the soil surface during part of their life cycle (Naulleau 1992, Kazmaier et al. 2001, Lagarde et al. 2002), and are not exposed to sampling effort. Individuals may temporarily leave the sampling area and become unavailable for capture. These behaviors result in temporary emigration, i.e., individuals are alive but not available for capture during sampling periods. Temporary emigration probability (γ') may vary spatially and temporally, and its occurrence violates key assumptions for CMR models (Seber 1982, Pollock et al. 1990), resulting in biased estimates of population parameters (Kendall et al. 1997, Kendall 1999). Furthermore, for those individuals available for capture, several factors such as habitat characteristics, time, sex, or age may affect their capture

probability (p). These factors can be explicitly modeled, therefore relaxing the assumption of equal catchability, which in turtles is known to bias abundance estimates obtained from methods assuming equal catchability (Koper and Brooks 1998). Therefore, the probability of detecting a turtle at a particular time is the product (($1 - \gamma) \times P$), and is referred to as effective capture probability (Kendall 1999).

Modeling approach.—We tested for possible effects of individual heterogeneity, trap-response behavior, and time-related variations on capture probabilities (Otis et al. 1978, Williams et al. 2002). We also modeled temporary emigration (the probability of an individual not being available for trapping during one or more primary sampling periods), transience (the probability that a newly captured individual was just passing through the study area, with a near-zero chance of returning to be recaptured during the study), and apparent survival (the probability of surviving from one primary period to the next and of staying in the study area). The number of animals not captured was modeled for each primary period as time dependent or constant and added to the number of animals known to be in the population to provide an estimate of the population size $N(t)$ and $N(.)$, respectively. Survival was modeled on an annual scale, and was either year dependent, $S(t)$ or constant $S(.)$.

Temporary emigration was modeled with two parameters: $\gamma'(t)$ was the probability that a turtle was absent from the study site at time t if absent at time $t - 1$, and $\gamma''(t)$ was the probability that a turtle was absent from the study site at time t if present at time $t - 1$. Temporary emigration was modeled as either random ($\gamma'(t) = \gamma''(t) = \gamma(t)$), or Markovian ($\gamma'(t) \neq \gamma''(t)$). The temporary emigration parameters were either time dependent or not.

To model capture probability we included heterogeneity, time, and behavioral response. Heterogeneity was modeled using a finite mixture model (Norris and Pollock 1996, Pledger 2000) with two groups of individuals. Heterogeneity was included in the model as a mixing parameter, π, indicating the proportion of the populations in one of the two groups of individuals. The proportion of individuals in the other group is ($1 - \pi$), and the two groups have different capture probabilities that are estimated. The mixing parameter either differed between years, $\pi(t)$, or not $\pi(.)$, although the number of secondary samples might have been too low to be able to assess heterogeneity for some years. Two kinds of capture probabilities were modeled: p, the probability of capture in any secondary period for initial captures and applied to individuals not previously caught in the primary period, and c, the probability of capture in any secondary period for recaptures and applied to individuals previously caught in the primary period. Initial capture and recapture probabilities were estimated for each primary period, $p(t)$ and $c(t)$,

respectively, or not, $p(.)$ and $c(.)$, respectively, or with two-group heterogeneity, $p(g)$ and $c(g)$, respectively. To limit the number of parameters in our initial models capture and recapture probabilities were modeled as constant within secondary periods. Because turtles were physically captured and manipulated, we thus assumed a priori that trap response was more important than time variation within primary periods. For models with no trap response in which capture probabilities do not depend on previous capture history, the parameter p is used, and there is no parameter c.

To test the effect of cattle density on adult survival, we used the proportion of individuals with repaired shell fractures as a covariate. The rationale is that the higher this proportion is, the higher the probability that some turtles died because of trampling by cattle. We used the observed proportion of individuals with repaired shell fractures in year t as a covariate of adult survival between year $t - 1$ and t. Our hypothesis is that the observed proportion of cracked shells at time t reflects the level of trampling by cattle in the interval between $t - 1$ and t, and therefore if trampling increases the probability of mortality, we expect a negative relationship between the proportion of individuals with cracked shells in year t and adult survival between year $t - 1$ and t. Assuming identical capture probabilities, the proportion of individuals with repaired shells was estimated for each year and for each sex by dividing the number of individuals with repaired shells captured by the total number of individuals captured. The effect of the covariate was tested using an analysis of deviance with a one-sided test, and the fraction of the variation in adult survival explained by the covariate was evaluated following Skalski et al. (1993). We recognize that our approach does not permit modeling of the immediate mortality rate. A more logical approach would be to use a multistate robust design model involving shells with cracked and uncracked states, but the proportion of turtles with cracked shells was too small in our data set to obtain robust estimates.

All these models were implemented in program MARK (White and Burnham 1999) for each sex and for each site. We used an information theoretic approach to select the most appropriate model for the data (Burnham and Anderson 2002) based on the AIC. We used the small-sample modification (AIC_c) proposed by Hurvich and Tsai (1989). Using program CAPTURE (Rexstad and Burnham 1991), we also investigated the modeling of capture probabilities by assessing the discriminant function model selection statistics.

Goodness-of-fit testing.—There is no goodness-of-fit test for our initial models including heterogeneity. We thus assessed the fit of our initial models using program RDSURVIV (Hines 1996) by modifying the predefined models in the program so as to expand the number of parameters. Program RDSURVIV uses a cell-pooling algorithm to compute Pearson's χ^2 test statistic, and

PLATE 1. Female European pond turtle (*Emys orbicularis*). Photo credit: © Jean E. Roché, used by permission.

permits testing the fit of robust design models including time and behavioral effects, but not heterogeneity (Kendall et al. 1995, 1997). Goodness-of-fit tests were performed for each sex and for each site separately. The assumption of closure within primary periods was tested using program CloseTest (Stanley and Burnham 1999). Although a closure test is available in program CAPTURE (Rexstad and Burnham 1991), Type I error rates for this test exceed nominal rates in the presence of time or behavioral variation in capture probabilities (White et al. 1982), and the test is sensitive to temporary violation of closure occurring during the middle of the study (Otis et al. 1978).

Estimating population growth rate.—We estimated the rate of change in abundance between primary sampling periods t and $t + 1$ as $\hat{\lambda}_t = \hat{N}_{t+1}/\hat{N}_t$. The average rate of change over the study period was computed as the geometric mean of the annual rates of increase, $\hat{\lambda}_t = (\hat{N}_{10}/\hat{N}_1)^{0.1}$. Variances of the rates of increases were estimated using the delta method approximations (Seber 1982, Williams et al. 2002), and estimates are given ±SE.

RESULTS

Closure tests

Closure tests indicated that the closure assumption within primary periods was supported in 64% of years with data adequate to assess closure (Appendix B). Most violations of the closure assumption occurred in 1999 and 2002, and there was no systematic violation of the closure assumption for each year. Among the top six models receiving the highest model selection scores based on the CAPTURE algorithm for model selection, the model with time and behavioral response of capture, M_{tb}, was selected for most (74%) data sets. Since models with heterogeneity response, M_{bh} or M_h, were selected in 13% of the cases, we considered models with heterogeneity, behavioral response, and time variation across primary periods (note that models without heterogeneity not presented here had much lower quasi-AIC$_c$ [QAIC$_c$] values).

To further assess the closure assumption and because the width of the primary periods may appear large in relation to the time scale at which we modeled the demographic parameters, especially for the first three years of the study, we performed an additional analysis for these years. We considered months as primary periods and days of capture within each month as secondary samples, and conducted a model selection using a robust design using the same modeling approach as described above. Results (not presented here) indicated that monthly survival was ~1 and that abundance varied little (and not significantly) between months for each year. These results suggest that the closure assumption was reasonable for both sexes in both populations.

Goodness of fit

Goodness-of-fit analyses using program RDSURVIV indicated a lack of fit of the most general models to the data (Esquineau females: $\chi^2_{144} = 282.4$, $P < 0.001$; Esquineau males: $\chi^2_{76} = 116.6$, $P = 0.001$; Moncanard females: $\chi^2_{72} = 140.3$, $P < 0.001$; Moncanard males: $\chi^2_{50} = 68.7$, $P = 0.041$). We thus calculated the variance inflation factor for each data set, which varied between 1.374 and 1.961, and based model selection on AICc corrected for overdispersion (QAIC$_c$ [Lebreton et al. 1992, Burnham and Anderson 2002]).

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TABLE 1. Estimated survival ($\hat{S}$) and temporary emigration ($\hat{\gamma}'$ and $\hat{\gamma}''$) for primary periods for the European pond turtle (*Emys orbicularis*) at two locations in the Tour du Valat, France, 1997–2006.

	Females, Esquineau			Males, Esquineau		
Period	$\hat{S}$	$\hat{\gamma}''$	$\hat{\gamma}'$	$\hat{S}$	$\hat{\gamma}''$	$\hat{\gamma}'$
1	0.905 (0.063)			0.878 (0.026)		
2	0.999 (0.000)	0.239 (0.036)		0.878 (0.026)	0.370 (0.163)	
3	0.963 (0.049)	0.239 (0.036)	0.928 (0.221)	0.878 (0.026)	0.000 (0.001)	0.000 (0.001)
4	0.999 (0.000)	0.239 (0.036)	0.568 (0.243)	0.878 (0.026)	0.291 (0.088)	0.291 (0.088)
5	0.880 (0.079)	0.239 (0.036)	0.920 (0.258)	0.878 (0.026)	0.725 (0.077)	0.725 (0.077)
6	0.829 (0.079)	0.239 (0.036)	0.683 (0.137)	0.878 (0.026)	0.533 (0.084)	0.533 (0.084)
7	0.999 (0.003)	0.239 (0.036)	0.328 (0.150)	0.878 (0.026)	0.000 (0.003)	0.000 (0.003)
8	0.618 (0.081)	0.239 (0.036)	1.000 (0.001)	0.878 (0.026)	0.839 (0.065)	0.839 (0.065)
9	1.000 (0.000)	0.239 (0.036)	0.000 (0.001)	0.878 (0.026)	0.447 (0.123)	0.447 (0.123)
Mean	0.939 (0.023)	0.239 (0.036)	0.677 (0.103)	0.878 (0.026)	0.382 (0.050)	0.382 (0.050)

Notes: Values in parentheses are estimated standard errors. Blank cells indicate quantities that were not estimated at the beginning of the study for temporary emigration parameters. For time-varying parameters, mean indicates the arithmetic mean of the parameters with its associated standard deviation approximated using the delta method. See *Methods* for definitions of parameters. The symbol $\hat{\gamma}'$ is the probability that a turtle absent from the study site at time t is absent at time $t - 1$, and $\hat{\gamma}''$ is the probability that a turtle absent from the study site at time t is present at time $t - 1$.

Model selection

Inferences about relevant sources of variation in the parameters are provided using model selection statistics in Appendices C–G.

For females at Esquineau, the model with the lowest QAIC$_c$ is substantially better than the others in the set of models, and we thus based inferences on this model. Under this model {S(t), γ''(.), γ'(t), π(t), p(t), c(h)}, capture probabilities were modeled using time-specific capture ($\bar{p} = 0.383 \pm 0.023$) and constant group-specific recapture ($\hat{c} = 0.645 \pm 0.080$; $\hat{c} = 0.156 \pm 0.022$) probabilities, with the proportion of animals in each group changing over time. The estimates of group composition were approximately 0 or 1 in 4 of the 10 years, indicating no evidence of heterogeneity in some years. Capture and recapture probabilities differed, indicating some trap response behavior. Temporary emigration was Markovian. The probability of becoming a temporary emigrant was constant ($\hat{\gamma}'' = 0.238 \pm 0.036$; ~24% temporary emigrants in each primary period), whereas the probability of staying a temporary emigrant from one occasion to the next was time specific (Table 1). About 68% of temporary emigrants remained temporary emigrants in each primary period ($\hat{\gamma}' = 0.677 \pm 0.103$). Survival probabilities varied between primary sampling periods (Table 1) and were estimated at 0.939 $\pm$ 0.023. For males at Esquineau there was considerable support for time-specific capture probabilities and group-specific recapture probabilities, with the proportion of individuals in each group changing over time. Capture probabilities ($\bar{p} = 0.465 \pm 0.092$) were higher than group-specific recapture probabilities ($\hat{c} = 0.376 \pm 0.068$; $\hat{c} = 0.053 \pm 0.022$). As for females, the estimates of group composition were ~0 or 1 in 4 of the 10 years, indicating no evidence of heterogeneity in some years. There was also considerable support for random time-specific temporary emigration. The sum of the QAIC$_c$ weights for models that included these effects on capture

and temporary emigration parameters was 0.997. Random temporary emigration was time specific (Table 1) and indicated an average of ~38% temporary emigrants between primary periods ($\hat{\gamma}' = \hat{\gamma}'' = 0.382 \pm 0.050$), although it varied from 0% to 81.5%. There was more uncertainty in model selection for inference on survival. Models with constant or time-specific survival rates had similar QAIC$_c$ weights. Model-averaged parameter estimates (Burnham and Anderson 2002) provided support for constant survival, particularly when one considers the low precision of these estimates. Survival rates between primary periods were estimated at 0.878 $\pm$ 0.026.

Model selection for females at Moncanard gave considerable support for constant survival ($\hat{S} = 0.993 \pm 0.057$), Markovian temporary emigration ($\hat{\gamma}'' = 0.218 \pm 0.056$; $\hat{\gamma}' = 0.819 \pm 0.131$), capture probabilities, and group-specific recapture probabilities ($\hat{c} = 0.898 \pm 0.063$; $\hat{c} = 0.137 \pm 0.029$). However, there was some uncertainty in model selection for inference on group composition and capture probabilities. Average group composition was $\hat{\pi} = 0.199 \pm 0.051$ and never equaled 0 or 1 in any of the primary periods. Again, model-averaged estimates gave support for constant group composition given the low precision of these estimates. There was evidence for trap response, and annual capture probability was estimated at 0.327 $\pm$ 0.038. Because model-averaged estimates were nearly equal ($\hat{p} = 0.364 \pm 0.093$; $\hat{p} = 0.320 \pm 0.041$), and since the confidence intervals considerably overlapped, there was support for capture probabilities being not group-specific.

For males at Moncanard, model selection gave support for constant Markovian temporary emigration ($\hat{\gamma}'' = 0.282 \pm 0.063$; $\hat{\gamma}' = 0.533 \pm 0.150$), the sum of QAIC$_c$ weights for models with constant Markovian temporary emigration was 0.61, constant capture probabilities ($\hat{p} = 0.405 \pm 0.0420$), constant group-

TABLE 1. Extended.

	Females, Moncanard			Males, Moncanard	
$\hat{S}$	$\hat{\gamma}''$	$\hat{\gamma}'$	$\hat{S}$	$\hat{\gamma}''$	$\hat{\gamma}'$
0.993 (0.057)			0.849 (0.040)		
0.993 (0.057)	0.218 (0.056)		0.849 (0.040)	0.282 (0.065)	
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)
0.993 (0.057)	0.218 (0.056)	0.819 (0.131)	0.849 (0.040)	0.282 (0.065)	0.592 (0.159)

specific recapture probabilities ($\hat{c} = 0.625 \pm 0.080$ and $\hat{c} = 0.096 \pm 0.035$), and constant group composition ($\hat{\pi} = 0.336 \pm 0.090$). However, there was important uncertainty in model selection for inference on survival. Model-averaged parameter estimates provided support for constant annual survival, given the low precision of these estimates. Survival between primary periods was estimated at $\hat{S} = 0.849 \pm 0.040$.

The proportion of females with repaired shell fractures was 0.046 ± 0.007 at Esquineau, and zero at Moncanard. This proportion tended to increase during the study period from 0.025 in 1998 to 0.081 in 2006 and, when entered as a covariate of adult survival, significantly explained 44.2% of the variation in survival (Anodev: $F_{1,9} = 5.554$, $P = 0.021$). Female survival at Esquineau was negatively related to the proportion of individuals with repaired shell fractures (slope $= -2.772 \pm 1.027$ for a standardized covariate). For males, the proportion of repaired shell fractures was similar at the two sites (Esquineau: 0.036 ± 0.011; Moncanard: 0.023 ± 0.009), and was not related to survival ($F_{1,9} = 0.687$, $P = 0.21$; $F_{1,9} = 0.001$, $P = 0.50$).

Estimates of time-specific abundance for the first time period were discarded, since this year corresponded to the initiation of the study. Estimates of abundance and effective capture probabilities are shown in Table 2. For females and males at Esquineau the geometric mean rates of population change were estimated at $\hat{\lambda} = 0.959 \pm 0.109$ and $\hat{\lambda} = 0.984 \pm 0.069$, respectively, suggesting 4.1% and 1.6% annual decreases between 1998 and 2006. This was supported by the higher $QAIC_c$ of models where N was constrained to be constant across years (females: $\Delta QAIC_c = 11.28$; males: $\Delta QAIC_c = 8.54$). The effective capture probability averaged $\bar{p}* = 0.315 \pm 0.055$ for females and $\bar{p}* = 0.235 \pm 0.074$ for males.

For females and males at Moncanard, the geometric mean growth rates were estimated at $\hat{\lambda} = 1.017 \pm 0.049$ and $\hat{\lambda} = 1.066 \pm 0.082$, respectively, suggesting 1.7% and 6.6% annual increases. This was supported by the lower $QAIC_c$ of models where N was constrained to be constant across years (females: $\Delta QAIC_c = 5.73$; males: $\Delta QAIC_c = 2.81$). The effective capture probability was $\hat{p}* = 0.256 \pm 0.039$ for females and $\hat{p}* = 0.284 \pm 0.047$ for males.

DISCUSSION

Modeling capture probabilities

There was clear evidence for trap response in both sexes at both localities, which could be modeled under the robust design to obtain unbiased estimates. Behavioral effects on conditional capture probabilities suggest that estimation methods assuming equal capture

TABLE 2. Estimated abundance and effective capture probability for primary periods for the European pond turtle (*Emys orbicularis*) at Tour du Valat, France, 1997–2006.

Primary period	Females, Esquineau		Males, Esquineau		Females, Moncanard		Males, Moncanard	
	$\hat{N}_t$	$\hat{p}t*$	$\hat{N}_t$	$\hat{p}t*$	$\hat{N}_t$	$\hat{p}t*$	$\hat{N}_t$	$\hat{p}t*$
1	106 (75.7)		37 (15.0)		30 (4.4)		12 (1.7)	
2	112 (19.1)	0.135 (0.035)	42 (6.3)	0.178 (0.091)	43 (3.3)	0.256 (0.039)	23 (1.4)	0.284 (0.047)
3	127 (7.5)	0.246 (0.038)	91 (12.9)	0.181 (0.036)	41 (3.2)	0.256 (0.039)	38 (1.9)	0.284 (0.047)
4	106 (4.9)	0.396 (0.060)	63 (4.3)	0.343 (0.089)	54 (6.2)	0.256 (0.039)	26 (2.6)	0.284 (0.047)
5	101 (26.9)	0.127 (0.034)	28 (3.7)	0.151 (0.071)	30 (7.6)	0.256 (0.039)	26 (5.1)	0.284 (0.047)
6	79 (9.5)	0.300 (0.080)	38 (1.4)	0.291 (0.073)	28 (3.3)	0.256 (0.039)	27 (2.1)	0.284 (0.047)
7	66 (5.1)	0.361 (0.075)	39 (2.8)	0.278 (0.087)	43 (4.2)	0.256 (0.039)	33 (2.3)	0.284 (0.047)
8	106 (18.8)	0.273 (0.049)	75 (26.5)	0.157 (0.046)	30 (7.6)	0.256 (0.039)	13 (3.5)	0.284 (0.047)
9	40 (0.0)	0.705 (0.057)	17 (0.0)	0.161 (0.065)	59 (8.4)	0.256 (0.039)	39 (4.6)	0.284 (0.047)
10	77 (11.8)	0.289 (0.063)	36 (2.0)	0.374 (0.110)	50 (10.2)	0.256 (0.039)	42 (6.7)	0.284 (0.047)

Notes: Values in parentheses are estimated standard errors. Blank cells indicate quantities that were not estimated at the beginning of the study for effective capture probability. See *Methods* for definitions of parameters.

probabilities may lead to biased estimates of population size (Pollock et al. 1990). Temporal variations in conditional capture and recapture probabilities were detected for one site (Esquineau), but capture and recapture probabilities did not vary between primary periods for the other site (Moncanard). This suggests that variations in capture probabilities can occur at small spatial scales (the two sites were only separated by 1.5 km). These differences in the factors influencing the capture process suggest caution against using capture–recapture methods that assume equal capture probability through time, space, and different segments of a population (e.g., males and females) without first testing these assumptions. Evidence for heterogeneity in recapture probabilities (but not in capture probabilities) at both sites and for both sexes suggests that after their first capture in traps, turtles vary in their willingness to enter traps in following encounters, and/or their chances of finding any traps at all. In addition, the proportion of the population in one of the two groups of animals with different recapture probabilities varied between primary occasions at Esquineau but not at Moncanard, again highlighting small-scale variations in the capture process. Heterogeneity in capture probabilities is expected in wildlife populations due to factors such as age or sex, and can lead to biased estimates of population size (Pollock et al. 1990). Heterogeneity in these European pond turtle populations could be the source of the slight lack of fit we observed in our goodness-of-fit tests. We suspect that such effects on capture and recapture probabilities are relatively common in many species of reptiles and amphibians (Lowe 2003, Bailey et al. 2004, Frétey et al. 2004, Muths et al. 2006, Kinkead and Otis 2007, Mazerolle et al. 2007), and because these probabilities are influenced by many factors they need to be estimated in each study.

Modeling temporary emigration

To our knowledge these results represent one of the few attempts to rigorously estimate temporary emigration in turtles. For males and females at both sites, our models identified that a percentage of the turtles in the sampled populations may not be available for capture during some primary periods, although they are still in the superpopulation, i.e., they are temporary emigrants. About 20% to 40% of the turtles in the sampled area from year to year were estimated to be unavailable for capture in traps during each primary sample period. Estimates are relatively high, but fall within the range of temporary emigration estimates obtained in other species using a similar methodology (Kendall and Bjorkland 2001, Bailey et al. 2004, Frétey et al. 2004, Bradford et al. 2006, Karanth et al. 2006, Muths et al. 2006, Kinkead and Otis 2007). Temporary emigration may be caused by individuals moving outside the trapping area. It is likely that the range of some individuals overlapped the sampling areas only partially, and these individuals may or may not be present during

the times of sampling in some years. Our results indicate that individuals absent in year $t - 1$ were more likely to be absent in year t than individuals present in year $t - 1$, and support this hypothesis. Dispersal in these two populations seem very low (see *Modeling survival*, below), and certainly lower than temporary emigration probabilities. Temporary emigration may also be caused by individuals changing their behavior in some years and avoiding traps. Among several species of turtles, it has been shown that some individuals skip breeding opportunities (Kuchling 1993, Miller 1997, Doody et al. 2003, Rivalan et al. 2005, Bertolero et al. 2007a), most probably because they may not be able to acquire sufficient food for reproduction in some years (Bull and Shine 1979), and some desert tortoise species aestivate and/or skip breeding when environmental conditions become too harsh (Henen 2002, Largarde et al. 2002). In our study the breeding status for a sample of females (*n* = 128) was determined as part of a companion study between 1997 and 2000 (Olivier 2002). There was evidence that some female European pond turtles skip reproduction during some years, as found in other populations of the same species (Keller 1997, Kotenko 2000, Naulleau 2000). Olivier (2002) found that during a given year ~26.5% of females did not lay a single clutch, ~50% laid one clutch, and ~23.5% laid two or more clutches, suggesting the existence of different breeding behaviors, as found in the other species (Rivalan et al. 2005, Bertolero et al. 2007a). Moreover, both sexes are known to aestivate when environmental conditions deteriorate (e.g., when bodies of water dry up [Naulleau 1991]). Skipping of reproduction, and aestivation, are consistent with a pattern of Markovian, or state-dependent, temporary emigration. The extent of Markovian temporary emigration was equivalent for females at both sites and for males at Moncanard, but it was higher for males at Esquineau, which also showed random temporary emigration. Overall mean temporary emigration was higher in males (0.344 ± 0.046) than in females (0.228 ± 0.071; $\chi_1^2 = 3.905$, $P = 0.048$), in accordance with Duguy and Baron (1998), who found lower site fidelity in males than in females. However, the probability that an individual is absent from the study area at time t if absent at time $t - 1$ was relatively high (from 0.407 to 0.819), indicating that a significant proportion of the population was unavailable for capture during several consecutive years. For example, ~10% of females at Esquineau are within the study area every second year, and about 30% of males at Moncanard remain outside the study area during four consecutive years. Although these patterns are not consistent with biennial breeding in the European pond turtle, as found for other turtles (Doody et al. 2003, Rivalan et al. 2005), they may reflect differences in condition and/or quality between individuals (Swingland and Coe 1979, Chastel et al. 1995, Cam et al. 1998, Wallis et al. 1999, Bertolero et al. 2007a). This may also be related to interactions between the

differences in the ecology of the two sexes and site characteristics.

Modeling survival

Assuming no mortality or permanent emigration during sampling periods, overall adult annual survival rates for European pond turtles were 86.4% in males and 96.6% in females, corresponding to a mean life expectancy for adult females of ~30 years (calculated as $1/M$, where M is the complement of survival [Charnov 1993]). For females reaching the mean age of first reproduction (~8 years [Olivier 2002]), one might expect a mean life expectancy of 38 years. On the Tour du Valat estate, some European pond turtles marked as adults in 1976 were still alive in 2006 (A. Olivier, *unpublished data*), and European pond turtles have been documented to live >70 years (Biegler 1966). At both sites survival estimates were lower for males than for females, as found for other turtle species (Converse et al. 2005, but see Bertolero et al. 2007*b*). The complement of survival estimates includes deaths and permanent emigration out of the study area. This annual loss of females is likely to be from mortalities, since permanent emigration out of both study sites estimated from capture–recapture data and multistate models is extremely low for adult females (<0.1%; A. Olivier and C. Barbraud, *unpublished data*). However, permanent emigration is higher for males, with estimates ranging from 3% to 9% (A. Olivier and C. Barbraud, *unpublished data*). Apparent differences in adult survival between males and females may thus only reflect differences in permanent emigration, but further analyses are needed for stronger inference. Our estimates are consistent with results from previous studies indicating that adult survival in chelonians approaches or exceeds 90% (Shine and Iverson 1995), but to our knowledge adult survival has not been previously estimated under a robust design for any freshwater turtle species. Most studies have used CJS models, which tend to underestimate survival in the presence of temporary emigration (Kendall et al. 1997). Given the relatively high probabilities of temporary emigration found in our own studies and others on reptiles and amphibians (see above *Modeling temporary emigration*), using the robust design approach should be encouraged for these species.

Population dynamics

Average turtle densities were slightly higher at Moncanard (69.7 ± 7.3 turtles/km^2) compared to Esquineau (55.7 ± 11.1 turtles/km^2; Appendix H). These estimates are consistent with those obtained for other populations in similar habitats (Mazzotti 1995, Duguy and Baron 1998). Estimates of population growth rate suggest that the turtle population at Esquineau is declining, particularly females, whereas the population appears increasing or stable at Moncanard. The demographic mechanisms involved remain unclear, but the lower adult survival for females at Esquineau is consistent with the observed decline, which could be partly caused by higher mortality rates (given that permanent emigration is extremely low). Indeed, the proportion of newly marked adults between 2001 and 2006 was similar at both sites (females at Esquineau: 0.062 ± 0.009; females at Moncanard: 0.079 ± 0.013; males at Esquineau: 0.170 ± 0.019; males at Moncanard: 0.199 ± 0.031), and the proportion of newly marked immature individuals was 0.063 ± 0.008 at Moncanard and 0.067 ± 0.008 at Esquineau. Therefore, results support the hypothesis of a decline of the female population at Esquineau caused by a higher mortality compared to the Moncanard female population. Given the proximity of the two sites, these differences can not be caused by climate effects. Our results strongly suggest a negative effect of cattle at Esquineau, at least with this density of cattle. Ideally, several populations (replicates) should be studied for each situation for stronger inference, but this would require a substantial increase in resources (time, personnel, funds). Although we did not detect a relationship between survival and the proportion of cracked shells in males, we can not exclude that in fact the effect was more acute than in females, since we modeled a lagged mortality rate. Although the introduced red-eared slider (*Trachemys scripta elegans*) may have detrimental effects for the European pond turtle (Cadi and Joly 2004), we do not believe it is a cause of the decline, since red-eared slider has never been captured at our study sites (Olivier 2002).

Conclusion

We have focused on this species of turtle to illustrate how the robust design CMR approach can be used in population studies on reptiles and amphibians, and more generally in species for which imperfect detectability is particularly acute. Our results emphasize the importance of intensive sampling and the usefulness of the robust design to obtain reliable estimates of population parameters critical to studies in ecology, the evolution of life history traits, and for the design of effective conservation plans. Our results suggest that a significant proportion of European pond turtle populations are unavailable for capture during a given year, and that capture probability of individuals varies due to behavioral effects, time effects, and between individuals. Therefore, using unadjusted count indices to compare populations over time and space without estimating detection probability and its sources of variation is very likely to produce biased estimates of survival and population size and erroneous conclusions. Given their cryptic behavior and life history attributes, we suspect that this may also apply to many reptile and amphibian species. Our results suggest a negative effect of cattle grazing on adult survival in European pond turtles in these populations, and illustrate how methods and sampling designs accounting for detectability can help in designing management plans for reptiles and am-

phibians. For example, in the case of the European pond turtle, several management decisions regarding the impact of cattle grazing can be envisaged. Managers confronted with declining European pond turtle populations in grazed habitats might decide to stop cattle grazing, following a precautionary principle. Managers may also consider preventing access by cattle to areas most frequently used by pond turtles either for feeding or for egg-laying, based on knowledge acquired through radio-tracking studies. Ideally, experimental studies are needed where the density of cattle could be manipulated and the demographic parameters of several turtle populations estimated from a capture–mark–recapture robust design. This would allow estimation of an optimal cattle density compatible with a stable turtle population. At our study sites, the density of cattle has been reduced since 2007 at Esquineau, and we expect an increase in adult survival and population size in future years. Finally, population parameters differed between two populations of turtles at a small spatial scale, probably in relation to different management practices, and one population is declining. Given the relatively limited dispersal abilities of several species of reptiles and amphibians, the influence of local environmental factors on their population dynamics might be higher than expected from species with greater dispersal capacities (e.g., birds). Therefore, care must be taken when inferring population dynamics from single-site studies in these species, and we encourage researchers and managers to study several population units to obtain less biased inferences.

Literature Cited

Bailey, L. L., T. R. Simmons, and K. H. Pollock. 2004. Estimating detection probability parameters for Plethodon salamanders using the robust capture-recapture design. Journal of Wildlife Management 68:1–13.

Banks, B., T. J. C. Beebee, and K. S. Cooke. 1994. Conservation of the natterjack toad Bufo calamita in Britain over the period 1976–1990 in relation to site protection and other factors. Biological Conservation 67:111–118.

Bertolero, A., J.-P. Nougarède, M. Cheylan, and A. Marín. 2007a. Reproduction traits in two Western populations of Hermann's tortoise Testudo hermanni hermanni. Amphibia–Reptilia 28:77–85.

Bertolero, A., D. Oro, and A. Besnard. 2007b. Assessing the efficacy of reintroduction programmes by modelling adult survival: the example of Hermann's tortoise. Animal Conservation 10:360–368.

Biegler, R. 1966. A survey of recent longevity records for reptiles and amphibians in zoos. International Zoo Yearbook 6:487–493.

Bradford, A. L., P. R. Wade, D. W. Weller, A. M. Burdin, Y. V. Ivashchenko, G. A. Tsidulko, G. R. VanBlaricom, and R. L. Brownell, Jr. 2006. Survival estimates of western gray whales Eschrichtius robustus incorporating individual heterogeneity and temporary emigration. Marine Ecology Progress Series 315:293–307.

Bull, J. J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. American Naturalist 114:296–306.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cadi, A., and P. Joly. 2004. Impact of the introduction of the red-eared slider (Trachemys scripta elegans) on survival rates of the European pond turtle (Emys orbicularis). Biodiversity and Conservation 13:2511–2518.

Cadi, A., M. Nemoz, S. Thienpont, and P. Joly. 2004. Home range, movements, and habitat use of the European pond turtle (Emys orbicularis) in the Rhône-Alpes region, France. Biologia 59, Supplement 14:89–94.

Cagle, F. R. 1939. A system for marking turtles for future identification. Copeia 1939:170–193.

Cam, E., J. E. Hines, J.-Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. Ecology 79:2917–2930.

Castanet, J. 1988. Les méthodes d'estimation de l'âge chez les chéloniens. Mésogée 48:21–28.

Charnov, E. L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford, UK.

Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76:2240–2246.

Cheylan, M. 1998. Evolution of the distribution of the European pond turtle in the French Mediterranean since the post-glacial. Mertensiella 10:47–65.

Converse, S. J., J. B. Iverson, and J. A. Savidge. 2005. Demographics of an ornate box turtle population experiencing minimal human-induced disturbances. Ecological Applications 15:2171–2179.

Defos du Rau, P., C. Barbraud, and J.-Y. Mondain-Monval. 2005. Incorporating uncertainty into analyses of red-crested pochard habitat selection. Biological Conservation 125:355–367.

Doody, J. S., A. Georges, and J. E. Young. 2003. Twice every second year: reproduction in the pig-nosed turtle, Carettochelys insculpta, in the wet-dry tropics of Australia. Journal of Zoology 259:179–188.

Duguy, R., and J.-P. Baron. 1998. La cistude d'Europe, Emys orbicularis, dans le marais de Brouage (Char.-Mar.): cycle d'activité, thermorégulation, déplacements, reproduction et croissance. Annales de la Société des Sciences de Charente-Maritime 8:781–803.

Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. American Naturalist 126:231–237.

Frétey, T., E. Cam, B. Le Garff, and J.-Y. Monnat. 2004. Adult survival and temporary emigration in the common toad. Canadian Journal of Zoology 82:859–872.

Furness, R. W., and J. J. D. Greenwood. 1993. Birds as monitors of environmental change. Chapman and Hall, London, UK.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Gregory, R. D., A. van Strien, P. Vorisek, A. W. Gmelig Meyling, D. G. Noble, R. P. B. Foppen, and D. W. Gibbons. 2005. Developing indicators for European birds. Philosophical Transactions of the Royal Society B 360:269–288.

Henen, B. T. 2002. Reproductive effort and reproductive nutrition of female desert tortoises: essential field methods. Integrated and Comparative Biology 42:43–50.

Hines, J. E. 1996. RDSURVIV User's Manual. Patuxent Wildlife Research Center, USGS, Laurel, Maryland, USA. ⟨http://www.mbr-pwrc.usgs.gov/software/index.html⟩

Hurvich, C. M., and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Karanth, K. U., J. D. Nichols, N. S. Kumar, and J. E. Hines. 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. Ecology 87:2925–2937.

Kazmaier, R. T., E. C. Hellgren, D. R. Synatzske, and J. C. Rutledge. 2001. Mark–recapture analysis of population parameters in a Texas tortoise (Gopherus berlandieri) population in southern Texas. Journal of Herpetology 35:410–417.

Keller, C. 1997. Ecologia de poblaciones de Mauremys leprosa y Emys orbicularis en el Parque Nacional de Donana. Dissertation. University of Seville, Seville, Spain.

Keller, C., A. C. Andreu, and C. Ramo. 1998. Aspects of the population structure of Emys orbicularis hispanica from southwestern Spain. Pages 147–158 in U. Fritz, U. Joger, R. Podloucky, and J. Servan, editors. Proceedings of the EMYS Symposium, Dresden '96. Mertensiella 10:147–158.

Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology 80:2517–2525.

Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture–recapture data. Biometrics 57:1113–1122.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

Kéry, M. 2002. Inferring the absence of a species: a case study of snakes. Journal of Wildlife Management 66:330–338.

Kinkead, K. E., and D. L. Otis. 2007. Estimating superpopulation size and annual probability of breeding for pond-breeding salamanders. Herpetologica 63:151–162.

Koper, N., and R. J. Brooks. 1998. Population-size estimators and unequal catchability in painted turtles. Canadian Journal of Zoology 76:458–465.

Kotenko, T. I. 2000. The European pond turtle (Emys orbicularis) in the steppe zone of Ukraine. Stapfia 69:87–106.

Kuchling, G. 1993. Possible biennial ovarian cycle of the freshwater turtle Erymnochelys madagascarensis. Journal of Herpetology 27:470–472.

Lagarde, F., X. Bonnet, K. Nagy, B. Henen, J. Corbin, and G. Naulleau. 2002. A short spring before a long jump: the ecological challenge to the steppe tortoise (Testudo horsfieldi). Canadian Journal of Zoology 80:493–502.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lenk, P., U. Fritz, U. Joger, and M. Wink. 1999. Mitochondrial phylogeography of the European pond turtle, Emys orbicularis (Linnaeus 1758). Molecular Ecology 8:1911–1922.

Lowe, W. H. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. Ecology 84:2145–2154.

Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.

Mazzotti, S. 1995. Population structure of Emys orbicularis in the Bardello (Po delta, northern Italy). Amphibia–Reptilia 16:77–85.

Miller, J. D. 1997. Reproduction in sea turtles. Pages 51–81 in P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida, USA.

Morrison, C., and J.-M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: a review. Journal of Animal Ecology 72:270–279.

Muths, E., R. D. Scherer, P. S. Corn, and B. A. Lambert. 2006. Estimation of temporary emigration in male toads. Ecology 87:1048–1056.

Naulleau, G. 1991. Adaptations écologiques d'une population de cistudes (Emys orbicularis L.) (Reptilia, Chelonii) aux grandes variations du niveau d'eau et à l'asséchement naturel du milieu aquatique fréquenté. Bulletin de la Société Herpétologique de France 58:11–19.

Naulleau, G. 1992. Study of terrestrial activity and aestivation in Emys orbicularis (Reptilia, Chelonia) using telemetry. Pages 343–346 in Z. Korsos and I. Kiss, editors. Proceedings of the Sixth Ordinary General Meeting of the Societas Europaea Herpetologica. S.E.H, Budapest, Hungary.

Naulleau, G. 2000. Reproduction and growth in Emys orbicularis under extreme variations in water levels in Dordogne, France. Chelonii 2:49–52.

Norris, J. L., and K. H. Pollock. 1996. Nonparametric maximum likelihood estimators for population size under two closed capture–recapture models with heterogeneity. Biometrics 52:639–649.

Olivier, A. 2002. Ecologie, traits d'histoire de vie et conservation d'une population de cistude d'Europe Emys orbicularis en Camargue. Dissertation. Ecole Pratique des Hautes Etudes, Université de Montpellier II, Montpellier, France.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference for capture data on closed animal populations. Wildlife Monographs 62, the Wildlife Society, Bethesda, Maryland, USA.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impact from natural fluctuations. Science 253:892–895.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models for mixtures. Biometrics 56:434–442.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107, Wildlife Society, Bethesda, Maryland, USA.

Pounds, J. A., et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161–167.

Rexstad, E., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, USA.

Rivalan, P., A.-C. Prévot-Julliard, R. Choquet, R. Pradel, B. Jacquemin, and M. Girondot. 2005. Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. Oecologia 145:564–574.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Shine, R., and J. B. Iverson. 1995. Patterns of survival, growth and maturation in turtles. Oikos 72:343–348.

Skalski, J. R., A. Hoffmann, and S. G. Smith. 1993. Testing the significance of individual and cohort level covariates in

animal survival studies. Birkhäuser Verlag, Basle, Switzerland.

Stanley, T. R., and K. P. Burnham. 1999. A closure test for time-specific capture–recapture data. Environmental and Ecological Statistics 6:197–209.

Swingland, I. R., and M. Coe. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment. Philosophical Transactions of the Royal Society B 286:177–188.

Tamisier, A., and P. Grillas. 1994. A review of habitat changes in the Camargue: an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biological Conservation 70:39–47.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.

Wallis, I. R., B. T. Henen, and K. A. Nagy. 1999. Egg size and annual egg production by female desert tortoises (*Gopherus agassizii*): the importance of food abundance, body size, and date of egg shelling. Journal of Herpetology 33:394–408.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture removal methods for sampling closed populations. Los Alamos National Laboratory Publication LA-8787-NERP, Los Alamos, New Mexico, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16:446–453.

Zuffi, M. A. L., and A. Gariboldi. 1995. Sexual dimorphism of the European pond terrapin *Emys orbicularis* (L. 1758) from Italy. Pages 124–129 *in* G. A. Llorente, A. Montori, X. Santios, and M. A. Carretero, editors. Scientia Herpetologica. Sociedad Europea Herpetologica, Barcelona, Spain.

APPENDIX A

A photograph of a European pond turtle caught at Tour du Valat, France, with a repaired shell fracture caused by cattle (*Ecological Archives* A020-035-A1).

APPENDIX B

Primary and secondary sampling periods, sampling effort, and number of individual turtles caught at Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A2).

APPENDIX C

Sex- and site-specific tests for population closure and model selection statistics based on turtle capture history data from Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A3).

APPENDIX D

Model selection statistics for robust design analysis of female European pond turtle capture data from Esquineau, Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A4).

APPENDIX E

Model selection statistics for robust design analysis of male European pond turtle capture data from Esquineau, Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A5).

APPENDIX F

Model selection statistics for robust design analysis of female European pond turtle capture data from Moncanard, Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A6).

APPENDIX G

Model selection statistics for robust design analysis of male European pond turtle capture data from Moncanard, Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A7).

APPENDIX H

Estimated densities (individuals/km^2) for primary periods for the European pond turtle at Tour du Valat, France, 1997–2006 (*Ecological Archives* A020-035-A8).