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Abstract. Climate is globally changing. In Europe, studies have highlighted an increasing trend in both the frequency and magnitude of droughts. Abrupt changes in the frequency, location, or intensity of extreme heatwaves and droughts can have direct and severe effects on wild populations. Amphibians are the planet's most threatened group of vertebrates, with over 40% of known species considered in decline. To date, researchers have mainly focused on the influence of repeated droughts on species occurrence and community composition; however, evidence of the direct impact of climatic factors on the demographic parameters of amphibians is currently not well documented. Further investigation of this issue is therefore of critical importance in order to optimize local and global wildlife conservation policies in the context of a changing climate. This study used capture–recapture data to investigate the impact of severe drought on the survival and fecundity of a threatened amphibian, the yellow-bellied toad (*Bombina variegata*, L.), as well as to predict how potential changes in the frequency of droughts might influence the population growth rate. By developing multievent capture-recapture models, we showed that severe drought has a negative impact on fecundity and postmetamorphic survival at different ontogenetic stages. Then, using stochastic matrix population models, we predicted that changes in drought frequency negatively influence the population growth rate, which is a warning sign for population persistence. Direct conservation actions are then proposed to mitigate the detrimental effects of drought on population dynamics.

Key words: amphibian; *Bombina variegata*; drought; multievent capture–recapture models.

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INTRODUCTION

Extreme climate events have been recorded to increase during the last century (McCarthyn 2001). In Europe, records indicate that the frequency and magnitude of heatwaves and droughts have increased in Europe over the last 45 yr, especially in the southern and western regions (Fink et al. 2004, Vautard et al. 2007). In combination with other environmental factors (e.g., habitat loss, disease, and biological invasion), abrupt changes in the frequency, location, or intensity of these climatic events can have direct and severe effects on wild populations (Parmesan et al. 2000). Understanding how such climatic events may influence population

persistence is therefore a critical issue in conservation biology.

Amphibians are the planet's most threatened group of vertebrates, with over 40% of known species considered in decline (Stuart et al. 2004). Many factors contribute to explain this global decline (reviewed by Houlahan et al. 2000, Kiesecker et al. 2001), including habitat loss and landscape fragmentation (Cushman 2006, Becker et al. 2007), disease (Voyles 2009), and biological invasion (Kats and Ferrer 2003). Furthermore, climate change is expected to lead to changes in population dynamics (Griffiths et al. 2010, Lowe 2012), species distribution (Scheele et al. 2012), and community composition (McMenamin et al. 2008). To date, researchers have mainly focused on the two latter areas; the direct impact of climatic factors on demographic parameters and, in turn, population viability remains poorly documented. Of the few studies considering the effect of climate change on amphibian population dynamics, low annual survival rates at adult stage have been reported due to mild winters during hibernation (Reading 2007 on *Bufo bufo*, Griffiths et al. 2010 on *Triturus cristatus*), due to heavy rainfall during breeding activity (Griffiths et al. 2010 on *T. cristatus*), and due to drought during breeding activity (Church et al. 2007 on *Ambystoma tigrinum*). A drop in recruitment has also been sometimes linked to drought (Richter et al. 2003 on *Rana sevosa*, Taylor et al. 2006 on *Ambystoma opacum*) or to heavy rainfall leading to increased flood severity (Lowe 2012 on *Gyrinophilus porphyriticus*).

However, the consequences of climatic effects on the population persistence of amphibians are unfortunately often based on supposition, and few studies have attempted to predict how potential changes in climatic conditions might affect population viability (Church et al. 2007). Investigating the influence of extreme climate events such as droughts is therefore of critical importance in order to optimize local and global wildlife conservation policies in the context of a changing climate (Shoo 2011).

In this study, we examined how severe drought impacts the survival and fecundity of a small, long-lived anuran of Western and Central Europe, the yellow-bellied toad (*Bombina variegata*), as well as the impact of potential changes in drought frequency on its population growth rate. The recent extinction of this endangered amphibian in Belgium and Luxembourg, as well as in several regions of southern and western France, is alarming and supports the idea of a widespread decline (Massemin and Cheylan 2001, Lescure et al. 2011), although the proximate causes (i.e., habitat loss and fragmentation or disease) often remain poorly documented (Warren and Büttner 2008, Canessa et al. 2013, Cayuela et al. 2015, Scheele et al. 2015).

Using capture–recapture (CR) data collected on a population of *B. variegata* in southern France, we investigated whether or not drought had a negative impact on survival at three ontogenetic stages (juvenile, subadult, and adult). It is known that severe dehydration usually has detrimental effects on many amphibian physiological systems (Hillman 2009). As a deficit of rainfall may lead to high rates of larval mortality due to pond desiccation or density-dependent factors resulting from a reduction in oviposition site availability (Berven 1990, Walls et al. 2013), we also tested whether or not drought has a detrimental influence on fecundity. Then using a stochastic matrix population model (Caswell 2001), we examined how future changes in drought frequency might influence population persistence. We predicted that a combined reduction in both recruitment and survival after metamorphosis would lead to a negative relationship between the population growth rate and drought frequency. We then discussed possible conservation management perspectives for the yellow-bellied toad.

Methods

Study area and field sampling

The study was conducted on a population of *B. variegata* located in the Ardèche department, southeastern France. The population is located along a 2.5-km segment of the Bourge River. In the study area, the species breeds in rocky pools and residual puddles in close vicinity to the river channel and hibernates in the surrounding woodland (Cayuela et al. 2011, 2013). The breeding season extends from late April to late June, and tadpole metamorphosis occurs between June and early September. The study took place over a 5-yr period between 2010 and
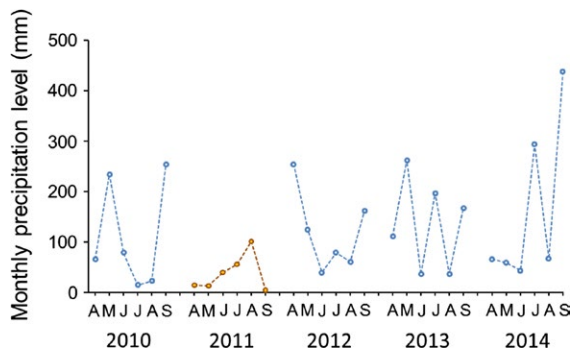
Fig. 1. Variation in precipitation levels during the active period (April to September) of *Bombina variegata* in a population in southern France between 2010 and 2014: in blue, "standard" years; in orange, drought.

2014. In France, the spring of 2011 was characterized by extremely low precipitation; the average amount of precipitation across the country was approximately 45% of the average recorded from 1971–2000. As such, it was the driest spring in the last 50 yr: drier than that of 1976 (54% of the average amount) or of 1997 (60%). During the study period in the surveyed area (see Fig. 1), monthly precipitation varied from 4.5 mm (April 2011) to 161.1 mm (September 2014), with 2011 being the driest year (a cumulative rainfall of 38.1 mm between April and September), and 2014 the wettest (438 mm between April and September).

The toads were surveyed using the CR method. Toads were caught by hand or with a dip net during daylight hours (09:00–19:00) during the breeding season, from late April to June. In the breeding season of each year, between six and nine capture sessions were carried out. At each capture session, we exhaustively sampled all the water bodies (around 500 rocky pools and residual puddles) located along the surveyed river segment. The time required to sample the whole river segment in a single session varied from 1 to 2 d. Three ontogenetic stages were considered: juveniles (captured after their first overwintering), subadults (captured after their second overwintering), and sexually mature adults (captured after at least three overwinterings). The snout–vent length ranged 22–29 mm in juveniles, 30–34 mm in

subadults, and 35–52 mm in adults. In this species, toads reach sexual maturity at the age of 3 (Plytycz and Bigaj 1993). Gender was identified on the basis of larger forearm size and the presence of nuptial pads in males (Kyriakopoulou-Sklavounou et al. 2012). We identified each individual by the specific black-and-yellow mottled pattern on its belly, which was recorded in photographs. We used the pattern-matching software Extract Compare (Hiby and Lovell 1990) to avoid misidentification.

Multievent capture–recapture model

The CR data set was modeled by extending the version of the robust design proposed by Cayuela et al. (2014). The model followed the typical structure of "standard" robust design (Kendall et al. 1997), which is made up of two nested levels of capture occasions. "Secondary sessions" include field sessions carried out in the same year. "Primary periods" correspond to yearly sessions (encompassing several secondary sessions), during which we assumed that the state of an individual was fixed and transitions between states were therefore considered between primary periods only. Because sex identification was not possible for juveniles and subadults (due to absence of nuptial pads in males), we used a multievent CR (Pradel 2005) approach to cope with the uncertainty in sex assignment, and sex was thus coded as a state instead of as a group as is usual in CR data modeling. From an initial departure state, individuals could be categorized as 1 of 11 distinct states: (UM) unborn male, (UF) unborn female, (JM) live juvenile male, (JF) live juvenile female, (SM) live subadult male, (SF) live subadult female, (BM) live sexually mature breeding male, (BF) live sexually mature breeding female, (NBM) live sexually mature nonbreeding male, (NBF) live sexually mature nonbreeding female, (†) dead individual.

The model was conditional on the first capture occasion and an "unborn individual" state was included, which allowed us to model the probability that an individual that had not yet been observed in the population recruited as a juvenile between two primary periods. Ten state transitions (detailed in Table 1) were possible for the recruitment and ontogenetic stage transition

probabilities between two primary periods as following:

Matrix (1)

$$
\begin{pmatrix}
1-\alpha^{\mathrm{JM}} & 0 & \alpha^{\mathrm{JM}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1-\alpha^{\mathrm{JF}} & 0 & \alpha^{\mathrm{JF}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \beta^{\mathrm{JM}} & 0 & 1-\beta^{\mathrm{JM}} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \beta^{\mathrm{JF}} & 0 & 1-\beta^{\mathrm{JF}} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \beta^{\mathrm{SM}} & 0 & 1-\beta^{\mathrm{SM}} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \beta^{\mathrm{SF}} & 0 & 1-\beta^{\mathrm{SF}} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\tag{1}
$$

Given that we examined recruitment without accounting for gender-dependency, $\alpha^{\mathrm{JM}}/\alpha^{\mathrm{JF}}$ were constrained to be equal (hereafter the parameter is shown as α). Moreover, age transition probabilities $\beta^{\mathrm{JM}}/\beta^{\mathrm{JF}}/\beta^{\mathrm{SM}}/\beta^{\mathrm{SF}}$ were fixed at 0 between secondary sessions and at 1 between primary periods.

After having recruited, individuals could successively transition between three ontogenetic stages, i.e., juvenile, subadult, or sexually mature adult, given that they survived. As is usual in a CR framework, survival estimates include both death and permanent emigration: i.e., apparent survival. Ten state transitions (detailed in Table 1) for survival were possible as following:

Matrix (2)

Given that the parameters ϕ^{BNM} and ϕ^{BNF} were not identifiable, $\phi^{\mathrm{BM}}/\phi^{\mathrm{BNM}}$ and $\phi^{\mathrm{BF}}/\phi^{\mathrm{BNF}}$ were constrained to be equal in the model. Survival transition probabilities were fixed at 1 between secondary sessions.

When an individual was sexually mature, we assumed that it could breed or skip breeding each year (Cayuela et al. 2014). As individuals were captured only in aquatic breeding sites, nonbreeding toads were considered as not available for capture and shifted to an unobservable state (for modeling unobservable states, see Kendall and Nichols 2002). In the model, transitions between breeding and nonbreeding states were assumed to obey a Markov chain process. Four state transitions (detailed in Table 1) for breeding or nonbreeding were possible as following:

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \phi^{\mathrm{JM}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{\mathrm{JM}} \\
0 & 0 & 0 & \phi^{\mathrm{JF}} & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{\mathrm{JF}} \\
0 & 0 & 0 & 0 & \phi^{\mathrm{SM}} & 0 & 0 & 0 & 0 & 0 & 1-\phi^{\mathrm{SM}} \\
0 & 0 & 0 & 0 & 0 & \phi^{\mathrm{SF}} & 0 & 0 & 0 & 0 & 1-\phi^{\mathrm{SF}} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi^{\mathrm{BM}} & 0 & 0 & 0 & 1-\phi^{\mathrm{BM}} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{\mathrm{BF}} & 0 & 0 & 1-\phi^{\mathrm{BF}} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{\mathrm{NBM}} & 0 & 1-\phi^{\mathrm{NBM}} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{\mathrm{NBF}} & 1-\phi^{\mathrm{NBF}} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\tag{2}
$$

Matrix (3)

$$\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BM} & 0 & 1-\gamma^{BM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BF} & 0 & 1-\gamma^{BF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBM} & 0 & \gamma^{NBM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBF} & 0 & \gamma^{NBF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix} \quad (3)$$

The transition probabilities γ^{BM}/γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$ were fixed at 1 between secondary sessions.

Concerning field observation, i.e., events *sensu* multievent modeling formulation, six observation probabilities (detailed in Table 1) were considered as following

Matrix (4)

$$\begin{pmatrix}
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1-p^{JM} & p^{JM} & 0 & 0 & 0 \\
1-p^{JF} & p^{JF} & 0 & 0 & 0 \\
1-p^{SM} & 0 & p^{SM} & 0 & 0 \\
1-p^{SF} & 0 & p^{SF} & 0 & 0 \\
1-p^{BM} & 0 & 0 & p^{BM} & 0 \\
1-p^{BF} & 0 & 0 & 0 & p^{BF} \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0
\end{pmatrix} \quad (4)$$

Note that as nonbreeding individuals were not available for recapture, their recapture probability was fixed at 0.

Biological scenarios using the E-SURGE program

This parameterization was implemented in the E-SURGE program (Choquet et al. 2009). Competitive models were ranked through a model selection procedure using Akaike information criteria adjusted for a small sample size and their derivate quantities (QAICc).

Hypotheses concerning capture and state transition probabilities were tested in an umbrella model [α(YEAR), φ(AGE × DRY), γ(SEX), p(-YEAR + AGE + SEX)]. We built 32 competing models considering all the possible combinations of factors on survival, breeding, and recapture probabilities. We tested whether survival probability differed between ontogenetic stages (AGE) by specifying state transition differences between the three stages coded as states in the model. We also examined whether survival probability varied according to drought (DRY) by including a time-specific effect in the model; transitions between the primary period 2011 (a drought year) and 2012 were specified as different from the others. In terms of breeding probability, we tested whether or not breeding/nonbreeding transitions varied according to gender by considering state transition differences between genders coded as states in the model. We also examined if recapture probability varied according to year (YEAR), gender (SEX), or ontogenetic stage (AGE). Initial-state probability IS was consistently held to be different between ontogenetic stages and gender. Moreover, we only considered year-specific recruitment probability α.

From the best-supported model, we derived the number of recruited juvenile females at t per breeding female at $t-1$ per year by using the number of individuals captured in each age class and their capture probability. The confidence interval of these estimates was calculated using parametric bootstrapping. We used this recruitment as a measure of female fecundity in matrix model simulations.

Simulation matrix model

To examine how future changes in drought frequency might influence population persistence, we built a three age-class, female-dominant, and

Table 1. Description of the parameters of the multievent capture–recapture model.

Parameter	Definition
α^{JM}	Probability that a newly metamorphosed male would be recruited (Matrix 1, line 1)
α^{JF}	Probability that a newly metamorphosed female would be recruited (Matrix 1, line 2)
β^{JM}	Probability that a juvenile male would not reach subadult stage (Matrix 1, line 3)
β^{JF}	Probability that a juvenile female would not reach subadult stage (Matrix 1, line 4)
β^{SM}	Probability that a subadult male would not reach adult stage (Matrix 1, line 5)
β^{SF}	Probability that a subadult female would not reach adult stage (Matrix 1, line 6)
ϕ^{JM}	Probability that a juvenile male would survive (Matrix 2, line 3)
ϕ^{JF}	Probability that a juvenile female would survive (Matrix 2, line 4)
ϕ^{SM}	Probability that a subadult male would survive (Matrix 2, line 5)
ϕ^{SF}	Probability that a subadult female would survive (Matrix 2, line 6)
ϕ^{BM}	Probability that a sexually mature male would survive, given it has bred (Matrix 2, line 7)
ϕ^{BF}	Probability that a sexually mature female would survive, given it has bred (Matrix 2, line 8)
ϕ^{NBM}	Probability that a sexually mature male would survive, given it has skipped breeding (Matrix 2, line 9)
ϕ^{NBF}	Probability that a sexually mature female would survive, given it has skipped breeding (Matrix 2, line 10)
γ^{BM}	Probability that a sexually mature male bred at time t, given it has bred at $t-1$ (Matrix 3, line 7)
γ^{BF}	Probability that a sexually mature female bred at time t, given it has bred at $t-1$ (Matrix 3, line 8)
γ^{NBM}	Probability that a sexually mature male skipped a breeding opportunity at time t, given it skipped breeding at $t-1$ (Matrix 3, line 9)
γ^{NBF}	Probability that a sexually mature female skipped a breeding opportunity at time t, given it skipped breeding at $t-1$ (Matrix 3, line 10)
p^{JM}	Probability that a juvenile male was recaptured during a secondary session and was observed as a juvenile (sex nonidentified in the field) (Matrix 4, line 3)
p^{JF}	Probability that a juvenile female was recaptured during a secondary session and was observed as a juvenile (sex nonidentified in the field) (Matrix 4, line 4)
p^{SM}	Probability that a subadult male was recaptured during a secondary session and was observed as a subadult (sex nonidentified in the field) (Matrix 4, line 5)
p^{SF}	Probability that a subadult female was recaptured during a secondary session and was observed as a subadult (sex nonidentified in the field) (Matrix 4, line 6)
p^{BM}	Probability that a sexually mature male (sex identified in the field) was recaptured during a secondary session (Matrix 4, line 7)
p^{BF}	Probability that a sexually mature female (sex identified in the field) was recaptured during a secondary session (Matrix 4, line 7)

prebreeding Leslie matrix (juveniles, subadults, and adults) (Caswell 2001):

$$\text{Matrix (5)} \qquad \begin{pmatrix} 0 & 0 & F*BP \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{pmatrix} \qquad (5)$$

We used the survival probability (S_1, juvenile survival; S_2, subdult survival; S_3, adult survival) from the previous CR data analysis. Fecundity was possible only for adult individuals and consisted of the recruitment estimations (F) (number of recruited juvenile females at t per breeding female at $t-1$) multiplied by the proportion of breeding females BP. The proportion of breeding females was obtained using the stable stage distribution of a two-stage matrix (breeding and nonbreeding females) with transitions between states estimated in the CR data modeling step.

We built stochastic projections based on two matrices: one on the demographic parameter estimates of "standard" years, and one on the demographic parameters of "drought" years. The frequency of drought events was then increased from 1/10 yr to 1 per year. We simulated 1000 population trajectories over 10,000 yr (k) using the stochastic process and for each simulation calculated the population growth rate using $\log(t_k) - \log(t_0)/k$. We derived the median growth rate and its 95% confidence interval using the quantiles of the resulting population growth rate distribution.

RESULT

During the survey, we carried out a total of 7827 captures (3630 males, 1659 females, 1184 subadults, and 1354 juveniles), of which 768

Table 2. Variation of *Bombina variegata* vital rates in a population in southeastern France (Bourge River); model selection procedure: *r* = model rank, *k* = number of parameters, dev = residual deviance, QAICc = Akaike information criteria adjusted for a small sample size and their derivate quantities, AGE = variation between the three ontogenetic stages (juvenile, subadult, and adult), DRY = drought, YEAR = variation between years, CST = constant.

r	Survival	Breeding	Recruitment	Recapture	k	Dev	QAICc
1	AGE × DRY	SEX	YEAR	YEAR + AGE + SEX	24	21867.77	21915.93
2	AGE × DRY	CST	YEAR	YEAR + AGE + SEX	22	21875.12	21919.24
3	AGE	SEX	YEAR	YEAR + AGE + SEX	21	21886.96	21929.07
4	AGE	CST	YEAR	YEAR + AGE + SEX	19	21894.06	21932.16
5	DRY	CST	YEAR	YEAR + AGE + SEX	18	21925.39	21961.47
6	DRY	SEX	YEAR	YEAR + AGE + SEX	20	21923.47	21963.58
7	CST	CST	YEAR	YEAR + AGE + SEX	17	21930.53	21964.61
8	CST	SEX	YEAR	YEAR + AGE + SEX	19	21928.43	21966.52
9	AGE × DRY	SEX	YEAR	YEAR	21	22285.08	22327.20
10	AGE × DRY	CST	YEAR	YEAR	19	22291.56	22329.66
11	AGE	SEX	YEAR	YEAR	18	22302.97	22339.05
12	AGE	CST	YEAR	YEAR	16	22311.30	22343.36
13	DRY	CST	YEAR	YEAR	15	22343.78	22373.84
14	DRY	SEX	YEAR	YEAR	17	22340.32	22374.40
15	CST	CST	YEAR	YEAR	14	22349.20	22377.25
16	CST	SEX	YEAR	YEAR	16	22345.55	22377.62
17	AGE × DRY	SEX	YEAR	AGE + SEX	21	21899.63	21941.75
18	AGE × DRY	CST	YEAR	AGE + SEX	19	21904.88	21942.97
19	AGE	CST	YEAR	AGE + SEX	16	21924.69	21956.76
20	AGE	SEX	YEAR	AGE + SEX	18	21917.63	21953.71
21	DRY	CST	YEAR	AGE + SEX	15	21955.26	21985.31
22	DRY	SEX	YEAR	AGE + SEX	17	21953.24	21987.32
23	CST	CST	YEAR	AGE + SEX	14	21960.93	21988.98
24	CST	SEX	YEAR	AGE + SEX	16	21965.20	21994.25
25	AGE × DRY	SEX	YEAR	CST	17	22133.04	22167.12
26	AGE × DRY	CST	YEAR	CST	15	22139.15	22169.21
27	AGE	SEX	YEAR	CST	14	22151.78	22179.83
28	AGE	CST	YEAR	CST	12	22159.58	22183.62
29	DRY	CST	YEAR	CST	11	22190.76	22212.80
30	DRY	SEX	YEAR	CST	13	22187.16	22213.21
31	CST	CST	YEAR	CST	10	22196.51	22216.54
32	CST	SEX	YEAR	CST	12	22191.75	22216.79

individuals were identified (328 males, 237 females, 73 subadults, and 130 juveniles; state at last capture). The number of juveniles identified each year varied from 36 (in 2011: drought conditions) to 145 (in 2010), the number of subadults from 8 (in 2010) to 132 (in 2011), the number of females from 94 (in 2011) to 139 (in 2014), and the number of males from 150 (in 2011) to 221 (in 2014).

The model selection procedure is provided in Table 2. The best-supported model [a(YEAR), ϕ(AGE × DRY), γ(SEX), p(YEAR + AGE + SEX)] (deviance = 32893.87, QAICc = 32938.51, QAICc relative weight = 0.91) suggested that recapture probability depended on gender, ontogenetic stage, and year (Fig. 2a). The model also indicated that breeding propensity varied between genders (Fig. 2b). The probability of breeding in two consecutive years was slightly higher in males than in females, while the probability of skipping breeding for two consecutive years was lower in males than in females. Survival probability increased with age, but was negatively influenced by drought at the juvenile and adult stages (Fig. 2c). The survival rate fell by 12% in juveniles and 10% in adults when the population experienced a severe drought. Fecundity was slightly lower during a drought event than
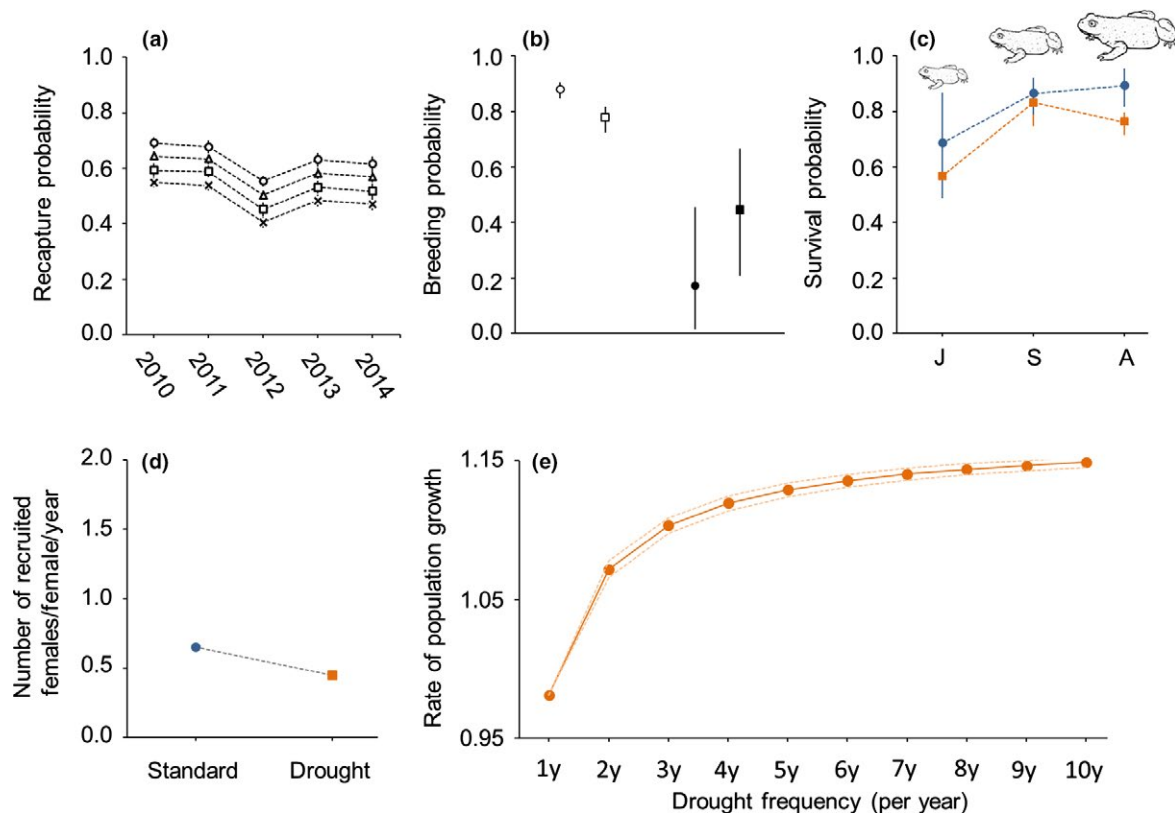
Fig. 2. Demographic parameters (mean and 95% CI) in a population of *Bombina variegata* in southern France: (a) recapture probability: circle = juvenile, triangle = subadult, cross = adult female, square = adult male, (b) breeding probability: empty circle = probability of a male breeding two consecutive times, empty square = probability of a female breeding two consecutive times, full circle = probability of a male skipping breeding two consecutive times, full square = probability of a female skipping breeding two consecutive times, (c) survival probability at three ontogenetic stages (J = juvenile, S = subadult, A = adult) in standard conditions (blue) and during a drought (orange), (d) Fecundity in standard conditions (blue) and during a drought (orange), (e) predicted population growth rate according to drought frequency (from 1 drought every year to 1 drought every 10 yr).

in normal conditions (Fig. 2d). Fecundity fell by 31% when the population experienced a severe drought.

Stochastic matrix models (Fig. 2e) predicted a 17% increase in the population growth rate from the most pessimistic scenario in which one drought is experienced every year to the most optimistic scenario of one drought per decade.

DISCUSSION

Our findings demonstrate that severe drought has an impact both on fecundity and survival at different ontogenetic stages in *B. variegata*.

Simulations show that population growth is strongly influenced by drought frequency, which is an alarming warning sign for population persistence of this endangered amphibian.

Fecundity is impacted by drought events

Our results indicate that fecundity is lower during droughts than in normal conditions; fecundity fell by 31% when the population experienced a severe drought. This decrease is likely the result of the direct effect of drought on tadpole mortality due to the desiccation of breeding sites. In *B. variegata*, high mortality rates during larval growth are usually a

consequence of hydroperiod unpredictability of oviposition sites (Morand 1997). In amphibians in general, a high deficit of rainfall leads to catastrophic breeding failure (Richter et al. 2003, Taylor et al. 2006), which may in turn strongly affect population dynamics and persistence (Scheele et al. 2012). This decrease in fecundity could also be the result of density-dependent factors (which affect larval survival, larval size, and time of metamorphosis) due to the reduction of available breeding sites during a drought leading to a concentration of tadpoles (Berven 1990). Likewise, an increase in water temperature and unstable water level of a breeding site during a drought could accelerate the development rate and lead to a lower growth rate at the larval stage. This usually results in a reduction of lipid levels and body size at metamorphosis, which leads to lower survival rates over the first overwintering (Scott et al. 2007, Tejedo et al. 2010, Schmidt et al. 2012).

Survival probability is impacted by age and drought

Our findings also show that survival is negatively influenced by drought at the juvenile and adult stages while no detrimental effect has been detected on subadult survival, likely because of a lack of statistical power (only 73 subadults in our data set). The survival rate fell by 12% in juveniles and by 10% in adults when the population experienced a severe drought. Such a deleterious effect has also been reported in frogs (Berven 1990) and salamanders (Church et al. 2007). This confirms the conclusions of a previous study in which we highlighted the adverse effect of rainfall deficit (that also occurred in spring 2011) on adult survival in *B. variegata* in a population in northeastern France (Cayuela et al. 2014). Severe dehydration has detrimental effects on the physiological systems, organs, and tissues of amphibians, affecting for instance the capacity of muscle contraction, locomotion, and aerobically supported activities (Hillman 2009). Pulmonary compliance and lung volume can facilitate lymph mobilization, which appears to be a key adaptation of anurans to dehydration because it stabilizes plasma volumes (Hillman et al. 2010). However, in bombinatorids, small lung and lymph volumes resulting from a small body

mass likely limit the species' ability to cope with severe dehydration (Withers et al. 2014). In *B. variegata*, this limitation is usually mitigated by microhabitat selection (springs and small cool streams) during the drier episodes of their annual breeding period (Beshkov and Jameson 1980, Pichenot 2008). However, in combination with a decrease in soil moisture, the desiccation of these microhabitats likely contributes to low survival rates during severe droughts.

Population growth rate is impacted by drought frequency

The stochastic matrix model predicts that potential changes in drought frequency will strongly affect the population growth rate. In this model, the population growth rate increases by 17% from the most pessimistic scenario in which one drought is experienced every year, to the most optimistic scenario of one drought per decade. Simulations using ECHAM4 and HadCM3 climate models predict that the frequency of droughts with an intensity of today's 100-yr events is likely to be more than one every 40 yr in the 2020s, and more than one every 10 yr in the 2070s in a large part of western and southern France (Lehner et al. 2006). As a result, it is likely that *B. variegata* populations located in western and southern France will experience a marked decline with a potential risk of local extinction. To test this prediction, we strongly encourage that future studies couple demographic processes and historical, present and predicted habitat suitability (using species distribution models) in order to fully understand the demographic response of this endangered amphibian to drought frequency and variation in soil moisture.

Conservation recommendations

Our results indicate that severe droughts in Western Europe can constitute a potential threat for *B. variegata* populations, which have experienced a significant decline during the last century (Massemin and Cheylan 2001, Lescure et al. 2011). We now propose conservation advices to guide management actions of conservationists.

Reducing exposure to stressful dehydration conditions is usually critical in mitigating

amphibian vulnerability and the impact of climate change on these vertebrates (Shoo 2011). *Bombina variegata* often use springs and small cool streams during the drier periods of the breeding season (Beshkov and Jameson 1980). These influence body temperature and control dehydration rates. Limiting the loss of water in an ecosystem, for example, by water retention, slowing water flow, reducing evapotranspiration, or bringing more water to ecosystems, e.g., by restoring hydraulic connections, could mitigate the detrimental effects of dehydration during droughts. Our conservation action recommendations are in line with these aims.

First, we strongly discourage draining operations in actively managed woodlands, wetland meadows used for grazing, and bogs, as this could reduce the availability of microclimate refuges. If draining is already taking place, the drains can be filled with mud. If draining operations cannot be avoided, the flow can be reduced with small dams in order to capture water during the wet season for later release during the dry season. The same result can be obtained if channels are coupled with irrigation systems in the vicinity of breeding sites. These storage devices should be located under canopy cover and close to natural springs and streams in order to maintain cool, moist conditions. Second, we stress the importance of vegetation cover, e.g., fringing riparian forests, in limiting evapotranspiration (Olson et al. 2007). In addition, large fallen logs provide a diversity of thermic refuges for amphibians, which, by limiting the desiccation risk, facilitate high species richness, especially in a floodplain area (Indermaur et al. 2009). In actively managed woodlands, harvesting should be limited in areas close to natural springs and streams (within a distance of 40–100 m) in order to preserve interstitial spaces in substrates, i.e., microhabitats (Olson et al. 2007). Third, reinstating or maintaining hydraulic connections is key. If springs are exploited for human water consumption, or the water is channeled off for irrigation, a common practice along the rivers of southeastern France, a reasonable proportion of the water volume should be left in the natural ecosystem.

Furthermore, studies showed landscape alteration may hinder or reverse the expected population response to changed climate conditions (Selwood et al. 2015). Populations in modified landscapes may decline faster than expected with the added pressures arising from climate change. For instance, Mantyka-Pringle et al. (2012) demonstrated that areas with high current temperatures and where average rainfall has decreased over time exacerbate the negative effects of habitat loss and fragmentation on species density. In addition to direct conservation actions, we thus encourage the suppression of additional stresses as habitat loss and fragmentation (see Cayuela et al. 2015), which could have, in combination with drought, synergistic detrimental effects on population dynamics of *B. variegata*.

Acknowledgments

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