



Temporal trends in agile frog *Rana dalmatina* numbers: results from a long-term study in western France

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Reports of amphibian declines have highlighted the urgent need for long-term data sets to increase understanding of population changes. To detect population changes in the agile frog *Rana dalmatina* in Vendée, western France, counts were made of spawn masses over 16 years and road mortalities over 13 years. Long-term trends were evaluated using regression analysis of the logarithmic transforms of annual mortalities and egg masses as dependent variables against year as the independent variable. Tests of the regressions against a 0 hypothetical coefficient, indicative of population stability, gave coefficients that were positive for road mortalities and negative for spawn counts. However, neither was significantly different from 0, indicating a stable population. Further analysis using jackknifing produced a series of pseudo-regression coefficients, which agreed with the true regressions. Results from both datasets were therefore congruent and indicated wide annual fluctuations, with a major increase in numbers between 2009 and 2014. Data from spawn deposition in a recently established pond suggested that the presence of invasive crayfish *Procambarus clarkii* influenced both deposition sites and long-term population changes.

Key words: Amphibians, *Rana dalmatina*, long-term populations, spawn counts, road mortalities.

INTRODUCTION

Amphibians are widely reported as the vertebrate class most affected by the worldwide biodiversity decline (e.g. Blaustein et al., 1994; Alford & Richards, 1999; Hitchings & Beebee, 1997; Houlahan et al., 2000; Fischer, 2000; Cushman, 2006). No single contributing factor has been identified in the decline, although multifaceted interactions have been proposed (e.g. Collins & Storfer, 2003). These include time lags in density dependent responses leading to chaotic dynamics (e.g. Wilbur, 1990), climatic effects and habitat alterations by humans (e.g. Hartel, 2005; Gollmann, et al., 2002). Given the role of amphibians as both predator and prey in many ecosystems, insight into changes in their population status provides key ecological information. Current knowledge indicates frequent widespread population fluctuations with high increases in certain years, offset by moderate decreases over periods of several years (Pechmann et al., 1991; Pechmann and Wilbur 1994; Meyer et al. 1998). This suggests that short-term monitoring may introduce a degree of error when attempting to evaluate trends and hence, longer time series are required.

The primary objective of this study was to examine for changes in the numbers of agile frog *Rana dalmatina*, a species found across Europe and listed as under threat in Appendix II of the Bern Convention. It is an example of a pond-breeding amphibian that moves widely

across the landscape. Population studies in several regions of Europe including Romania (Hartel, 2008a; 2008b), Sweden (Stromberg, 1995), Austria (Gollmann et al., 1998, 2002), Greece (Sofianidou et al., 1983) and France (Combes et al., 2018) have shown that numbers fluctuate widely but none showed evidence of major long-term declines. There have been few studies of *R. dalmatina* in fragmented landscapes (Wederkinch, 1988), environments that are universally implicated in the biodiversity decline (e.g. Fischer, 2000). This paper describes changes in *R. dalmatina* numbers in a fragmented habitat in western France that includes areas of extensive agriculture bisected by hedgerows, woodland and urban areas. Additionally, in the agricultural areas, fertilisers and pesticides are applied annually, including during the breeding season (Fig. 1) and have been implicated as contributing to population decline (Beebee & Griffiths, 2005).

The data are derived from two sources; counts of spawn masses and road mortalities. Egg mass counts have been used in previous studies of *R. dalmatina* and employed as proxies to estimate the size of breeding populations. As the spawn moves to the pond surface (see example in Meek, 2012b), it is relatively easy to count compared to breeding females (e.g. Pechmann & Wilbur, 1994; Grant et al., 2005) and so reduces observer error. In addition, these frogs are frequently killed on roads and in the study locality, second only to *Bufo bufo* in this respect (Meek, 2012a). However, they differ from sympatric

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Figure 1. Google Earth map of the study locality showing sampling areas for spawn masses and surrounding habitat consisting of agricultural fields, hedgerows, woodland and urban areas. Continuous lines indicate ditches adjacent to hedgerows or woodland, broken lines ditches alongside roads. New Pond and Old Pond locations are also highlighted.

amphibians in that the peak period for road mortalities is during the summer months and hence appear not to be primarily associated with migration (Meek, 2012a). Road mortalities have been used previously to estimate population changes in amphibians (e.g. Meyer et al. 1998), snakes (Capula et al., 2014; Rugiero et al., 2018), and mammals (e.g. Mallick et al., 1998; Baker et al., 2004; Widenmaier & Fahrig, 2006). Road mortalities give only an index of abundance but are independent of spawn count and avoids double counting and autocorrelation.

METHODS

The study area (46°27'N;1°53'W) is a fragmented landscape dominated by agriculture that had experienced little or no major changes in land use during the study period from 2003 to 2018. The climate is mild oceanic (June, July and August monthly mean air temperature = 26°C; November through to February monthly mean = 10.2°C), with a period of high precipitation usually falling from October until January (monthly mean = 85.7 mm). During the summer months of June, July, and August when rainfall is low (monthly mean = 51.3 mm) it is normal for all but the largest water bodies to dry up. Figure 1 shows a map of the area where spawn masses were counted with key areas identified.

Spawn is readily visible rising to the surface of the water within days of deposition (see examples in Meek, 2012b). Daily counts were made by a single observer each spring beginning February 2003 along the edge of ditches and ponds until the end of March 2018 after which no spawn masses were deposited. Annual peak

counts were derived from the maximum number of spawn masses counted at a site in a given year. Spawn deposition was recorded in three ditches and two ponds in a woodland/wetland area on the edge of the village of Chasnais (Fig. 1). Total ditch length, using the measuring tool in Google Earth, was 1,377 m of which 1,081 m was at the roadside and 296 m next to hedgerow or woodland. New Pond (see Fig. 1) had an approximate surface area of 945 m² and was created during the summer/autumn of 2009, with the first spawn recorded in February 2010. The smaller pond (Old Pond) with a surface area of 64.1 m² had been established prior to 2003.

Data on road mortalities were collected on roads (total distance ≈16 km) between a wetland area close to the village of St Denis du Payre and the wetland next to Chasnais. The distance between the two is approximately 6 km (see Meek, 2012a for a schematic view). Surveying for road mortalities commenced in January 2005 and was undertaken between four and six times every month throughout each year until December 2017 in both study localities. Surveys were carried out by a single observer on a bicycle travelling at 5–10 km/hour. Road traffic volume increased slightly during the 13 year period from initial surveying 2005–2017 (see Meek (2012a) for traffic volumes).

Statistical analysis

Road mortalities and spawn masses were tested for departures for equality of annual counts using a *G*-test goodness-of-fit at *n*-1 d.f.. This gives the expected annual probability for spawn mass across 16 years of sampling as 1/16 = 0.0625 and for 13 years of road mortality data

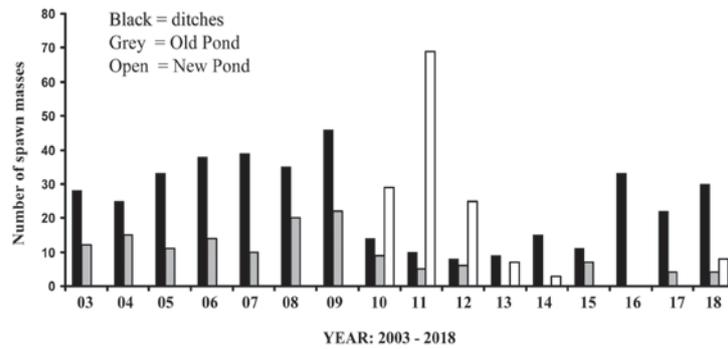


Figure 2. Changes in annual spawn counts in ditches (black bars), Old Pond (grey bars) and New Pond (open bars). See text for further details.

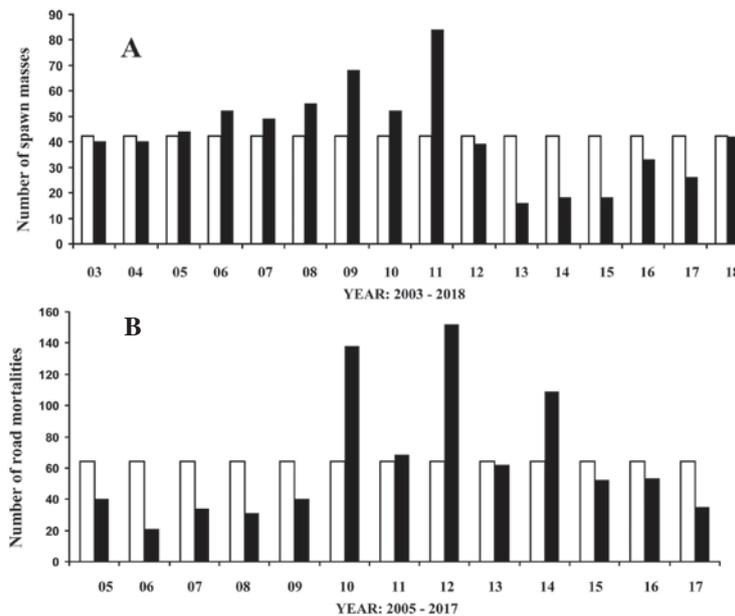


Figure 3. Histograms showing annual numbers of spawn mass (A) and road mortalities (B) as black bars. Open bars represent expected frequencies under a null hypothesis of equality of year counts. See text for further details.

as $1/13 = 0.077$. The data for road mortalities were not normally distributed (Anderson-Darling; $\alpha^2 = 0.996$, $P = 0.008$). Therefore to compare variation in annual counts of road mortalities with spawn masses, the data sets were subjected to a Leven’s test for homoscedasticity. This is less sensitive to departures from normality and considers the distances of the observations from their sample medians. The test is robust for smaller samples (Box & Jenkins, 1976) and rejects equality of variance when

$$W > F\alpha_{k-1, N-k}$$

where W is the test statistic, $F\alpha_{k-1, N-k}$ the upper critical value of the F -distribution $k-1$ and $N-k$ degrees of freedom with significance α .

To identify long-term trends in population parameters, regression analysis was applied to the logarithms of annual mortalities and spawn masses as dependent variables with year as the independent variable giving

$$\log_e N = b + m \cdot \text{year} ,$$

where $\log_e N$, represents either numbers of spawn masses or road mortalities, m the regression coefficient and b the y-intercept. The null hypothesis is that $\log_e N$ is stable when $m = 0$; significant departures from m indicate population change. Departures from 0 were evaluated using a t -test at $n-2$ d.f. (Bailey, 1995). Since unusually high or low year counts may have an inordinate effect on m , a test for influence function (Gotelli & Ellison, 2004) to estimate the errors of the true regression coefficients was made using jackknifing (Sahinler & Topuz, 2007). This method has the advantage of giving exact repeatable results by systematically removing one-year data sets from the sample. Regression analysis was re-applied to produce a series of pseudo- m values that were then compared against the true coefficients.

RESULTS

A total of 836 road mortalities were found in the surrounding area between 2005 and 2017, consisting of 338 large adults and 498 smaller frogs (*mean* number per year = 64.3 ± 42.2). Sexing adults was usually not possible

Table 1. Regression analysis of the logarithms of temporal changes in annual numbers of frog spawn masses or road mortalities as dependent variables against year as an independent variable. The regression coefficient m is shown with standard errors. The t -tests and P -values are derived from tests of the true coefficients against a hypothetical of $m = 0$, which would indicate long-term population stability. For comparison, data for *R. dalmatina* given by Stromberg (1995) and Hartel (2008b) has been subject to the same analysis. Length of the study in years is shown as n and actual numbers of spawn masses or road mortalities as Σn . See text for further details.

	m	\pm	t	p	n	source	Σn	Reference
France	-0.048	0.023	1.98	0.07	16	Spawn counts	678	This study
France	0.03	0.04	0.87	0.40	13	Rd/mortalities	836	This study
Sweden	0.067	0.037	1.18	0.10	12	Spawn counts	1692	Stromberg (1995)
Hungary	-0.013	0.03	0.46	0.66	11	Spawn counts	4484	Hartel (2008b)

due to carcass degradation due to the time present on roads. Snout to vent lengths ranged from 18 and 92 mm (mean = 49.7 ± 14.1) with the distribution skewed towards smaller individuals ($s = 0.34$, $\alpha^2 = 2.19$ $P < 0.0001$). Spawn masses totalled 678 between 2003 and 2018; 397 in 3 ditches, 139 in Old Pond and 141 in New Pond; hence the majority (58.6%) were found in ditches (Fig. 2).

Annual road mortalities differed significantly from equal year counts $G = 304.09$, $df = 12$, $P < 0.0001$). The regression of log annual road mortalities against year gave a coefficient of $m = 0.03 \pm 0.04$, which did not differ significantly from 0 ($t = 0.87$, $p = 0.40$) suggesting general long-term population stability. Mean of the tests for pseudo- m was 0.03 ± 0.038 , which was in agreement with the true m . The test for influence function of road mortalities highlighted 2012 and 2010 as unusually high observations, 2.41 and 2.2 times greater than expected respectively (Fig. 3b). None of the pseudo- m values exceeded the 95% confidence interval (P -values 0.06–0.67).

Spawn mass counts differed significantly from annual regularity ($G = 120.9$ $P < 0.0001$, $d.f. = 15$). Regression analysis of log spawn masses against year gave a negative coefficient -0.048 ± 0.023 that, although not significantly different from 0, was close to the 95% confidence interval ($t = 1.98$, $P = 0.07$). Jackknifing produced a mean pseudo- m of 0.046 ± 0.06 with the test for influence function indicating 2011 as unusually high ($\times 2.0$) and 2013 as unusually low ($\div 2.64$) years (Fig. 3a). Re-analysis after first removing 2011 and then 2013, gave marginally significant results ($P = 0.04$ in both). This represents 12.5% of the 16 samples and suggests a possible moderate long-term decline in numbers. Variances of annual road mortalities and annual spawn mass counts were not significantly different ($W = 3.3$, $p = 0.08$).

DISCUSSION

Road mortality and egg mass counts showed similar levels of population fluctuation and long-term trends. Spawn mass counts were closer to the 95% interval in the regression and might suggest moderate population decline but the jackknife analysis supported the true regression. Changes in population levels indicating decline in amphibians have been misinterpreted in earlier studies, especially when data sets are gathered

over limited time periods and populations fluctuate widely (Pechmann et al., 1991). For example, Pechmann & Wilbur (1994) suggested that amphibian populations are likely to be in decline most of the time, followed by short increases after a period of high recruitment (but see Alford & Richards, 1999). This agrees with the general pattern of change found here and with *R. dalmatina* in other areas where wide annual variation appears to be the norm, including in France (e.g. Combes et al., 2018). Application of coefficients of variation ($Cv = \delta/mean$, where δ is the standard error; Scherer & Tracey, 2011) to other *R. dalmatina* time series gave 0.5 for Sweden (Stromberg, 1995) and 0.29 for populations in Romania (Hartel, 2008b). This compares to 0.46 for egg mass counts and 0.64 for road mortalities in the present study indicating similar levels of fluctuation and long-term trends (Table 1). Values ranging from 0.29 to 1.29 have been found in North American time series for anuran egg masses cited in Scherer & Tracey (2011).

Breeding phenology showed little change during the study period and Combes et al. (2018) found no effect of precipitation and temperature on egg-clutch abundance during the active period leading up to reproduction. However, climate data from the weather station at La Rochelle-Le Bout Blanc (around 25 km from the study locality) indicated rainfall from 2009 – 2011 was higher than average, which is in good agreement with high frog numbers from 2009–2014. The subsequent years of a general decline in frog numbers could involve these high densities, since increases in intra-specific competition in larvae may impact on metamorphosis (Scott, 1990; Scott 1994). Periods of extreme cold can increase embryo mortality by encasing floating egg masses in ice. This was observed during February 2012 (Meek, 2012b) and 2018. Estimates of larval mortalities in two spawn masses in a period of freezing during 2012 that lasted for several weeks indicated survivorship of 2.7 and 3.4% (Meek, 2012b) but inspection of several ice-impacted spawn during a 7 day freezing in 2018 indicated fewer eggs were affected, especially those positioned lowest in the egg mass.

Frequent cohort failure in amphibians is often connected to pond hydroperiod and cited as an underlying cause of population fluctuation (Beebee & Griffiths, 2005; Denoel & Ficetola, 2008). Extensive dry periods with low precipitation, especially during

February, may impact on the survival of *R. dalmatina* larvae through ditch drying. This has been observed in other *R. dalmatina* populations (Hartel 2005; 2008b). Throughout the study period water was present in the ditches until around June /July but from 2016 through to 2017, low precipitation resulted in early ditch drying. Additionally, topsoil from agricultural fields (see Fig. 1) drifting into ditches during dry summers and bank burrowing activities of Coypu (*Myocastor coypus*) result in ditch silting and early drying. Larval survival was more likely affected by hydroperiod in ditches than in deeper ponds where reasonable levels were usually present later into summer.

In other areas of France, introduced predators have been cited as partly influencing the reproduction dynamics of *R. dalmatina* (Combes et al., 2018), which is in agreement with the present study. Spawn mass number decline in New Pond were likely due to the presence of alien crayfish *Procambarus clarkii*, which is known to impact on adult and especially the larvae of *R. dalmatina* and other amphibians (Ficetola et al., 2011). The decline in spawn mass numbers began 2012 and continued to 2015 when they reached zero. This trend coincided with first sightings of *P. clarkii* in New Pond during 2012 with numbers peaking in 2015. However, breeding female *R. dalmatina* returned in small numbers in spring 2018 (see Fig. 3) coinciding with *P. clarkii* absence from at least 2017. The return of algae and some macrophytes, which are heavily grazed by *P. clarkii* and mostly not present during peak numbers, suggests the decline/absence was real. Although its natural dispersal capability has been cited as low (e.g. Geiger et al., 2005), *P. clarkii* fulfils the criteria of Article 4(3) of Regulation (EU) No 1143/2014 of the European Parliament—a species wide spread in Europe and impossible to eradicate in a cost-effective manner (Souty-Grosset et al., 2016). However, an adaptive trait in *R. dalmatina* may be wide foraging behaviour (up to 1,100 m from the egg deposition site; Blab, 1986) and lack of site fidelity (Waringer-Loschenkohl, 1991; Gollmann et al., 2002; Ficetola et al., 2006) enabling breeding site selection and avoidance of *P. clarkii*. Five out of nine European species of anurans showed behaviour changes in response to *P. clarkii* presence, signalled by chemical cues from predated or injured conspecifics (Nunes et al., 2013). Removal of alien species, for example introduced goldfish (*Carassius auratus*), successfully restored *Triturus carnifex* populations in Central Italy (Mori et al., 2016) and trout removal enabled rapid recovery of *Rana muscosa* in North America (Vredenberg, 2004).

A potential weakness in any long-term study of amphibian populations concerns funding limitations and time factors involved in field work. There is also the question of whether or not the study populations form a series of meta-populations with boundaries that are difficult to delimit. Wide foraging and lack of breeding site fidelity suggests that individual *R. dalmatina* may reproduce in areas outside the study locality in certain years. However, the data for road mortalities were collected up to 6 km from the spawning area and when split into an approximate 50/50 east–west geographic, were congruent in both fluctuations and long-term

trends. Hence, breeding aggregations may have some continuity and are valuable as sampling sites. Continual monitoring of spawn mass and road mortality in addition to collecting potentially important environmental/climatic data alongside monitoring to try and identify population drivers remains a useful tool in monitoring population trends (Temple & Cox, 2009).

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REFERENCES

- Alford, R.A., Richards, S.J., (1999). Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30, 133–165.
- Bailey, N.T.J. (1995). *Statistical Methods in Biology*. Cambridge University Press, UK, pp. 255.
- Baker, P., Harris, S., Robertson, C., Saunders, G. & White, P. (2004). Is it possible to monitor mammal population changes from counts of road traffic casualties? An analysis using Bristol's red foxes *Vulpes vulpes* as an example. *Mammal Review* 34, 115–130.
- Beebee, T.J.C & Griffiths, R.A. (2005). The amphibian decline crisis: A watershed for conservation biology? *Biological Conservation* 125, 271–285
- Blab, J. (1986). *Biologie, Ökologie und Schutz von Amphibien (Biology, Ecology and Protection of Amphibians)*. Schriftenreihe für Landschaftsplege und Naturschutz. Heft 18. Kilda Verlag, Bonn, pp. 150.
- Blaustein, A. R., Wake, D. B. & Sousa, W. P. (1994). Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8, 60–71.
- Box, G. E. P. and Jenkins, G. (1976). *Time Series Analysis: Forecasting and Control*, Holden-Day, pp 575.
- Capula, M., Rugiero, L., Capizzi, D., Luiselli, L. (2014). Long-term, climate change-related shifts in monthly patterns of roadkilled Mediterranean snakes (*Hierophis viridiflavus*). *Herpetological Journal* 24, 97–102.
- Collins, J.P & Storfer, A. (2003). Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9, 89–98.
- Combes, M., Pinaud, D., Barbraud, C., Trotignon, J. & Brischox, F. (2018). Climatic influences on the breeding biology of the agile frog (*Rana dalmatina*). *The Science of Nature* (2018) 105: 5.
- Cushman S. A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128, 231–240.
- Denoel, M, & Ficetola, G. F. (2008) Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 714–728
- Ficetola, G. F., Valota M. & de Bernardi F. 2006. Temporal variability of spawning site selection in the frog *Rana dalmatina*: consequence for habitat management. *Animal Biodiversity and Conservation* 29, 157–163.
- Ficetola, G.F., Siesa, M.E., Manenti, R., Bottoni, L., De Bernardi,

- F., Padoa-Schioppa, E. (2011). Early assessment of the impact of alien species: differential consequences of an invasive crayfish on adult and larval amphibians. *Diversity and Distributions* 17, 1141–51
- Fischer, M. (2000). Species loss after habitat fragmentation. *Trends in Ecology & Evolution* 15, 396.
- Geiger, W. P., Alcorlo, P., Baltanas, A. & Montes, C. (2005). Impact of an introduced crustacean on the trophic webs of Mediterranean wetlands. *Biological Invasions* 7, 49–73
- Gollmann, G., Baumgartner, C., Gollmann, B. & Waringer-Löschenkohl, A. (1998). Breeding phenology of syntopic frog populations, *Rana dalmatina* and *R. temporaria* in suburban Vienna. *Verhandlungen der Gesellschaft für Ökologie* 29, 357–361.
- Gollmann, G., Gollmann, B., Baumgartner, C. & Waringer-Löschenkohl, A. (2002). Spawning site shifts by *Rana dalmatina* and *R. temporaria* in response to habitat change. *Biota* 3/1–2, 35–42.
- Gotelli, N.J. & Ellison, A.M. (2004). *A Primer of Ecological Statistics*. Sinauer Associates, Sunderland, USA, pp. 510
- Grant, E.H.C, R.E. Jung, J.D. Nichols, & Hines, J.E. (2005). Double-observer approach to estimating egg mass abundance of pool-breeding amphibians. *Wetlands Ecology and Management* 13, 305–320.
- Hartel, T. (2005). Aspects of breeding activity of *Rana dalmatina* and *R. temporaria* reproducing in a semi-natural pond. *North-Western Journal of Zoology* 1, 5–13.
- Hartel, T. (2008a). Long-term within pond variation of egg deposition sites in the agile frog, *Rana dalmatina*. *Biologia* 63, 1–4.
- Hartel, T. (2008b). Weather conditions, breeding date and population fluctuation in *Rana dalmatina* from central Romania. *Herpetological Journal* 18, 40–44.
- Hitchings, S. P. & Beebee, T. J. C. (1997). Genetic sub-structuring as a result of barriers to gene flow in urban *Rana temporaria* (common frog) populations: implications for biodiversity conservation. *Heredity* 79, 7117–27.
- Houlahan J. E., Findlay, C. S., Schmidt, B.R., Meyer, A. H., Sergius, L. & Kuzmin, S. L. (2000). Quantitative evidence for global amphibian population declines. *Nature* 404, 752–55.
- Mallick S. A., Hocking G. J., & Driessen M. M. (1998). Road kills of the eastern barred bandicoot (*Perameles gunnii*) in Tasmania: an index of abundance. *Wildlife Research* 2, 139–145.
- Meek, R. (2012a). Patterns of amphibian road-kill in the Vendée region of western France. *Herpetological Journal* 22, 51–58.
- Meek, R. (2012b). Low survivorship of *Rana dalmatina* embryos during pond surface freezing. *Herpetological Bulletin* 120, 32–33.
- Meyer, A. H., Schmidt, B.R. & Grossenbacher, K. (1998). *Analysis of three amphibian populations with quarter century long time series*. Proceedings of the Royal Society, London 265, 523–28.
- Mori, E., Menchetti, M., Cantini, M., Bruni, G., Santini, G & Bertolino, S. (2016). Twenty years monitoring of a population of Italian crested newts *Triturus carnifex*: strong site fidelity and shifting population structure in response to restoration. *Ethology, Ecology & Evolution* 2016, 1–14.
- Nunes, A.L., Richter-Boix, A., Laurila, A., Rebelo, R., (2013). Do anuran larvae respond behaviourally to chemical cues from an invasive crayfish predator? A community-wide study. *Oecologia* 171, 115–27.
- Pechmann, J. H. K., Scott, D. E., Semlitsch, R. D., Caldwell, J. P., Vitt, L. J. & Gibbons, J.W. (1991) Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253, 892–95.
- Pechmann, J. H. K. & Wilbur, H. M. (1994). Putting declining amphibian populations into perspective: natural fluctuations and human impacts. *Herpetologica* 50, 65–84.
- Rugiero, L., Capula, M., Capizzi, D., Amori, G., Milana, G., Lai, M., Luiselli, L. (2018). Long-term observations on the number of roadkilled *Zamenis longissimus* (Laurenti, 1768) in a hilly area of central Italy. *Herpetozoa* 31, in press.
- Sahinler, S & Topuz, D. (2007). Bootstrap and jackknifing resampling algorithms for estimation of regression parameters. *Journal of Applied Quantitative Methods* 2, 188–99.
- Scherer, R. D., & Tracey, J.A. (2011). A power analysis for the use of counts of egg masses to monitor wood frog (*Lithobates sylvaticus*) populations. *Herpetological Conservation and Biology* 6, 81–90.
- Scott, D. E. (1990). Effects of larval density in *Ambystoma opacum*: an experiment in large scale field enclosures. *Ecology* 71, 296–306.
- Scott, D. E. (1994). The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75, 1383–1396.
- Sofianidou T.S. & Kyriakopoulou-Sklavounou P. (1983). Studies on the biology of the frog, *Rana dalmatina*, during the breeding season in Greece. *Amphibia-Reptilia* 4, 125–36.
- Souty-Grosset, C., Anastácio, P.M., Aquiloni, L, Banha, F, Choquer, J., Chucholld, C. & Tricarico E. (2016). The red swamp crayfish *Procambarus clarkii* in Europe: Impacts on aquatic ecosystems and human well-being. *Limnologica* 78–93.
- Stromberg G. (1995). The yearly cycle of the jumping frog (*Rana dalmatina*) in Sweden. A 12 year study. *Scientia* (1995), 185–86.
- Temple H. J. & Cox N. A. (2009). European Red List of Amphibians. Luxembourg: Office for Official Publications of the European Communities.
- Vredenberg, V.T. (2004). Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proceedings of the National Academy of Sciences USA* 101, 7646–50.
- Waringer-Loschenkohl A. 1991. Breeding ecology of *Rana dalmatina* in Lower Austria: a 7-year study. *Alytes* 9, 121–34.
- Wederkinch, E. (1988): Population size, migration barriers and other observations of *Rana dalmatina* populations near Koge, Zeeland, Denmark. *Memoranda Societatis pro Fauna et Flora Fennica* 64, 101–03.
- Widenmaier K., & Fahrig L., (2006). Inferring white-tailed deer (*Odocoileus virginianus*) population dynamics from wildlife collisions in the City of Ottawa. In: Irwin C.L., Garrett P., McDermott K.P. (Eds.). Proceedings of the 2005 International Conference on Ecology and Transportation. Center for Transportation and the Environment, San Diego, California, 589–602.
- Wilbur, H. M. (1990). Coping with chaos: toads in ephemeral ponds. *Trends in Ecology & Evolution* 5, 37.

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