# Estimating the demographics of an ocellated lizard (*Timon lepidus* Daudin, 1802) population through photo identification capture-recapture

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Received: 28 Oct., 2022; First decision: 12 Nov., 2022; Revised: 18 Nov., 2022; Second decision: 7 Dec., 2022; Revised: 9 Dec., 2022; Accepted: 20 Dec., 2022

#### **Abstract**

This study used photo identification "capturerecapture" to monitor a population of ocellated lizards (Timon lepidus Daudin, 1802), providing the first data on the demography of this species in the wild. The monitoring was conducted over a period of six years in a valley of the Var River in southeast France, with an average rate of 25 visits per year. This resulted in 1870 exploitable photographs that allowed the identification of 138 different individuals along a 1,600m linear path. For the 114 lizards that were over the age of one, the life history data was analysed with MARK software using the Cormack-Jolly-Seber (CJS) model. This analysis enabled survival estimates - both annual and seasonal (mid-May to end of September versus October to mid-May) - for both sexes. Annual survival appears to be higher in males than in females (0.65 versus 0.48), with a life expectancy of 2.3 years for adult/subadult males and 1.4 years for adult/subadult females. During the winter period, monthly survival is close to 1 for both sexes. It is lower during the summer period: 0.92 in males and 0.87 in females. These survival and longevity rates are surprisingly low for a species of this size. However, they can be considered reliable given

the high "recapture" (via photo identification) rates (between  $0.465 \pm 0.053$  and  $0.986 \pm 0.014$  in spring, lower in autumn) and the isolation of the study site.

#### Résumé

L'étude utilise la photo-identification pour suivre une population de lézards ocellés (Timon lepidus Daudin, 1802) dans le sud-est de la France. Les données de capture-marquage-recapture (CMR) issues de la photo-identification fournissent les premières données sur la démographie de cette espèce dans la nature. Le suivi a été réalisé sur une période de six ans dans la vallée du fleuve Var (Alpes-Maritimes), avec un rythme moyen de 25 visites par an. Mille huit cent soixante-dix photographies exploitables ont permis d'identifier 138 individus différents le long d'un parcours linéaire de 1 600 mètres. Les données d'histoire de vie ont été analysées pour 114 lézards âgés de plus d'un an, avec le logiciel MARK en utilisant le modèle Cormack-Jolly-Seber (CJS). L'analyse permet d'estimer la survie annuelle et saisonnière (de mi-mai à fin septembre versus octobre à mi-mai) chez les deux sexes. La survie annuelle

**Keywords:** *Timon lepidus*, demography, CMR, south of France, photo identification, monitoring, ocellated lizard.

**Mots-clés :** *Timon Lepidus*, démographie, CMR, sud de la France, identification photo, monitoring ; lézard ocellé.

semble être plus élevée chez les mâles que chez les femelles (0,65 contre 0,48), avec une espérance de vie de 2,3 ans pour les mâles adultes et subadultes (> 1 an) et de 1,4 an pour les femelles adultes et subadultes. Pendant la période hivernale, la survie mensuelle est proche de 1 pour les deux sexes. Elle est plus faible pendant la période estivale: 0,92 chez les mâles et 0,87 chez les femelles. Les taux de survie mis en évidence sont étonnamment bas pour une espèce de cette taille. Ils peuvent cependant être considérés comme fiables étant donné l'isolement du site d'étude et les forts taux de « recapture » obtenus via la photo d'identification (entre 0,465 ± 0,053 et 0,986 ± 0,014 au printemps, plus faibles en automne).

## Introduction

Knowledge of the demographic parameters of a species – age at maturity, adult survival, mean generation time - is fundamental to understanding its population dynamics, especially when modelling the viability of a threatened population (Akçakaya & Sjögren-Gulve 2000; Brook et al. 2000; Beissinger 2002). Unfortunately, acquiring this information is laborious, especially for discreet and uncapturable species: the case of many reptiles. Estimating the survival rate or life expectancy of a species in the wild requires multi-year monitoring involving recognition of individuals – generally by individual marking – which is difficult to put into practice for most lizard species. As a result, demographic studies on lizards mainly concern abundant and easily captured species such as, for example, in Europe, Zootoca vivipara, Lacerta agilis or Podarcis sp. (Barbault & Mou 1988; Strijbosch & Creemers 1988; Galán 1999; Berglind 2000; Le Galliard et al. 2010; Rotger et al. 2020; Diego-Rasilla et al. 2021).

The ocellated lizard (Timon lepidus Daudin, 1802) is a shy species that is difficult to capture except in very specific situations: rabbit burrows allowing the use of traps, artificial or natural shelters facilitating the manual capture of lizards (Grillet et al. 2010; Cheylan et al. 2011; Doré et al. 2015). The demographic data available on this species is therefore almost non-existent, apart from information derived from skeletochronology almost four decades ago (Castilla & Castanet 1986), an invasive technique that can only be performed on dead animals or on an amputated phalange (Comas et al. 2016). Furthermore, this technique does not provide information on survival rates, which require multi-annual monitoring by capture-mark-recapture surveys. As a result, no reliable data is available on the demography of this threatened species (Grillet *et al.* 2006; Cheylan *et al.* 2011) (near threatened species on the IUCN species list; Pleguezuelos *et al.* 2009).

To improve demographic knowledge of this species, this study used a technique that has not yet been widely used on reptiles: photo identification (Jackson *et al.* 2006; Bengsen *et al.* 2011; Bolger *et al.* 2012; Cruickshank & Schmidt 2017). It was possible to use it in this case because of the distinctive patterns of this species, but also because of the singular configuration of the study site (the site is isolated; see site description below). The findings allow the first estimates of survival rates and longevity in the wild for this species.

#### **Materials and methods**

# The study site

The monitoring was carried out at a site located in the valley of the Estéron River, which flows into the Var River in the south of France, about 16km north of Nice (43.821°N/7.183°E). The study area covered a length of 1,600 m and an average width of about 50m along the western bank of the Estéron River, stretching south from the Nucera bridge (Figure 1). It was embanked between 1920 and 1970 to protect the valley from recurrent severe flooding of the Var River, although the exact date of these works on this part of the river is unknown. The embankment consists of a concrete foundation covering the side of the embankment at an approximate 45° angle, with a 70cm wide horizontal lip at the top (Figure 2). Concrete blocks are stacked on the slope. Since the end of 2014, the top of the embankment has been made into a cycle path with a railing on the river side to make walking and cycling safer. Due to its configuration, the study area is virtually isolated: to the east by the river bed, to the west by a road with heavy traffic and then a water body, all in a highly urbanised context. Exchanges with the surroundings are therefore very limited and, although the species is present at the edge of the water body on the other side of the road, no individuals have ever been observed alive or dead on the road despite regular visits to the site. The ocellated lizards at the site shelter in the maze of concrete blocks lining the bank and venture



Figure 1 – View of the study site. The route taken to photograph the lizards is indicated in red (photo M. Belaud).



Figure 2 – View of the study site – Details of the dike with the blocs and cycle path (photo M. Belaud).

little outside this refuge. This zone has the advantage of being relatively inaccessible to humans due to the incline of the bank and a safety barrier separating the embankment from the cycle path. The concrete blocks provide valuable hiding places for the lizards, especially the gap that has developed over time between the blocks and the concrete base.

Lizards cross the cycling path to assess grassy areas between the cycling path and the road where they feed (one lizard was found dead on the cycle path, probably due to a collision with a bike over the study period). Excluding the area of the cycle track, which is not used by lizards for feeding, the site exactly covers 81,400m².

#### **Data collection**

The cycle path provides an ideal vantage point to view and photograph the lizards below. Accustomed to frequent human traffic, they are much more confident here than elsewhere. Over a period of six years (2015-2020), from March to November, an observer (MB) walked the cycle path from the Nucera bridge and then back (a distance of 3,200m), generally in the morning (between 9:00 and 13:00), equipped with 10×40 binoculars and a 300mm lens mounted on a digital SLR camera (Canon 7D mark II - 20.2 megapixels). The observer walked slowly along the railing, stopping every 10m. The immediate vicinity along the track was examined first, as that would offer the closest view of any lizards hidden in the grass. Attention was then focused on the concrete blocks to the left and right and then on the lower part of the embankment.

During the six-year study, the number of annual monitoring visits varied between a minimum of 4 (2015) and a maximum of 38 visits (2019) (Table 1), representing a total of 315 hours of prospecting over a cumulative distance of 451km. During the 150 visits of the site, 996 ocellated lizards were observed and 4026 photographs were taken of individuals. The precise time of the photograph was also noted so that it could be referenced to the previously calibrated time-stamped photos, which were then labelled with the specific code for the lizard.

#### Identification of individuals

Photo identification is a commonly used monitoring technique today, especially for mammals (Kelly 2001; Nipko *et al.* 2020). It is less frequently used for reptiles, due to the difficulty of photographing these animals

from a distance and of detecting distinguishing marks between individuals (Steinicke et al. 2000; Perera & Perez-Mellado 2004; Sacchi et al. 2016). From this point of view, the ocellated lizard has the identification advantage that individuals have varied lateral patterns. Moreover, the size of this lizard allows an image resolution that is sufficiently satisfactory to examine the colouration details (see photo examples in Figure 3). During the survey visits, whenever possible lizards were photographed from both sides, so that the right and left side patterns were available. Individuals photographed only on one side were excluded from the results to allow for unambiguous subsequent identification.

For the identification of individuals, we did not use image recognition software (Matthé et al. 2017), given the relatively small number of individuals (138 different individuals over the six years of the study). The identification was carried out by directly comparing the photos onscreen. This allowed us to use several criteria to identify individuals: size, sex, side patterns (blue markings, flank reticulation), head scales and wounds. Flank patterns are a good means of recognition (as shown in Figure 3), as well as both the number and arrangement of lateral blue markings and some dorsal patterns. Head scales, particularly the labial scales, can also be used as an identification criterion given their variability. They also have the advantage of being very similar on both sides of the head. Wounds, which are quite common in males due to fighting, are also an aid to identification, as is the state of regeneration of the tail if it has been severed (14% of individuals in our study). The main difficulty lies in the identification of juveniles under one year of age, for which profound marking/ colouration changes are observed. Without obtaining frequent close-up photographs over

Table 1 – Sampling effort during the multi-year survey: number of annual visits; distance travelled during visit; time spent on site (hours: minutes); number of photographs taken and used; number of ocellated lizard individuals seen; number of different individuals observed.

Year	# of visits	km	Time spent	# of photographs		# of lizards	# of individuals	
				taken	used	seen	different	total
2015	4	1	3:10	66	14	4	4	4
2016	10	16	12:08	267	68	28	19	19
2017	36	115	98:12	1225	431	286	53	66
2018	34	109	78:39	1034	407	283	64	100
2019	38	122	71:20	925	543	252	58	125
2020	28	88	52:15	509	407	143	36	138
	150	451	315:04	4,026	1,870	996		138

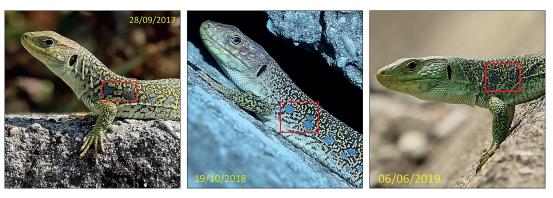


Figure 3 – Example of patterns allowing the identification of the same adult individual over three years (photo M. Belaud).



Figure 4 – Change in the pattern of a juvenile photographed on four occasions over less than a year (photo M. Belaud).

time, for example from week to week, their identification is almost impossible, as shown in the photographs (Figure 4). For this reason, juveniles under the age of one were excluded from the demographic analyses.

# **Demographic analyses**

Only capture histories of adult and subadult lizards (age > 1 year) observed during the period 2016 to 2020 were used for the analyses. Each "recapture" corresponded to an observation validated by at least one photograph. To estimate apparent survival ( $\varphi$ ) and recapture rates (p), we used the Cormack-Jolly-Seber model (CJS: Lebreton  $et\,al.$  1992) implemented in program MARK (White & Burnham 1999).

The recapture probability for autumn 2016 was fixed at p = 0 (no sampling was carried out during this period; Table 2). In order to distinguish between summer and winter survival, we selected observations made in spring (April to June) and autumn (September to October) and eliminated observations from July and August (Table 2). The time interval between spring and autumn of each year was set at 4.5 months to estimate summer survival (mid-May to end of September), and the interval between autumn and the following spring was set at 7.5 months to estimate winter survival (October to mid-May). In this way, the monthly survival estimates  $(\phi)$  were directly comparable between summer (su) and winter (wi). In the survival modelling, we tested different biological hypotheses: variation due

Table 2 – Number of ocellated lizards identified in each season and the seasonal observation effort.

Year	Season	Observation effort (hours)	Lizards identified
2016	Spring	9	18
	Autumn	0	0
2017	Spring	61	40
	Autumn	7	8
2018	Spring	38	45
	Autumn	17	24
2019	Spring	32	38
	Autumn	12	17
2020	Spring	18	24
	Autumn	12	8

to (1) sexual differences (s), (2) differences between seasons and years (t), and (3) differences between summer and winter (season), but without year differences for each season (i.e. no difference between years for a given season). We also assessed the existence of a linear relationship between observation effort (e: number of hours spent searching for lizards each season) and recapture probability. Factors and covariates were tested with interactions (noted by \*) or as additive effects (noted by +). The average life expectancy for lizards older than one year was calculated with the formula LE =  $-1/\ln(\varphi)$ , where  $\varphi$  was the annual survival probability of each sex. Annual survival was calculated from seasonal survival  $\varphi_{annual}$  =  $\varphi_{su}^{4.5} * \varphi_{wi}^{7.5}$  and the variation in  $\varphi_{annual}$  was estimated by the Delta method (Seber 1982). Because the site is considered as isolated, population size (spring data only) was calculated with closed population models (Otis et al. 1978), using the Huggins design in the program MARK (White & Burnham 1999) (to make sure, open population models were also tested (Jolly-Seber model, POPAN program in MARK) but did not provide good estimates). We evaluated models that were constant  $(M_0)$ , time dependent  $(M_t)$ , dependent on behaviour on first capture  $(M_{\nu})$ , with individual heterogeneity between capture probability  $(M_b)$ , and a combination of these models  $(M_{th}, M_{th})$  and  $M_{th}$ ; Otis et al. 1978; Williams et al. 2001). Prior to the survival analysis, we verified the goodness-of-fit of the overall model ( $\varphi_{s*t}$ ,  $p_{s*t}$ ) and the CJS model with U-Care software (Choquet et al. 2009). The selection of survival and population size models was carried out with the Akaike information criterion corrected for small samples (AICc; Burnham & Anderson 2002). The difference between

the AICc of each model and the AICc of the

model with the smallest value ( $\Delta$ AICc) and the Akaike weight ( $\omega_i$ ) were used to select the best model.

The graphs were made with R software (R Core Team 2018) and the package *tidyverse* (Wickham *et al.* 2019).

#### Results

# Recapture rate

Recapture rates varied according to the observation effort made in each season (Figure 5; Table 1). In all cases, they were higher in spring than in autumn (between  $0.465 \pm 0.053$  and  $0.986 \pm 0.014$  in spring and between  $0.219 \pm 0.052$  and  $0.439 \pm 0.052$  in autumn; first model in Table 4), reflecting both the intensity of lizard activity and the frequency of site visits.

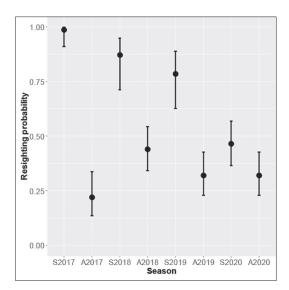


Figure 5 – Resighting probability in spring (S) and autumn (A) over 2017-2020 as estimated from the model \$\Phi\_{\text{steason}}\$, \$\phi\_{\text{e}}\$ (resighting probabilities can only be estimated from 2017 onward). The bars show the 95% confidence intervals.

#### Population size and density

Autumn sampling did not allow for reliable population estimates (Table 2). The population estimates are therefore based on spring 2017 to 2020, using closed population models. The population size varied between a maximum

The population size varied between a maximum de  $54.0 \pm 4.9 (\pm SE)$  lizards in spring 2018 and a minimum of  $34.2 \pm 7.8$  lizards in spring 2020 (Table 3), with no significant difference

between the four analysed years of monitoring (2017-2020). Based on the most reliable population estimate (54 individuals in 2018), the density of individuals older than age one is estimated to be in the range of a minimum of 5.98 ind/ha and a maximum of 8.59 ind/ha.

#### Sex ratio

In spring 2018, 25 adult females and 21 adult males were identified, resulting in a balanced sex ratio (1 female to 0.84 males;  $\chi^2 = 0.044$ , df = 1, p = 0.835). In the same season, the estimated population size was  $34.2 \pm 7.4$  females ( $\pm$  SE; model Mh) and  $30.4 \pm 11.2$  males (model Mb), i.e. also a balanced sex ratio (1 female to 0.89 males;  $\chi^2 = 0.031$ , df = 1, p = 0.860).

# Survival rate and life expectancy

Survival rates were calculated from the life histories of 114 lizards older than one year (66 females and 48 males). The data fitted the CJS model satisfactorily (global GOF test  $\chi^2 = 29.514$ , df = 30, p = 0.491). The retained survival model was supported with an Aikake weight of 89.1% (Table 4). It shows that the survival rates were higher for males than females and, for both sexes, lower in summer than winter (Figure 6). The annual survival was  $0.480 \pm 0.062$  ( $\pm$  SE) for females and  $0.650 \pm 0.064$  for males. From the second year, average life expectancy was 1.4 years for females and 2.3 years for males.

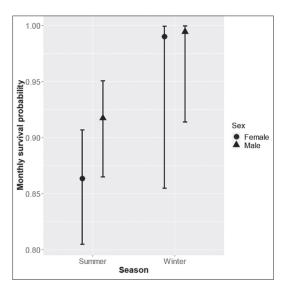


Figure 6 – Monthly survival probability in summer (mid-May to September) and winter (October to mid-May) estimated from the model  $\varphi_{\text{s-season'}}$   $p_{\text{e}}$ . The bars show 95% confidence intervals.

Table 3 – Estimated ocellated lizard population size (n) in spring 2017-2020. Models:  $M_{\rm h}$  = capture probability varies with individual;  $M_{\rm bh}$  = capture probability varies with individual and behavioural response to capture; and  $M_{\rm tbh}$  = capture probability varies with behavioural response to capture, time and individual (Otis et al. 1978). SE = 95% confidence interval.

Spring	Model	n	SE	Inf95	Sup95
P2017	Mh	53.08	10.88	44.80	99.43
P2018	Mh	54.04	4.88	48.68	70.12
P2019	Mtbh	43.37	6.54	38.83	72.79
P2020	Mbh	38.84	43.63	24.78	307.70

Table 4 – Models of apparent survival  $(\Psi)$  and recapture probability (p) for the ocellated lizard population in the study site from 2016 to 2020. Models were evaluated by comparing the  $\triangle$ AICc,  $\omega_i$  is the Akaike weight and k is the number of estimable parameters. Subscript notations in the models: t = time; s = sex; season = summer and winter; e = observation effort for recapture; and constant e = season no variation.

Model	AICc	ΔAICc	$\omega_{i}$	k	Deviance
$\varphi_{s+season}$ , $P_e$	407.993	0	0.891	5	166.846
$\varphi_{s+season}$ , $P_t$	413.166	5.173	0.067	10	161.224
$\varphi_{\text{season}}$ , $P_{\text{t}}$	415.156	7.163	0.025	9	165.415
$\varphi_s$ , $P_t$	417.975	9.982	0.006	9	168.235
$\varphi_{s+t}$ , $P_t$	418.953	10.959	0.004	15	155.670
$\varphi_s$ , $P_{s+t}$	420.168	12.175	0.002	10	168.226
$\varphi_t, P_t$	420.468	12.475	0.002	13	161.790
$\varphi_{s+t}$ , $P_{s+t}$	420.748	12.755	0.002	16	155.128
$\varphi_{constant}$ , $P_t$	421.210	13.217	0.001	8	173.146
$\varphi_t$ , $P_{s+t}$	422.546	14.552	0.001	14	161.577
$\varphi_{constant}$ , $P_{s+t}$	422.886	14.893	0.001	9	173.146
$\varphi_{s+t}$ , $p_{s*t}$	428.170	20.176	0	20	152.959
$\varphi_{s^*t}$ , $P_{s^*t}$	436.455	28.462	0	24	151.248

## **Discussion**

The unique conditions of this study – good visibility of the animals, their habituation to human presence, and the isolation of the population - allowed a multi-year survey via photo identification of this shy species, which has been little accessible to population dynamics studies. The study also allowed the reliability of photo identification to be tested as a long-term population monitoring method. We found that the technique was effective for the identification of subadults and adults older than one year, but was problematic in juveniles, due to rapid changes in their colouration pattern. In contrast to capture, which is generally traumatic for individuals and difficult to carry out on this species, photo identification offers the advantage of not disturbing the

animals. However, the quality of the photos can lead to significantly less information compared to physical capture, and only photographing both sides of an individual's body allows for unambiguous subsequent identification. The use of this method with other populations of ocellated lizards or other species of lizards may be problematic, except in very specific situations allowing good visibility of the animals.

Given the sampling effort (an average of 25 visits per year, with a maximum of 38 visits in 2019), recapture rates per season were high, ranging from a minimum of 29% in autumn 2017 to a maximum of 98% in spring 2017. As would be expected, the findings show that the "recapture" probability of an animal is closely linked to the "capture" effort as well as to the activity of the animals, which is more intense in spring (April, May and June) than in autumn (September and October). These high "recapture" rates provide satisfactory survival estimates, allowing an analysis of whether these are differentiated by sex and by season. Seasonally, there was a strong contrast between apparent winter survival (October to mid-May) and apparent summer survival (mid-May to late September). Both sexes taken together, survival was 99% in the winter and 89% in the summer, showing that the mortality risk, mainly due to predation, is almost nil in the lizard's winter phase and higher during its active period. During the active period (in this case, mid-May to end September), females have a survival rate of around 86%, while that of males is 92%, a difference of 6%. This difference in survival can probably be explained by the risks involved in reproduction: e.g. high food and thermoregulation requirements during the gestation phase and less agility during pregnancy. In our study site, the main predator could be the Montpellier snake (Malpolon monspessulanus), as it was frequently observed on site and is a great consumer of lizards, in particular ocellated lizards (Pleguezuelos 2021). The other potential diurnal predators (corvids, gulls and a pair of short-toed snake eagles nesting nearby) do not hunt on this site because the cycling path, which is highly frequented, is a disturbance.

Based on the estimated survival rates, the average life expectancy of subadult and adult ocellated lizards in this population is only 1.4 years for females and 2.3 years for males, which are very low values for a lizard of this size. Indeed, these are similar survival rates

to most small lacertid species, which have a body mass 40 times lower than the ocellated lizard. However, we found that one male reached the age of 7, two reached the age of 6, and two reached the age of 5.

Two studies using the skeletochronology method allow comparisons with our findings. In the south of France, the examination of 16 individuals resulted in an average age of 4.6 years (taking into account animals older than one year) and a maximum age of 10 (Cheylan 1984). In central Spain, an average age of 4.9 years was found in a sample of 76 individuals over the age of one, with a maximum age of at least 11 (Castilla & Castanet 1986). In captivity, the longest recorded life spans are 14 and 17 years (Decaux 1897; Flower 1925). Skeletochronology studies therefore indicate much higher life expectancy and longevity than the survival rates we obtained, which could be due to either (1) strong predation pressure at the site or (2) an underestimation of the estimated survival rate. Although it is impossible to conclusively determine which of these two hypotheses is at play in our case, it should be noted that apparent survival rates estimated by capture-mark-recapture are always intrinsically lower than the reality, since they do not distinguish between an individual that has died and one that has left the study site. Despite the fact that our study site is highly isolated, it can be assumed that a few individuals leave the site, especially subadult individuals during the dispersal phase.

The size of the subadult and adult population, estimated at between 48 and 70 individuals, shows that this is a small population, although we know that this estimate is low given that some insufficiently photographed individuals were excluded from the analysis. Due to the small size and the isolation of this population, it can be considered vulnerable in the medium term. The risk of its disappearance is exacerbated by the fact that the possibility of exchange with the closest populations is near non-existent. Previous studies on the ocellated lizard in Liguria in Italy and the French region of Alpes-Maritimes show the extent to which these populations are threatened - several have already become extinct (Deso et al. 2015). As major redevelopment work on the Var River is currently being considered, it is to be feared that this will hasten the disappearance of the ocellated lizard in this eastern part of its distribution.

# **Acknowledgements**

We would like to thank our naturalist colleagues Patrick Kern, Gérard Joannes, Monique and Guy Poncet for the photos of geo-localised individuals they kindly sent us and Elise Bradbury for the translation of this article into English.

# References

- Akçakaya, H.R. & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecological Bulletins* 48, 9-21.
- Barbault, R. & Mou, Y. P. (1988). Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. *Herpetologica* 44, 38-47.
- Beissinger, S. R. (2002). Population viability analysis: past, present, future. *In: Population viability analysis* (ed Beissinger S.R.). University of Chicago Press, Chicago, 5-17.
- Bengsen, A., Butler, J. & Masters, P. (2011). Estimating and indexing feral cat population abundances using camera traps. *Wildl. Res.* 38, 732-739.
- Berglind, S.Å. (2000). Demography and management of relict sand lizard *Lacerta agilis* populations on the edge of extinction. *Ecological Bulletins* 48, 123-142.
- Bolger, D.T., Morrison, T.A., Vance, B., Lee, D. & Farid, H. (2012). A computer-assisted system for photographic mark-recapture analysis. *Methods Ecol. Evol.* 3, 813-822.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, H.R. & Frankham, R. (2000). Predictive accuracy of population viability analysis in conservation biology. *Nature*, 404 (6776), 385-387.
- Burnham, K.P. & Anderson, D.R. (2002): Model Selection and Inference, second edition. A Practical Information-Theoretic Approach. Springer, New York.
- Castilla, M.A. & Castanet, J. (1986). Growth, age and longevity of *Lacerta lepida* assessed by skeletochronology. *In: Studies in Herpetology* (ed Rocek Z.). Charles University, Prague, 331-336.
- Cheylan, M. (1984). Croissance et détermination de l'âge chez le lézard ocellé (groupe *Lacerta lepida*, Sauria, Lacertidae) de France et du Maroc à partir de la squelettochronologie. *Bull. Mus. Hist. Nat. Marseille* 44, 29-37.
- Cheylan, M., Grillet, P. & Doré, F. (2011). Dynamique populationnelle du lézard ocellé. *In*: Thompson J. & Gauthier P. (eds), *Activités humaines et dyna*mique de la biodiversité en région méditerranéenne, CEFE, Montpellier, 25-26.
- Choquet, R., Lebreton, J.-D., Reboulet, A.-M., Pradel, R. & Gimenez, O. (2009). U-CARE: Utilities for performing goodness-of-fit tests and manipulating CApture-REcapture data. *Ecography* 32, 1071-1074.
- Comas, M., Reguera, S., Zamora-Camacho, F.J., Salvadó i Cabré, H. & Moreno-Rueda, G. (2016). Comparison of the effectiveness of phalanges vs. humeri and femurs to estimate lizard age with

- skeletochronology. *Animal Biodiversity and Conservation* 39, 237-240.
- Cruickshank, S.S. & Schmidt, B.R. (2017). Error rates and variation between observers are reduced with the use of photographic matching software for capture-recapture studies. *Amphi. Reptil.* 38, 315-325.
- Decaux C. (1897). Un lézard ocellé conservé en captivité depuis 14 ans. *La Nature* 49, 43-44.
- Deso, G., Cevasco, J-M., Salvidio, S., Ottonella, D., Oneto, F. & Cheylan, M. (2015). Statut des populations franco-italiennes de Lézard ocellé *Timon lepidus* (Daudin, 1801). *Bull. Soc. Herp. France* 156, 45-53.
- Diego-Rasilla, F. J., & Pérez-Mellado, V. (2004). Density dependence of survival in the Iberian wall lizard (*Podarcis hispanica*). *In: The Biology of Lacertid lizards. Evolutionary and Ecological Perspectives* (eds Pérez-Mellado V., Riera N., Perera A.). Institut Menorquí d'Estudis. Recerca 8, 177-200.
- Doré, F., Cheylan, M. & Grillet, P. (2015). *Le lézard* ocellé. *Un géant sur le continent européen*. Biotope, Mèze.
- Flower, S.S. (1925). Contributions to our Knowledge of the Duration of Life in Vertebrate Animals. III. Reptiles. *Proceedings of the Zoological Society of London* 95(3), 911-981.
- Galán, P. (1999). Demography and population dynamics of the lacertid lizard *Podarcis bocagei* in north-west Spain. *Journal of Zoology* 249, 203-218.
- Grillet, P., Cheylan, M. & Dusoulier, F. (2006). Évolution des habitats et changements climatique: quelles conséquences pour les populations de lézard ocellé, *Lacerta lepida* (Saurien, Lacertidés) en limite nord de distribution? *Ecologia Mediterranea* 32, 63-72.
- Grillet, P., Cheylan, M., Thirion, J.M., Doré, F., Bonnet, X., Dauge, C., Chollet, S. & Marchand, M.A. (2010). Rabbit burrows or artificial refuges are a critical habitat component for the threatened lizard *Timon lepidus* (Sauria, Lacertidae). *Biodiversity and Conservation* 19, 2039-2051.
- Jackson, R.M., Roe, J.D., Wangchuk, R. & Hunter, D.O. (2006). Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildl. Soc. Bull. 34, 772-781.
- Kelly, M. J. (2001). Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. *Journal of Mammalogy* 82, 440-449.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs* 62, 67-118.
- Le Galliard, J.F., Marquis, O. & Massot, M. (2010). Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology* 79, 1296-1307.
- Matthé, M., Sannolo, M., Winiarski, K., Spitzen-van der Sluijs, A., Goedbloed, D., Steinfartz, S. & Stachow, U. (2017). Comparison of photo-matching algorithms commonly used for photographic capture-recapture studies. *Ecol. Evol.* 7, 5861-5872.
- Nipko, R.B., Holcombe, B.E. & Kelly, M.J. (2020). Identifying Individual Jaguars and Ocelots via Pattern-Recognition Software: Comparing HotSpotter and Wild-ID. Wildl. Soc. Bull. 44, 424-433.

- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. Wildlife Monogr. 62, 1-135.
- Perera, A. & Perez-Mellado, V. (2004). Photographic identification as a non-invasive marking technique for Lacertid lizard. *Herpetol. Rev.* 35, 349-350.
- Pleguezuelos, R. M, Sá-Sousa, P., Pérez-Mellado, V., Marquez, R., Cheylan, M., Corti, C. & Martínez-Solano, I. (2009). *Timon lepidus*. The IUCN Red List of Threatened Species 2009: e.T61583A12498949. https://dx.doi.org/10.2305/IUCN.UK.2009.RLTS. T61583A12498949.en Accessed on 04 January 2023.
- Pleguezuelos, J.M. (2021). Culebra bastarda Malpolon monspessulanus. In: Enciclopedia Virtual de los Vertebrados Españoles (eds López P., Martín J., Martínez-Freiría F.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos. org/
- R Development Core Team. (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Rotger, A., Igual, J. M., & Tavecchia, G. (2020). Contrasting size-dependent life history strategies of an insular lizard. *Current Zoology* 66, 625-633.

- Sacchi, R., Scali, S., Mangiacotti, M., Sannolo, M. & Zuffi, M.A. (2016). Digital identification and analysis. *In: Reptile Ecology and Conservation. A Handbook of Techniques* (ed Dodd C.K.). Oxford University Press, New York, 59-72.
- Seber, G.A.F. (1982). *The Estimation of Animal Abundance and Related Parameters*, 2nd ed. Charles Griffin & Company Ltd, London.
- Steinicke, H., Ulbrich, K., Henle, K. & Grosse, W.R. (2000). Eine neue Methode zur fotografischen Individualidentifikation mittelerupäischer Halsbandeidechsen (Lacertidae). *Salamandra* 36, 81-88.
- Strijbosch, H. & Creemers, R.C.M. (1988). Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. *Oecologia* 76, 20-26.
- White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird study* 46, 120-139.
- Wickham, H. *et al.* (2019) Welcome to the tidyverse. *Journal of Open Source Software* 4, 1686. https://doi.org/10.21105/joss.01686
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2001). Analysis and management of animal populations, Academic Press. San Diego.