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Hugo Cayuela

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Hugo Cayuela

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Pour l'obtention du grade de

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Réponses à un environnement spatio-temporellement variable:

Sexe, dispersion et tactiques d'histoire de vie

Chez le sonneur à ventre jaune (*Bombina variegata* L.)

Devant le jury composé de :

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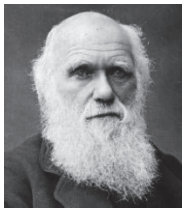
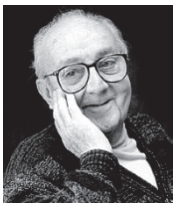


It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is most adaptable to change.

Charles Darwin (1809 – 1882)



Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful.

George Box (1919 – 2013)

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Résumé

Si la variabilité spatio-temporelle de l'environnement constitue un agent sélectif clé qui agit sur les stratégies adaptatives, la pression qu'elle exerce sur les traits d'histoire de vie, la dispersion et les choix liés à la reproduction revêt une complexité particulière pour laquelle un corpus conceptuel particulier a été développé. En affectant les schémas d'allocation de ressources aux trois principales composantes de valeur sélective que sont la maintenance, le développement et la reproduction, la variabilité environnementale régule les tactiques d'histoire de vie et le positionnement des espèces le long du slow-fast continuum. Lorsque le succès reproducteur est incertain, il est attendu qu'une longue durée de vie et un fort degré d'itéroparité, permis par une canalisation de la survie adulte, soient favorisés par la sélection naturelle. A l'échelle intraspécifique, des changements dans le régime de stochasticité de l'environnement sont aussi susceptibles d'induire des modifications des schémas d'allocation de ressources et de modifier la vitesse des cycles vitaux. Sous l'effet de fluctuations environnementales affectant la disponibilité spatiale et temporelle des ressources, ces accélérations et décélérations peuvent être accompagnées de modifications de la propension et des capacités dispersives des individus. Ces changements, potentiellement permis par des adaptations morphologiques, physiologiques ou comportementales, conduisent à l'existence d'un polymorphisme de dispersion et à l'émergence de syndromes de dispersion parmi les populations. A l'échelle individuelle, les variations spatio-temporelles de l'environnement sont aussi susceptibles d'influencer les processus de décision de reproduction et de choix de partenaires, conduisant à de profondes modifications dans la force, la forme et la direction de la sélection sexuelle.

Parce qu'il se reproduit dans des environnements aquatiques généralement instables et imprévisibles, le sonneur à ventre jaune (*Bombina variegata*) constitue un excellent modèle pour l'étude de ces processus biologiques. Dans le premier volet de ma thèse, je me suis intéressé à l'influence des variations spatio-temporelles de l'environnement sur les patrons de covariation entre les traits d'histoire de vie, la dispersion et les types comportementaux à l'échelle inter-populationnelle. J'ai examiné comment le degré de stochasticité interannuel de l'habitat de reproduction (réseaux de pièces d'eau) est susceptible de réguler le positionnement des populations le long du slow-fast continuum. J'ai par la suite étudié comment une décélération ou une accélération de ces rythmes de vie est susceptible d'être accompagnée par un syndrome de dispersion, impliquant une covariation entre la propension à disperser et des traits comportementaux (types comportementaux réactif *vs* proactif). J'ai ensuite analysé les conséquences de ce syndrome de dispersion sur les patrons de différenciation génétique dans plusieurs métapopulations exposées à des degrés contrastés de stochasticité de l'habitat de reproduction. Dans le second volet de ma thèse, je me suis intéressé au rôle de la canalisation environnementale dans la stratégie d'histoire de vie et j'ai évalué comment diverses formes de variations météorologiques (moyennes et événements climatiques extrêmes) pouvaient affecter la

dynamique de différentes populations. Dans chacune des populations, j'ai mesuré l'impact de facteurs météorologiques sur différents paramètres démographiques tels que la survie, le recrutement et les probabilités de reproduction. Mon attention s'est en particulier portée sur la contexte-dépendance des effets météorologiques sur la dynamique des populations. Dans le troisième et dernier volet de ma thèse, je me suis intéressé au choix d'accouplement des femelles de *B. variegata*, en examinant successivement les hypothèses de *bons gènes* et de *gènes compatibles* puis en me focalisant sur le rôle de la qualité et de la disponibilité des sites de reproduction sur les décisions d'accouplement des femelles. J'ai en particulier examiné comment les risques de compétition larvaire intraspécifique, un facteur déterminant pour la valeur sélective des jeunes chez les amphibiens se reproduisant dans des habitats aquatiques hautement temporaires, pouvait affecter les préférences d'accouplement des femelles. J'ai enfin ouvert des perspectives quant au rôle potentiel de la polyandrie dans l'évolution des stratégies adaptatives.

Mots-clés : stochasticité environnementale, stratégies d'histoire de vie, slow-fast continuum, syndrome de dispersion, type comportemental, démographie, différenciation génétique, choix d'accouplement, modèle des bons gènes, modèle des gènes compatibles, polyandrie, amphibien.

Abstract

Spatio-temporal variability of the environment is one of the major selective forces shaping adaptive strategies that have brought the challenge of interplay of several fields of causality. The investigation of the links between environmental variability and life history traits, dispersal and breeding decisions has indeed led to the development of a specific conceptual framework. By affecting the schedule of resource allocation during the whole lifetime between three main fitness components, namely maintenance, growth and reproduction, environmental variability regulates life history tactics and the position of the focal species along a slow-fast continuum. When the breeding success is uncertain, one might expect that a long life span and a high degree of iteroparity, allowed by a canalization of adult survival, should be favored by natural selection. At intraspecific scale, shifts in the regime of environmental stochasticity may also cause consistent modifications in the schedule of resource allocation and is expected therefore to modify the speed of life cycles. Resulting from environmental fluctuations that affect the spatio-temporal availability of resources, these acceleration or deceleration of the life cycles may be associated with modifications in both propensity and capacity of dispersal. These changes, potentially related to morphological, physiological and behavioral adaptations, lead to the emergence of a dispersal polymorphism and dispersal syndromes among populations. At individual scale, spatio-temporal variation of the environment may also influence breeding decisions and mate choice, leading to substantial shifts in the force, the form and the direction of mate selection.

The yellow-bellied toad (*Bombina variegata*) is a useful model to investigate these biological processes because it usually breeds in highly instable and unpredictable aquatic habitats. In the first part of my thesis, I have examined the influence of spatio-temporal variation of the environment on the covariation patterns between life history traits, dispersal and behavioral types at inter-population scale. I have investigated how the level of breeding habitat stochasticity (at the scale of pond archipelagoes) may regulate the position of *B. variegata* populations along the slow-fast continuum. Then, I have studied how acceleration or deceleration of the pace of life may be associated to a dispersal syndrome, implicating covariation between dispersal propensity and behavioral traits (i.e. reactive *vs* proactive behavioral types). Then I have analyzed the consequence of this dispersal syndrome on population genetic differentiation in different populations experiencing contrasting degrees of breeding habitat stochasticity. In the second part of my thesis, I have focused on the role of the environmental canalization in the life history strategy of *B. variegata* and I have evaluated how various forms of weather variation (mean and extreme events) could affect the dynamics of different populations. In each studied populations, I have quantified the impacts of weather variation on various demographic parameters as survival, recruitment and breeding probabilities. I have especially emphasized that the impact of weather variation on *B. variegata* populations is heavily context-dependent. In the third part of my thesis, I have investigated female mate choice by successively examining *good genes* and *compatible gene* hypotheses, and then by evaluating the role of breeding

habitat quality and availability on mating decision. I have especially evaluated how the risk of intraspecific larval competition, a critical factor affecting offspring fitness in amphibians breeding in highly temporary ponds, might affect female mate preferences. I have finally opened up prospects regarding potential role of polyandry in the evolution of adaptive strategies.

Keywords: environmental stochasticity, life history strategies, slow-fast continuum, dispersal syndrome, behavioral type, demography, genetic differentiation, mate choice, good gene model, compatible gene model, polyandry, amphibian.

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ANNEXE 2 . Matériel supplémentaire de l'article : Cayuela Hugo, Joly Pierre, Besnard Aurélien, Lengagne Thierry, Kaufmann Bernard, Bonnaire Eric, Pichenot Julian, Konecny Lara, Grolet Odile, Bellec Arnaud, Léna Jean-Paul. Habitat unpredictability shapes dispersal behavioral syndromes, dispersal dynamics and population genetic differentiation. Ecology, 97:2658-2670. DOI: 10.1002/ecy.1489.....228

ANNEXE 3. Matériel supplémentaire de l'article : Cayuela Hugo, Arsovski Dragan, Thirion Jean-Marc, Bonnaire Eric, Pichenot Julian, Boitaud Sylvain, Miaud Claude, Joly Pierre, Besnard Aurélien. Demographic responses to weather fluctuation are context dependent in a long-lived amphibian. Global Change Biology, 22:2076-2087. DOI: 10.1111/gcb.13290 236

INTRODUCTION GENERALE

Evolution des stratégies d'histoire de vie

Emergence du concept de stratégie d'histoire de vie

Un organisme peut être appréhendé comme le produit de trois processus biologique majeurs : la maintenance, la croissance et la reproduction. Ces trois composantes des histoires de vie sont en compétition pour des ressources limitées. Cette compétition se traduit par des compromis (i.e. des corrélations négatives) entre les différentes composantes d'histoire de vie (Gadgil & Bossert 1970, Stearns 1976, 1989). Dans cette ligne d'idée, la théorie du « soma disponible » (*disposable soma theory*, Kirkwood & Holliday 1979) postule que l'investissement dans la croissance et la reproduction constitue un détournement de ressources énergétiques au détriment de la maintenance somatique. Ainsi, la longévité est déterminée au travers de compromis entre la croissance et la reproduction d'une part et la maintenance somatique d'autre part, des modulations dans ces compromis conduisant à l'émergence de différentes stratégies d'histoire de vie (Cole 1954, Cody 1966, Williams 1966, Murphy 1968, Gadgil & Bossert 1970, Bryant 1971, Charnov & Schaffer 1973, Schaffer 1974, Stearns 1976, 1989).

Théorie des stratégies *r* et *K*

Le concept originel proposé par MacArthur & Wilson

La théorie des stratégies *r-K* a été proposée et popularisée par MacArthur et ses collaborateurs dans les années 60 et au début des années 70 (MacArthur 1962, 1972, Cody 1966, MacArthur & Wilson 1967, Pianka 1970). MacArthur & Wilson (1967) ont formulé l'idée qu'une île, lorsqu'elle était colonisée pour la première fois, possède des ressources abondantes. A mesure qu'elle est colonisée, les ressources de celle-ci s'amenuisent de telle façon que le régime de sélection auquel sont exposés les organismes passe de densité-indépendant à densité-dépendant. Cette idée a ensuite été transposée aux « îles continentales », en postulant que tous les organismes subissent des fluctuations de la taille de leurs populations à des degrés variables. De fréquentes baisses de la taille de population, causées par des facteurs extrinsèques tels que des perturbations environnementales, exposent les individus à une mortalité indépendante de la densité ; cette baisse des effectifs est suivie par une augmentation des ressources disponibles et la possibilité d'un fort accroissement démographique. Dans les populations en expansion et/ou occupant un habitat fortement fluctuant, où la capacité de charge n'est pas atteinte, la théorie des stratégies *r-K* postule que la sélection naturelle devrait favoriser les individus présentant de forts taux reproductifs. MacArthur & Wilson (1967) ont désigné cette stratégie sous le terme de « *r*-

selection » (correspondant au *r* du taux d'accroissement démographique). Chez les populations occupant des environnements plus stables, où celles-ci atteignent leur capacité de charge maximale, les individus font face à une mortalité densité-dépendante, étant exposés à une intense compétition intraspécifique. Ce régime de sélection est appelé « *K*-selection » (correspondant à la capacité de charge *K*) ; dans celui-ci, la sélection naturelle favorise les traits biologiques permettant aux individus de faire face à de faibles ressources en situation de forte compétition intraspécifique.

Application du concept à l'évolution des traits de vie

Quelques années après la parution de l'ouvrage de MacArthur & Wilson (1967) *The theory of island biogeography*, Pianka (1970) a proposé une application des principes de la théorie des stratégies de sélection *r*-*K* au cadre d'étude des traits d'histoire vie, en formulant des prédictions explicites à propos de leur évolution dans des environnements *r*-*K* et en suggérant l'existence de différentes stratégies d'histoire de vie. Ainsi, un environnement *r* présentant d'importantes ressources et une faible compétition intraspécifique devrait conduire à la sélection d'un ensemble de traits d'histoire de vie, inter-corrélés par le biais compromis d'allocation de ressources (Gadgil & Bossert 1970, Stearns 1976, 1989), favorisant une augmentation du taux d'accroissement démographique : une maturité sexuelle précoce, une petite taille corporelle, un important effort reproductif relativement à la taille du soma, une forte fécondité (gamètes femelles de petite taille) et une répartition des reproductions selon un mode sémelpare. A l'inverse, un environnement *K* avec de faibles ressources et une forte compétition intraspécifique devrait conduire à la sélection de traits favorisant une longue durée de vie, une faible fécondité et un fort de degré d'itéroparité, et de bonnes aptitudes compétitives. Ce concept a ensuite conduit à la production d'une large littérature concernant l'évolution des stratégies d'histoire de vie (voir la synthèse de Reznick 2002) et la publication d'importantes méta-analyses confirmant ces patrons de covariation entre traits d'histoire de vie (Tinkle et al. 1970, Dunham et al. 1988).

Quelques années plus tard, Stearns (1976, 1977) lançait la première critique de cette transposition du modèle *r*-*K*, en montrant que les modèles démographiques stochastiques, i.e. intégrant l'effet de variations environnementales aléatoires (Murphy 1968, Schaffer 1974), prédisent l'évolution des mêmes combinaisons de traits d'histoire de vie que celles prédites par le modèle *r*-*K*, mais pour d'autres raisons. Quand des variations aléatoires de l'environnement entrainent une forte variabilité de la survie juvénile, la sélection naturelle devrait conduire à l'évolution de stratégies d'histoire de vie combinant une maturité sexuelle tardive, un faible effort reproducteur, une faible fécondité et une forte longévité. En d'autres termes, les traits d'histoire de vie sont susceptibles de covarier entre eux dans le sens du schéma attendu sans qu'on puisse déterminer si le patron de covariation observé est mieux expliqué par le modèle *r*-*K* que par des modèles stochastiques, ni même qu'on puisse garantir que l'un

ou l'autre ne soit impliqué (voir les 6 critères proposé dans Stearns 1977). Au travers de cette critique, Stearns a proposé une alternative au modèle *r-K*, connue plus tardivement sous le terme « demographic theory » (Stearns 1992), laquelle reconnait comme principaux agents sélectifs des facteurs de mortalité extrinsèques (e.g. variations météorologiques) et établit que les patrons d'évolution des traits d'histoire de vie dépendent étroitement des classes l'âge sur lesquelles ces facteurs de mortalité agissent (*age-specific mortality*).

Théorie du slow-fast continuum

Concept et définition

Le *slow-fast continuum* apparait dans le milieu des années 1980 (Stearns 1983, 1984), même si le terme est utilisé pour la première fois par Sæther en 1987. Ce concept postule que les traits d'histoire de vie des espèces présentent des patrons de forte covariation (Stearns 1983, Harvey & Clutton-Brock 1985, Gittleman 1986, Read & Harvey 1989), permettant de les classer le long d'un continuum allant de lent (*slow*) à rapide (*fast*). A la différence du modèle *r-K*, le concept de *slow-fast continuum* ne fait aucun a priori sur les facteurs de régulation démographiques (densité-dépendants *vs* non-densité-dépendants) susceptibles de générer l'évolution de ces patrons de covariation. Chez les espèces de type *slow*, il est attendu que la sélection naturelle favorise une maturité sexuelle tardive, une faible fécondité et une longue durée de vie; les caractéristiques inverses sont attendues chez les espèces *fast*. Ce concept est supporté par des études empiriques chez une large gamme de taxons incluant les plantes (García et al. 2008), les poissons (Bjørkvoll et al. 2012), les reptiles (Clobert et al. 1998), les oiseaux (Sæther et al. 2004) et les mammifères (Promislow & Harvey 1990, Gaillard et al. 1998, 2003).

Hypothèse de canalisation environnementale

Les premiers modèles de mortalité âge-spécifique (Schaffer 1974) se sont principalement intéressés à des changements de valeur moyenne des paramètres de survie pour prédire les réponses adaptives des espèces aux variations environnementales. Ces modèles ont prédit qu'un fort degré d'itéroparité, et donc une longue durée de vie, constitue une stratégie de reproduction optimale lorsque des fluctuations environnementales induisent d'importantes variations du succès reproducteur ; à l'inverse, des variations dans la survie des reproducteurs induites par l'environnement devraient favoriser la sélection d'un mode de reproduction sémelpare. Néanmoins, ces modèles n'ont fourni aucune prédiction concernant l'amplitude des fluctuations temporelles des paramètres démographiques. Plus tard, Stearns (1992) puis Mills et al. (1999) ont mis l'accent sur l'importance conjointe de la moyenne

et de la variance temporelle des composantes de valeur sélective (survie, reproduction, âge à la maturité sexuelle). Puisque la variabilité environnementale affecte négativement les taux d'accroissement démographiques (Haldane & Jayakar 1963, Cohen 1966, Bulmer 1985, Lande & Orzack 1988, Boyce et al. 2006), il est attendu que les composantes de valeur sélective, dont les variations ont le plus fort impact sur le taux d'accroissement démographique, bénéficient d'une pression de sélection pour l'évolution de traits phénotypiques limitant l'amplitude de leurs fluctuations temporelles. Cette hypothèse est connue sous le terme de canalisation environnementale (Gaillard et al. 1998, Gaillard & Yoccoz 2003), désignant la réduction de la variabilité d'un trait donné (Gibson & Wagner 2000). Dans les histoires de vie structurées par stades ontogénétiques ou par classes d'âge, des changements identiques de valeur dans les composantes de valeur sélective peuvent avoir des effets divers sur le taux d'accroissement démographique selon la position de l'espèce le long du *slow-fast continuum.* Chez les espèces occupant l'extrémité *slow* du *slow-fast continuum*, un changement de valeur de la survie juvénile affecte moins le taux d'accroissement démographique qu'un changement proportionnellement équivalent surla survie adulte (Gaillard et al. 1998, Sæther & Bakke 2000). Chez les espèces *slow*, il est donc attendu que les traits phénotypiques minimisant les variations temporelles de survie adulte bénéficient d'une pression de sélection pour l'évolution de traits comportementaux et physiologiques (e.g. saut de reproduction, voir Cubaynes et al. 2011, Rideout & Tomkiewicz 2011, Shaw & Levin 2011). Cette hypothèse est étayée par des études empiriques chez une large gamme de taxons incluant les reptiles (Miller et al. 2011), les oiseaux (Jenouvrier et al. 2005, Rolland et al. 2010) et les mammifères (Owen-Smith & Mason 2005, Gaillard et al. 2000, Rotella et al. 2012).

Continuum de rythme de vie (*pace of life continuum*) : un concept intégrateur

Continuum de rythme de vie à l'échelle interspécifique

En incluant des caractéristiques physiologiques à l'examen des différences de traits d'histoire de vie entre espèces, le concept de continuum de rythme de vie (*pace of life continuum*) apparait comme une généralisation des concepts antérieurs de stratégies *r-K* et de *slow-fast continuum*. Celui-ci postule que des espèces fortement apparentées sont susceptibles de différer en termes de traits physiologiques (e.g. activité métabolique, activité hormonale, immunité) parce que ceux-ci coévoluent avec les caractéristiques d'histoire de vie (i.e. survie, fécondité, âge à la maturité sexuelle) de chaque espèce (Ricklefs & Wikelski 2002). Plus particulièrement, il est attendu que les espèces présentant de forts taux reproductifs et une faible survie (stratégie *r*-sélectionnée ou *fast*) aient aussi un métabolisme élevé, et vice versa(Ricklefs & Wikelski 2002, Réale et al. 2010, Careau et al. 2010). A l'échelle interspécifique, ce concept est notablement soutenu par les démonstrations empiriques proposées par Wiersma et al. (2007), puis quelques années plus tard par Williams et al. (2010), chez les oiseaux des

zones tropicales et tempérées. Ces démonstrations suggèrent que, à taille corporelle égale, les oiseaux des zones tempérées, incluant un grand nombre de migrant à long-distance, présentent des taux métaboliques basaux plus élevés que ceux des zones tropicales ; ces derniers occupent l'extrémité *slow* du *slow-fast continuum*, présentant des nichées de taille réduite (Cardillo 2002), des taux de croissance faibles (Ricklefs 1976), une longue période de dépendance aux parents après l'envol (Russell et al. 2004, Schaefer et al. 2004) ainsi qu'une survie adulte plus élevée (Fogden 1972, Snow & Lill 1974, Ricklefs 1976, 1997, Francis 1999). Par ailleurs, chez 12 espèces d'oiseaux tropicaux, une autre analyse a montré une relation négative entre le taux métabolique basal et les capacités de réponse immunitaire innée, suggérant que les espèces *slow* bénéficient d'un système immunitaire plus robuste et donc une plus grande longévité (Tieleman et al. 2005).

Continuum de rythme de vie à l'échelle intraspécifique

A l'échelle intraspécifique, plusieurs études ont proposé quasi-simultanément une nouvelle extension du concept de rythme de vie par l'inclusion de traits comportementaux (Stamps 2007, Wolf et al. 2007) ou traits de personnalité (Réale et al. 2010). Par personnalité [autrement nommé syndrome comportemental (Sih et al. 2004), *coping style* (Koolhaas et al. 1999) ou tempérament (Clarke & Boinski 1991, Boissy 1995)], il faut comprendre un ensemble de traits comportementaux inter-corrélés (Buss 1991, Gosling 2001), persistants dans le temps, généralement sous contrôle génétique (e.g. polymorphisme de séquence ou différence de profil d'expression chez le gène candidat DRD4, voir Mueller et al. 2013, 2014, Rollins et al. 2015) et de ce fait héritables (Dingemanse & Réale 2005, 2013). Selon la théorie des traits d'histoire de vie (Stearns 1992), il est attendu que le compromis adaptatif entre reproduction en cours et reproduction future induit des variations dans les régimes d'allocation de ressources au sein des populations, certains individus privilégiant plus que d'autres les gains futurs de valeur sélective (Pianka 1976, Roff 1992, Stearns 1992, Reid et al. 2003, Nussey et al. 2006. De telles divergences dans les prévisions de gains de valeur sélective devraient conduire à des différences systématiques dans le comportement individuel de prise de risques, lié par exemple à la recherche de nourriture ou à la reproduction (Clark 1994). Sur la base de ce raisonnement, le modèle théorique proposé par Wolf et al. (2007) postule que les individus priorisant la survie (et donc un étalement des gains de valeur sélective dans le temps) devraient également présenter une stratégie comportementale basée sur une minimisation des risques (*risk-adverse strategy*). Ces individus seraient relativement timides, peu agressifs, peu actifs et faiblement explorateurs (i.e. type comportemental « réactif »). A l'inverse, les individus privilégiant un fort taux reproductif devraient adopter une stratégie comportementale favorisant la prise de risques (*risk-prone strategy*). Doté d'un type comportemental « proactif », ils seraient relativement audacieux, agressifs, ainsi que plus fortement actifs et explorateurs.

Une validation empirique de l'hypothèse de Wolf et al. (2007) a été fournie par une récente étude chez une espèce de lémurien (*Microcebus murinus*). Chez cette espèce, les jeunes mâles avec de faibles gains actuels de valeur sélective mais de fortes prévisions de gains futurs présentent un type comportemental réactif alors que les mâles plus âgés, avec de forts gains actuels de valeur sélective, sont de type pro actif (Dammhahn 2012). De la même manière, une autre étude (Hall et al. 2015) chez un passereau (*Malurus cyaneus*) a montré que les individus âgés et en mauvaise condition physique, avec un faible potentiel de gains futurs de valeur sélective, présentent un type comportemental proactif et une survie apparente faible. Cette hypothèse est aussi supportée par une étude conduite chez le mouflon canadien (*Ovis canadensis*) montrant que les individus proactifs ont un plus fort succès reproducteur mais une durée de vie plus courte (Réale et al. 2009). Chez l'écureuil *Tamiasciurus hudsonicus*, les femelles présentant un type comportemental proactif ont une plus forte tendance à transmettre leur territoire à leur progéniture ce qui améliore la valeur sélective des jeunes en augmentant leur chance de survie durant l'hivernage ; ces femelles proactives ont par contre elle-même une faible survie (Boon et al. 2008).

Parallèlement aux travaux de Wolf et al. (2007), Stamps (2007) a émis l'hypothèse qu'un compromis entre la croissance et la mortalité est susceptible d'exister lorsque les traits physiologiques ou comportementaux favorisant un fort de taux de croissance impactent négativement la survie, soit durant la période de croissance soit plus tard dans la vie de l'individu (Arendt, 1997, Mangel & Stamps 2001, Biro et al. 2006). Par exemple, des individus avec un type comportemental proactif seraient plus susceptibles d'accroitre le temps alloué à la collecte de nourriture en présence d'un prédateur que les individus de type réactif, ce qui aurait pour effet d'accroitre le taux de développement tout en augmentant les risques de mortalité. L'année suivante, Biro & Stamps (2008) ont généralisé cette hypothèse en postulant que des différences interindividuelles de « productivité d'histoire de vie » (*life-history productivity*, le terme productivité correspond ici à la production de nouvelle biomasse via la croissance et la reproduction) seraient susceptibles de générer des divergences de traits de personnalité liés à l'acquisition de ressources alimentaires.

L'hypothèse proposée par Stamps (2007) et étendue par Stamps & Biro (2008) est soutenue empiriquement par de nombreuses études montrant qu'un type comportemental proactif est souvent positivement associé à de forts taux de prise alimentaire, ce qui a un effet positif sur la croissance (Yang et al. 1998, Pottinger & Carrick 2001, Ward et al. 2004, Johnson & Sih 2005, Müller & von Keyserlingk 2006, Pottinger 2006, Schjolden et al. 2006, Walsh et al. 2006), la taille à la maturité sexuelle (Johnson & Sih 2005, Walsh et al. 2006) et la fécondité (Rauw et al. 2000, Johnson & Sih 2005, Walsh et al. 2006). Les études démontrant l'existence d'un compromis entre la vitesse de développement et la mortalité sont en revanche plus rares. Par exemple, chez la demoiselle *Coenagrion hastulatum*, Brodin & Johansson (2004) ont montré que les larves issues de familles avec un type comportemental proactif (fort taux d'activité) présentaient des taux de croissance plus forts

que celles provenant de familles avec un type comportemental réactif (faible taux d'activité), mais que celles-ci subissaient aussi une plus forte mortalité en présence de prédateurs. De la même manière, chez la truite arc-en-ciel (*Oncorhynchus mykiss*), Biro et al. (2004, 2006) ont montré que les individus issus de souches domestiques artificiellement sélectionnées pour maximiser le taux de croissance intrinsèque utilisent des habitats plus productifs mais aussi plus risqués en terme de risque de prédation que les individus de souche naturelle. Ainsi, les truites de souche domestique se développent plus rapidement mais présentent une mortalité accrue en présence de prédateurs.

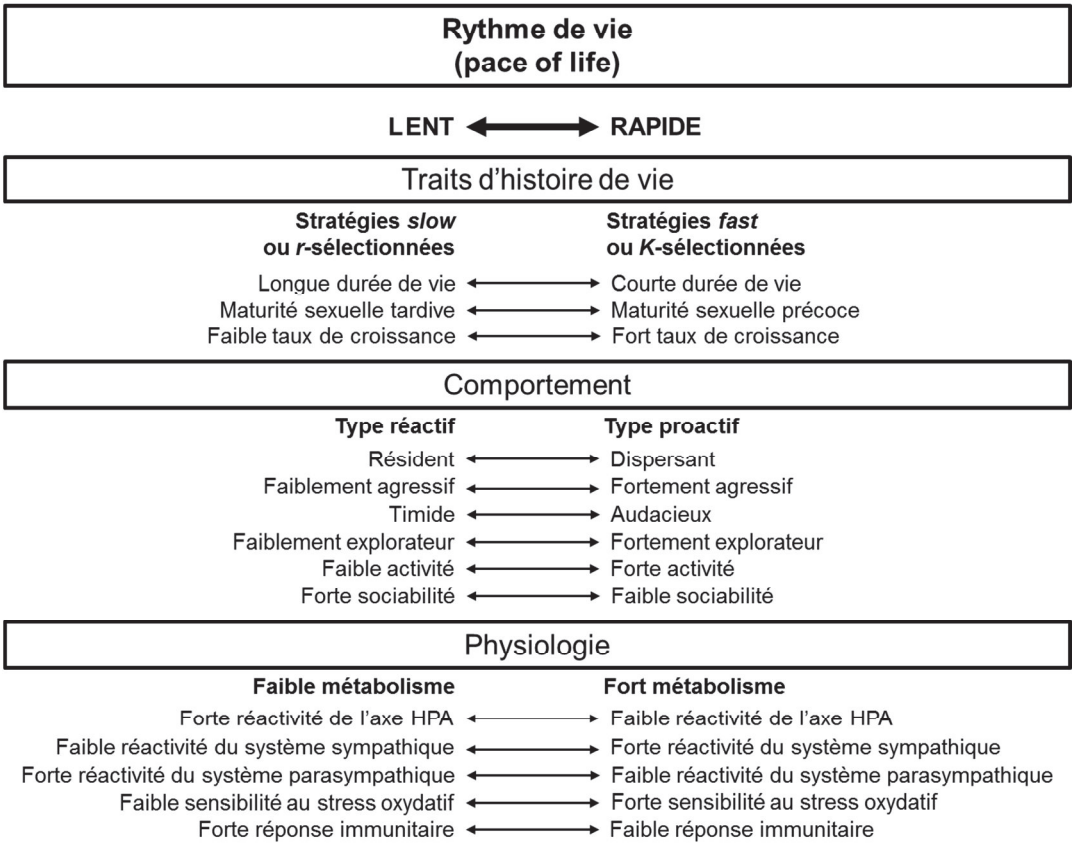

FIGURE 1. *Patron de covariations potentielles entre différents traits d'histoire de vie, traits comportementaux et traits physiologiques le long du continuum de rythme de vie (pace-of-life continuum) à l'échelle intraspécifique. Les doubles-flèches montrent les variations potentielles continues de stratégie d'histoire de vie au sein d'une population ou entre populations et leurs relations attendues avec des traits comportementaux et physiologiques (adapté de Réale et al. 2010). Axe HPA = axe hypothalamique – pituitaire – surrénal.*

Deux ans plus tard, Réale et al. (2010) propose l'inclusion du concept de personnalité animale dans l'analyse des syndromes de rythme de vie et identifie une série de covariations potentielles entre traits d'histoire de vie, traits comportementaux et traits physiologiques le long du continuum de rythme de vie, en mettant particulièrement l'accent sur des divergences intra- et inter-populationnelles (**FIGURE 1**). D'un point de vue évolutif, ces covariations entre traits pourraient résulter de facteurs génétiques tels que : la pléiotropie, c'est-à-dire un phénomène par lequel un gène code pour plusieurs caractères phénotypiques ; des liaisons génétiques, c'est-à-dire la tendance qu'ont les allèles partageant des

positions proches sur un chromosome à être hérités ensemble durant la méiose ; et des déséquilibres de liaison, impliquant une association non-aléatoire des allèles à différents loci indépendamment de leur position respective sur un chromosome Sinervo & Svensson 2002, Sih et al. 2004). Du reste, ces covariations entre traits pourraient aussi résulter de processus physiologiques et/ou développementaux communs (Sih et al. 2004).

Cas empiriques de régulation des rythmes de vie au niveau inter-populationnel

L'un des aspects novateurs de la synthèse proposée par Réale et al. (2010) est qu'elle insiste sur l'importance de rechercher ces patrons de covariation entre traits d'histoire de vie, traits comportementaux et traits physiologiques au niveau inter-populationnel. A cette échelle, des facteurs environnementaux tels que la disponibilité des ressources trophiques ou la pression de prédation semblent constituer d'importances forces sélectives agissant sur le positionnement des populations le long du continuum de rythme de vie. Concernant les traits histoires de vie, une forte pression de prédation ou de forts prélèvements cynégétiques conduisent étonnamment à une décélération des rythmes de vie chez les mammifères. Chez le chevreuil *Capreolus capreolus*, Nilsen et al. (2009) ont en effet montré que le temps de génération, une métrique robuste caractérisant la vitesse du cycle de vie (Gaillard et al. 2005), variait fortement entre populations et était inférieur à 4 ans chez les populations les plus productives tandis qu'il était généralement supérieur à 6 ans dans les populations exposées à forte pression de prédation et de chasse. Chez ces dernières, où le taux d'accroissement démographique est négatif, le ralentissement du rythme de vie n'est pas accompagné par des modifications de la fécondité ou de l'âge à la maturité sexuelle. L'interprétation de ces résultats faite par Nilsen et al. (2009) est que les populations de grands herbivores, n'étant pas capables de contrebalancer une augmentation de la mortalité par un accroissement de la fécondité et/ou une augmentation de l'effort reproductif à des âges précoces, devraient présenter un temps de génération allongé et un taux d'accroissement démographique réduit.

Chez *Thamnophis elegans*, un serpent d'Amérique du Nord, le patron temporel de disponibilité des proies génère simultanément des variations d'histoire de vie et de traits physiologiques parmi les populations. Chez les populations où la disponibilité interannuelle en proies est continue, les individus présentent une croissance plus rapide, une maturité sexuelle plus précoce, une plus forte fécondité et une plus faible survie que dans les populations exposées à une disponibilité en proies discontinue (Bronikowski & Arnold 1999, Bronikowski 2008, Miller et al. 2011). Sur le plan physiologique, les individus issus des populations à rythme de vie rapide ont une croissance plus rapide et ont en conséquence un taux moyen métabolique supérieur à ceux mesurés chez les individus provenant de populations à rythme de vie plus lent (Bronikowski & Vleck 2010). Cependant, ils présentent aussi des

taux d'activité métabolique masse-spécifique supérieurs quelques soit leur taille (Bronikowski & Vleck 2010). Par ailleurs, les taux de corticostérone plasmatiques résultant de l'induction d'un stress sont supérieurs chez les populations à rythme de vie lent (Palacios et al. 2012). Contre-intuitivement, les femelles gestantes issues de populations à rythme de vie rapide présentent des niveaux de corticostérone plus faibles que celles provenant de populations à rythme de vie lent ; néanmoins, le patron inverse est trouvé chez les jeunes produits par chaque type de femelles (Robert et al. 2009). Sur le plan comportemental, aucune étude ne semble à ce jour avoir été publiée concernant de possibles différences de types comportementaux selon de la vitesse du rythme de vie des populations de *Thamnophis elegans*.

La littérature traitant de l'influence des régimes de prédation et de disponibilité de nourriture sur les types comportementaux entre populations est relativement abondante (Sih et al. 2003, Bell 2005, Dingmanse et al. 2007, Urban 2007, Dingemanse et al. 2009, Herczeg et al. 2009). Chez l'épinoche (*Gasterosteus aculeatus*) par exemple, Dingmanse et al. (2007) ont montré que l'occurrence des types comportementaux varie entre populations et que le type proactif (dans leur cas d'étude, une forte agressivité, une activité élevé et un comportement explorateur marqué) n'est représenté que dans les grandes pièces d'eau où les prédateurs piscivores sont présents. Dans les mares de plus petite taille où les prédateurs sont absents, ces comportements sont faiblement exprimés. Chez une autre espèce d'épinoche (*Pungitius pungitius*), Herczeg et al. (2009) ont montré que les types comportementaux différaient selon que les individus proviennent de populations d'environnements marins (avec une forte abondance de prédateurs) ou de petites mares isolées (faible abondance de prédateurs). A l'inverse des résultats de Dingmanse et al. (2007), les épinoches issues des mares sans prédateurs présentent un comportement plus proactif que celles issus de l'environnement marin.

Les études empiriques montrant que différents régimes de disponibilité de nourriture ou de prédation peuvent entrainer simultanément des modifications des traits comportementaux, physiologiques et d'histoire de vie sont néanmoins plus rares. Chez les guppies (*Poecilia reticulata*), il semblerait que les populations occupant des têtes de bassins hydrographiques avec de faibles régimes de prédation aient un rythme de vie plus lent que celles présentent dans les zones situées plus en aval où la densité de prédateurs est plus importante. Chez ces dernières, les individus présentent un âge à la maturité sexuelle plus précoce, une fréquence de pontes plus importante et un investissement reproductif accru (Reznick et al. 1996). En plus de ces divergences d'histoire de vie, une étude indépendante de la première a montré que les individus provenant des populations de l'aval présentaient un type comportemental plus proactif (individus plus audacieux et plus tenaces) que ceux issus des populations l'amont (Fraser & Gilliam 1987). Un patron de covariation similaire entre traits d'histoire de vie et traits comportementaux a été mis en évidence chez une autre espèce de poissons (*Rivulus hartii*) dans ce même écosystème (Fraser & Gilliam 1987, Walsh & Reznick 2009). Néanmoins, aucune étude, même séparée, ne suggère qu'il existe des différences de traits physiologiques chez les

populations de ces deux espèces. La capucette (*Menidia menidia* ; poisson) fournit un des rares exemples empiriques d'une covariation simultanée entre des traits d'histoire de vie et des caractéristiques physiologiques et comportementales. Chez cette espèce, les populations de haute latitude exposées à des fenêtres temporelles réduites de développement, montrent un taux de prise alimentaire accru, un développement accéléré, des performances locomotrices réduites, une survie faible et une forte vulnérabilité face aux prédateurs en comparaison des populations de basses latitudes exposées à des risques de prédation plus intenses (Billerbeck et al. 2001, Lankford et al. 2001). Par ailleurs, les individus des populations de haute latitude présentent un taux d'activité métabolique plus élevé et un type comportemental plus proactif (une plus forte propension à se nourrir en présence d'un prédateur) que ceux de basses latitudes (Arnott et al. 2006, Chiba et al. 2007).

Synthèse

Le concept de continuum de rythme de vie constitue un paradigme intégrateur proposant l'existence de patron de covariation entre des traits physiologiques, comportementaux et d'histoire de vie. A l'échelle interspécifique, il postule que des espèces fortement apparentées sont susceptibles de différer en termes de traits physiologiques (e.g. activité métabolique, activité hormonale, immunité), de traits comportementaux (i.e. proactif, réactif) et de traits d'histoire de vie (i.e. survie, fécondité, âge à la maturité sexuelle) du fait de processus coévolutifs. A l'échelle intraspécifique, nos connaissances à propos de tels patrons de covariation restent fragmentaires. Par ailleurs, la majorité des études s'est intéressée à la prédation et la disponibilité des ressources alimentaires comme principaux agents sélectifs agissant sur la régulation des rythmes de vie à l'échelle intraspécifique. Le rôle de facteurs tels que la fréquence des perturbations et le degré de variabilité spatio-temporelle de l'environnement sur la régulation intraspécifique des rythmes de vie reste très méconnu.

Evolution des syndromes de dispersion

Dispersion : définition et concept

Dans cette partie, nous concentrons notre attention sur les patrons de covariations existants entre une composante particulière du continuum de rythme de vie, la dispersion, et les traits morphologiques, physiologiques, comportementaux et d'histoire de vie des organismes. La dispersion désigne le mouvement d'un individu de son site de naissance vers un site de reproduction ou entre sites de reproduction successifs (Matthysen 2012). De ce fait, il s'agit du principal mécanisme maintenant les flux de gènes au sein et entre les populations (Slatkin 1985, Bohonak 1999, Benton & Bowler 2012). La dispersion est généralement considérée comme un processus en trois étapes : l'émigration, le transfert (ou transience) et l'immigration (Ronce 2007, Matthysen 2012). Elle est multicausale, impliquant une combinaison de facteurs ultimaux et proximaux qui affectent les coûts et les bénéfices au cours des trois étapes du processus (Bonte et al. 2012). Parmi les causes ultimales, l'évitement de la dépression de consanguinité (Bengtsson 1978, Perrin & Mazalov 1999, Roze & Rousset 2005, Szulkin & Sheldon 2008, Banks & Lindenmayer 2014) et de la compétition avec des individus génétiquement apparentés (Gandon 1999, Cote & Clobert 2010, Scandolara et al. 2014) constituent deux importantes forces sélectives façonnant l'évolution du processus de dispersion lorsque l'environnement est spatio-temporellement stable. La variabilité spatio-temporelle de l'environnement, consistant notamment en des changements de stabilité ou de qualité de l'habitat, constitue aussi un facteur évolutif majeur dans l'évolution de la dispersion (Cohen & Levin 1991, McPeek & Holt 1992, Heino & Hanski 2001, Mathias et al. 2001, Friedenberg 2003, Blanquart & Gandon 2011). Parmi les causes proximales, des facteurs intrinsèques à l'individu tels que le développement (Ronce et al. 1998, Meylan et al. 2002, Vercken et al. 2007), l'état (e.g. sexe, âge, taille et condition physique : Chaput-Bardy et al. 2010, Selonen & Hanski 2010, Debeffe et al. 2012, Le Galliard et al. 2012), l'expérience (Serrano et al. 2001) et le pedigree (i.e. composante génétique du déterminisme des caractéristiques phénotypiques ; Sinervo et al. 2006, Doligez et al. 2009, Charmantier et al. 2011) affectent la propension et/ou les capacités de dispersion et d'installation. Des facteurs environnementaux et sociaux tels que des caractéristiques de l'habitat (Lin & Batzli 2001, Haynes et al. 2007, Selonen et al. 2007, Bestion et al. 2015) et des informations publiques telles que le succès reproducteur, présence et/ou la densité de conspécifiques (Doligez et al. 2004, Boulinier et al. 2008, Aragon et al. 2006) constituent aussi d'importants facteurs proximaux de la dispersion.

Les syndromes de dispersion

Syndrome de dispersion : définition et concept

Dans les années 1970, en s'appuyant sur l'idée préalablement émise qu'une population animale est constituée d'individus qualitativement différents (Chitty 1960), Myers & Krebs (1971) ont pour la première fois émis l'hypothèse et empiriquement montré que les dispersants et les résidents diffèrent qualitativement. Par suite s'est peu à peu établie l'idée que les dispersants ne constituent pas un sous-groupe aléatoire de la population mais qu'ils diffèrent des résidents sur le plan phénotypique et que la dispersion constitue de ce fait un processus phénotype-dépendant (e.g. Zera & Denno 1997, Zera et al. 2007, Philips 2009, Cote et al. 2010a). Ces différences phénotypiques constituent assez souvent des suites de traits morphologiques, physiologiques, comportementaux et d'histoire de vie inter-corrélés, dont la persistance justifie la dénomination de syndrome de dispersion (*dispersal syndome*, Clobert et al. 2009 Cote et al. 2010a, Ronce & Clobert 2012), et qui sont susceptibles d'accroitre le succès de la dispersion et/ou de modifier la balance des coûts-bénéfices de la dispersion (Ronce & Clobert 2012).

Patron de covariation entre capacités dispersives et traits démographiques

Les études empiriques suggérant l'existence de covariation entre la dispersion et les traits d'histoire de vie (survie, fécondité, décision de reproduction, âge à la maturité sexuelle) sont nombreuses, couvrant une large gamme de taxons (protozoaires ciliés : Fjerdingstad et al. 2007; papillons : Hanski et al. 2006, Saastamoinen 2007 ; amphibiens : Phillips et al. 2008a, 2010). Ces associations sont susceptibles de résulter de coûts immédiats et/ou différés induits durant les différentes phases du processus de dispersion (voir la synthèse de Bonte et al. 2012). Ces coûts, selon qu'ils soient associés à la phase d'initiation, de transfert ou d'immigration, peuvent par exemple se traduire par une hausse de la mortalité (Bonnet et al. 1999, Amo et al. 2007, Winne & Hopkins 2006, Serrano & Tella 2012, Cotto et al. 2014), une baisse de la fécondité (Karlsson & Johansson 2008, Nespolo et al. 2008, Saglam et al. 2008, Nevoux et al. 2013), ou une diminution des réponses immunitaires (Brown & Shine 2014), potentiellement associée à une augmentation de la charge parasitaire (Krkošek et al. 2009). Ces patrons de covariation peuvent aussi résulter de compromis adaptifs (*trade-off*) entre la dispersion et certains traits d'histoire de vie (e.g. durée de vie, fécondité), ces compromis pouvant être sous un contrôle génétique simple ou pléiotropique au travers de corrélations génétiques et/ou de phénomènes épistatiques (Bonte et al. 2012). Tant aux échelles interspécifiques qu'intraspécifiques, le sens et l'amplitude de ces associations entre dispersion et traits démographiques apparaissent variables, rendant la généralisation d'un patron difficile (voir la méta-analyse de Stevens et al. 2014 pour 740 espèces de vertébrés). Qui plus est, beaucoup d'études s'intéressant aux covariations entre les traits d'histoire de vie et la dispersion restent observationnelles et souffrent de certaines faiblesses

majeures, notamment en ce qui concerne la robustesse des estimations de paramètres démographiques tels que le recrutement et la survie (voir à ce propos la synthèse de Doligez & Pärt 2008).

Parmi les associations les plus communément rapportées, le syndrome du colonisateur (Baker & Stebbins 1965, Ronce et al. 2000), parfois nommé syndrome des espèces fugitives (Hutchinson 1951, Horn & MacArthur 1972, Tilman 1994) ou stratégie rudérale (Grime 1977), associe une forte capacité dispersive, une forte fécondité et une courte durée de vie à un groupe de traits coadaptés symptomatiques des habitats instables. Selon ce principe, la sélection naturelle devrait favoriser des individus avec une tactique d'histoire de vie rapide (extrémité *fast* du *slow-fast continuum*) et de fortes capacités dispersives dans les habitats instables ou nouvellement colonisés. A l'inverse, des individus avec stratégie lente (extrémité *slow* du *slow-fast continuum*) et de plus faible capacités dispersives devraient bénéficier d'un avantage sélectif dans les habitats stables et les populations établies plus anciennement (Gadgil & Solbrig 1972, Baker & Stebbins 1965, Burton et al. 2010, Perkins et al. 2013). Dans le premier cas, une faible survie et une forte fécondité caractérisent les individus avec un fort effort reproductif, lequel se définit comme la fraction de ressources allouées à la reproduction au cours de chaque épisode reproductif au détriment de la croissance et de la maintenance (William 1966, Gadgil & Bossert 1970, Stearns 1989). Une forte production de jeunes augmente les chances de colonisation de sites ou de patchs d'habitat vides avant leur colonisation par d'autres potentiels colonisateurs moins féconds et augmentent la production de propagules à partir de ces sites nouvellement colonisés (Ronce et al. 2000, Ronce & Olivieri 2004).

Cette covariation entre fortes capacités dispersives et stratégie *fast* a été récemment mise en évidence à l'échelle interspécifique Stevens et al. (2012, 2013) se sont intéressés aux patrons de covariation entre les capacités dispersives et les traits d'histoire de vie chez 142 espèces de papillons. Leurs résultats ont montré une forte association entre les caractéristiques démographiques de ces espèces et leur capacité de dispersion : une forte mobilité semble associée aux stratégies *fast* du *slow-fast continuum*. Chez ces espèces, la dispersion est mentionnée comme une stratégie permettant d'échapper temporairement à des conditions environnementales défavorable (Southwood 1988).

A l'échelle intraspécifique, cette association entre les tactiques d'histoire de vie et les capacités dispersives a été bien étudiée chez des espèces dont la répartition est en cours d'expansion (Perkins et al. 2013, Chuang & Peterson 2015). Chez *Rhinella marina*, un crapaud invasif sur le continent australien (Crossland et al. 2008, Letnic et al. 2008, Shine et al. 2010), Phillips (2009) a en effet montré que les individus situés sur le front d'invasion ont un taux de développement larvaire substantiellement supérieur à ceux issus de population plus anciennes situées dans la zone-cœur de l'aire de distribution, atteignant plus rapidement la maturité sexuelle. Ces variations de traits d'histoire de vie ont été interprétées comme un changement d'une stratégie-*K* dans les populations dans la zone-cœur vers une stratégie-*r* dans les populations localisées sur le front colonisation, contribuant à une

accélération de l'invasion (Phillips et al. 2008b, Perkins et al. 2013). Chez cette espèce introduite, ce syndrome est susceptible d'avoir évolué sous l'effet de deux forces sélectives majeures. Tout d'abord, les phénotypes dispersant sont spatialement agrégés sur le front de colonisation (seuls les meilleurs dispersants sont représentés sur le front), conduisant à des accouplements entre individus de statut de dispersion semblable (*Olympic Village effect*) (Shine et al. 2011). Deuxièmement, puisque la densité d'individus apparait plus faible sur le front de colonisation, les individus situés sur ce front subissent une compétition intraspécifique limitée et bénéficient de ce fait d'un avantage en termes de valeur sélective par rapport à leurs conspécifiques occupant les régions-cœur de l'aire de distribution. L'interaction entre ces deux forces évolutives a été nommée « spatial selection » (Phillips et al. 2008a, 2010).

Dispersion et traits morphologiques

De nombreuses études ont montré l'existence de patrons de covariation entre les capacités de dispersion des individus et leur morphologie, les résidents et dispersants étant susceptibles de varier d'un point de vue morphologique (Clobert et al. 2009, Ronce & Clobert 2012). A l'échelle intraspécifique, ce polymorphisme de dispersion implique l'existence de phénotypes spécialisés dont les caractéristiques morphologiques procurent un avantage de valeur sélective en modifiant la balance des coûts-bénéfices de la dispersion (Bonte et al. 2012). Chez les insectes par exemple, le polymorphisme de dispersion est un phénomène courant, apparaissant chez différentes lignées aux degrés d'apparentement phylogénétiques divers (Zera & Denno 1997). Deux grandes catégories de polymorphismes de dispersion ont été reconnues chez les insectes : tout d'abord, un polymorphisme alaire (*wing polymorphism*) qui s'exprime par l'existence de phénotypes volants dotés d'ailes complètement développées (ailés, macroptères) et de phénotypes non-volants dotés d'ailes réduites (brachyptères, microptères) ou tout simplement dénués d'aile (Harrison 1980, Roff 1986, Roff & Fairbairn 1991); ensuite un polymorphisme musculaire-alaire (*flight-muscle polymorphism*) lequel implique des variations dans la taille des muscles liés au vol (Fairbairn & Desranleau 1987, Zera et al. 1997, Marden 2000). Chez de nombreuses autres espèces animales, les différences morphologiques entre résidents et dispersants sont moins spectaculaires et sont plus généralement quantitatives que discrètes (Clobert et al. 2009). Par exemple, des contrastes de taille (ou de masse) et de condition corporelle entre phénotypes résidents et dispersants ont été rapportés chez différents organismes; en particulier, des études ont montré que les dispersants disposent d'une meilleure condition physique (mammifères : Wahlström & Liberg 1995 ; oiseaux : Belthoff & Dufty 1998, Barbraud et al. 2003 ; reptiles : Meylan et al. 2002) et/ou d'une plus grande ou d'une plus petite taille que les résidents (insectes : Anholt 1990, Saastamoinen et al. 2012 ; mammifères : O'Riain et al. 1996 ; reptiles : De Fraipont et al. 2000, Sinervo et al. 2006).

Dispersion et traits physiologiques

Des différences physiologiques ont aussi été observées entre résidents et dispersants (Clobert et al. 2009, Ronce & Clobert 2012). Tout d'abord, le développement de caractères phénotypiques affectant la dispersion au cours des phases d'émigration, de transfert et d'immigration qui sont régulés par des facteurs endocriniens. Chez les insectes par exemple, le polymorphisme allaire est placé sous le contrôle de régulateurs endocriniens, à travers l'action de deux types d'hormones majeures : l'hormone juvénile (JH) et la 20-OH ecdysone (Zera et al. 2007). Ces deux hormones régulent en particulier le développement des ailes et des muscles allaires associés chez les phénotypes ailés et macroptères (Zera & Denno 1997, Hartfelder & Emlen 2012, Hardie & Lees 2013). Chez les vertébrés, il a été montré que les dispersants peuvent présenter des taux de testostérone (Woodroffe et al. 1995, Holekamp & Smale 1998, Holekamp & Sisk 2003) et corticostérone/cortisol (Belthoff & Dufty 1998, Silverin 1997, Cease et al. 2007, Hamann et al. 2007) dans le plasma plus élevés que les résidents, sans qu'il soit néanmoins possible de déterminer si ces différences constituent une cause proximale ou résultent de processus physiologiques en cascade induits par l'augmentation générale de l'activité métabolique durant la phase de transfert. Par ailleurs, des différences de taux d'activité métabolique ont été mis en évidence entre les phénotypes résidents et dispersants, ces derniers présentant une activité respiratoire plus importante durant les épreuves de vol (Crnokrak & Roff 2002, Haag et al. 2005).

Dispersion et traits comportementaux

En plus de ces différences de traits démographiques, morphologiques et physiologiques, les phénotypes résidents et dispersants sont aussi susceptibles de différer sur le plan comportemental (Réale et al. 2010, Ronce & Clobert 2012). Si ces différences ont été largement mises en évidence chez une vaste gamme de taxons (arthropodes : Bonte et al. 2004 ; poissons : Fraser et al. 2001 ; amphibiens : Maes et al. 2013; reptiles : Aragon et al. 2006 ; oiseaux : Belthoff & Dufty 1998 ; mammifères : O'Riain et al. 1996), une question restée longtemps irrésolue était de savoir si les dispersants présentent des traits comportementaux différents de ceux des résidents au cours du processus de dispersion seulement (i.e. dispersion comportement-dépendante), ou si ces différences sont stables et persistantes à l'échelle de la vie des individus (i.e. dispersion personnalité-dépendante). Un nombre grandissant d'études indique que la propension à disperser, les capacités de transfert et d'installation semblent corrélées à des types comportementaux (i.e. personnalité) stables au cours de l'ontogénèse et au travers de différentes situations (voir les synthèses suivantes : Clobert et al. 2009, Cote et al. 2010a, Ronce & Clobert 2012, Sih et al. 2012). Un type comportemental proactif, incluant une forte activité, une forte propension à l'exploration, une forte agressivité, une faible sociabilité et

un fort niveau de hardiesse, est généralement associé à un phénotype dispersant ; à l'inverse, un type comportemental réactif est assez souvent corrélé à un phénotype résident (Ronce & Clobert 2012). Le type comportemental est susceptible d'influencer la dispersion au cours des trois stades du processus (i.e. émigration, transfert et immigration, Cote et al. 2010a). Concernant le stade d'émigration, chez la souris *Mus musculus* par exemple, le temps de latence avant l'initiation de la phase de transfert décroit à mesure que la propension à l'exploration augmente (Krackow 2003). Chez les macaques rhésus (*Macaca mulatta*), les mâles les plus agressifs dispersent plutôt durant leur adolescence que les mâles moins agressifs (Kaplan et al. 1995, Taub & Vickers 1995). Concernant la phase de transfert, chez la mésange charbonnière (*Parus major*), la propension à l'exploration et le niveau de hardiesse sont positivement corrélés à la distance de dispersion natale (Dingemanse et al. 2003 ; mais voir aussi Quinn et al. 2011). Fraser et al. (2001) ont mis en évidence un patron similaire chez les killis de Trinidad (*Rivulus hartii*). Par ailleurs, chez les gambusies (*Gambusia affinis*), le niveau de socialité est négativement corrélé à la distance de dispersion, suggérant qu'une dispersion personnalité-biaisée joue vraisemblablement un rôle prépondérant dans l'invasion biologique de cette espèce (Cote et al. 2010b). Enfin, concernant la phase d'immigration chez *Parus major*, Dingemanse et al. (2003) ont montré que les immigrants présentent un type comportemental plus proactif que les individus nés localement.

Facteurs environnementaux et régulation des syndromes de dispersion au niveau inter-populationnel

Au niveau inter-populationnel, des facteurs environnementaux tels que la fragmentation et la stabilité de l'habitat constituent d'importantes forces sélectives agissant sur l'évolution de la dispersion (Ronce et al. 2000, Baguette et al. 2012). La fragmentation de l'habitat résulte de la disparition progressive d'un habitat donné qui entraine des changements à la fois dans la surface et la configuration spatiale des patchs d'habitat restants, ce qui a des conséquences sur la connectivité fonctionnelle entre ceux-ci (Fahrig 2003). Des modèles théoriques (Travis & Dytham 1999, Heino & Hanski 2001, Mathias et al. 2001) postulent qu'en affectant la balance des coûts-bénéfices de la dispersion le degré de fragmentation de l'habitat, en combinaison avec des facteurs populationnels (e.g. *kin competition*, consanguinité, succès reproducteur) est susceptible de modeler l'évolution des taux dispersion. De façon intéressante, ces modèles prédisent aussi l'émergence d'un polymorphisme de dispersion en fonction de la configuration et de la qualité des patchs d'habitats restant. Des preuves empiriques soutiennent l'existence de tels polymorphismes dans les populations naturelles. Sur le plan morphologique, chez les insectes par exemple, un polymorphisme alaire existe chez les populations de paysages fragmentés et relativement continus (Taylor & Merriam 1995, Merckx et al. 2003, Merckx & Van Dyck 2006). Chez la demoiselle *Caleopteryx maculata* par exemple, les individus issus de populations de paysages fragmentés ont en moyenne des ailes plus longues et plus large que ceux

provenant de populations de paysages continus (Taylor & Merriam 1995), ce qui améliore leurs performances de vol et les chances de succès de la dispersion. De la même manière, Merckx & Van Dyck (2006) ont montré que les papillons issus de population de paysages fragmentés investissent plus d'énergie dans le développement du thorax comparés à ceux de population subissant des paysages moins fragmentés. Sur le plan comportemental, le degré de fragmentation de l'habitat est aussi susceptible d'entrainer un polymorphisme chez les traits comportementaux reliés à la dispersion. Par exemple, chez un lépidoptère (*Pararge aegeria*), les individus issus de populations de paysages faiblement fragmentés présentent une plus forte activité et une plus forte propension à l'exploration que ceux provenant de populations exposées à des paysages fortement fragmentés (Merckx et al. 2003). A l'inverse, une étude chez des amphibiens (*Bufo bufo*) a mis en évidence une relation positive entre la propension à l'exploration et le degré de fragmentation des habitats auxquels les populations sont exposées (Janin et al. 2012). Ce patron est aussi retrouvé dans les travaux de Brodin et al. (2012) chez une autre espèce d'anoures (*Rana temporaria*), lesquels ont montré que les individus de populations fortement isolées (insulaires) sont plus audacieux et plus explorateurs que les individus provenant de populations moins isolées (continentales), et que ces types comportementaux sont stables à différents stades ontogénétiques (têtards et métamorphes).

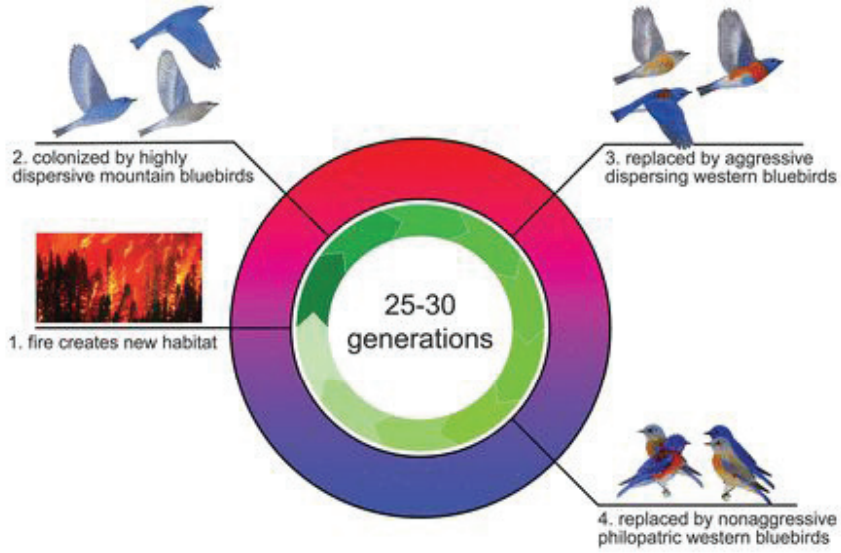

FIGURE 2. *Cycle de remplacement des espèces de Merles bleus dans des habitats post-incendie (extrait de Duckworth et al. 2015). Un nouveau patch d'habitat est produit à la suite d'un incendie (1) et est colonisé par des Merles bleus des montagnes (Sialia currucoides) qui sont exclus par compétition interspécifique par le phénotype dispersant-agressif de Merle bleus de l'ouest (Sialia mexicana) (3). Celui-ci est ensuite progressivement remplacé par le phénotype résident-social de Merle bleus de l'ouest (Sialia mexicana) (4). Le dégradé de rouge à violet montre la réduction du degré d'agressivité associé à une augmentation de la densité de conspécifiques. L'anneau vert indique la chute prédite dans la disponibilité des nids à mesure que la densité augmente.*

Des modèles théoriques prédisent que la variabilité spatio-temporelle de l'environnement (i.e. variations spatiale et temporelle de la capacité de charge, McPeek & Holt 1992 ; quantité et durée de persistance des patchs d'habitats, Paradis 1998, Travis & Dytham 1999 ; fréquence des perturbations,

Reigada et al. 2015) est susceptible de constituer une importante force sélective agissant sur l'évolution des taux de dispersion et favorisant la sélection d'un polymorphisme de dispersion aux échelles intra- et inter-populationnelles. Des études empiriques soutiennent l'hypothèse de l'existence d'un tel polymorphisme dans les populations naturelles. Par exemple, sur le plan morphologique, de nombreux travaux portant sur le polymorphisme alaire chez les insectes ont mis en évidence que la perte évolutive des ailes est souvent associée à l'utilisation d'habitats stables et persistants, que la fréquence d'individus macroptères dans les populations est négativement corrélées avec le degré de persistance de l'habitat (Harrison 1980, Roff 1990, Denno 1994, Denno et al. 1996, 2001, Zera & Denno 1997, Simmons & Thomas 2004) et que ces variations de longueur d'ailes sont héritables (Berggren et al. 2012). Le temps de persistance de l'habitat, en combinaison avec la densité de conspécifiques, est aussi susceptible de générer un polymorphisme des traits comportementaux reliés à la dispersion. Un bon exemple empirique est celui des Merles bleus de l'ouest (*Sialia mexicana*) (voir **FIGURE 2**), chez lesquels la disponibilité des sites de nidification (cavités dans les arbres morts) dépend de l'intensité des feux de forêt qui créent des patchs d'habitats temporairement favorables (Duckworth et al. 2012). Chez cette espèce, la propension à la dispersion est associée à deux phénotypes comportementaux distincts : les dispersants présentent un type comportemental proactif et sont hautement agressifs tandis que les résidents sont non-agressifs (Duckworth & Badyaev 2007, Duckworth 2008). Dans ce cas précis, l'agressivité et les capacités dispersives sont fonctionnellement intégrées parce que la colonisation de nouveaux patchs d'habitat par les mâles dispersants requiert de disposer d'aptitudes compétitives leur permettant d'éliminer les compétiteurs hétérospécifiques durant la colonisation de nouveaux sites. Dans ce système, la valeur sélective de chaque phénotype varie en fonction de l'âge des populations et de la densité de congénères (Duckworth et al. 2012). Dans les populations anciennes et bien établies, les mâles avec le phénotype résident-sociable, malgré leurs faibles aptitudes compétitives, bénéficient d'une meilleure valeur sélective que ceux avec un phénotype dispersant-agressif. En restant dans leur population natale, ils parviennent à obtenir un territoire en coopérant avec les individus apparentés. A l'inverse, les mâles avec le phénotype dispersant-agressif ont une meilleure valeur sélective dans les populations récentes où la densité de congénères est faible que dans les populations plus anciennes où le nombre de conspécifiques est plus important, ceci résultant vraisemblablement d'un trade-off entre la compétition entre mâles et la qualité des soins parentaux (Duckworth 2006).

Impact des syndromes de dispersion sur le fonctionnement des populations spatialement structurées

Dispersion et fonctionnement des populations spatialement structurées

Pour toute population isolée disposant de ressources finies, puisque l'environnement varie inexorablement dans le temps, la théorie prédit une extinction de celle-ci sur le long terme par le simple fait du hasard (Renshaw 1993). En conséquence, dans le cas des populations spatialement structurées, si aucun mouvement ne s'effectue entre sous-populations ou patchs d'habitat, la population globale s'éteindra inévitablement (Andrewartha & Birch 1954, Levins 1969, Harrison 1991, Hanski 1999). En permettant aux patchs éteints d'être recolonisés ou aux sous-populations de faible densité d'être alimentées par l'apport de nouveaux migrants (i.e. *rescue effect*), la dispersion module le degré d'interconnexion entre les sous-éléments de la population globale ; appelée métapopulation (Levin 1969, Hanski 1991, Hastings 1991) ou *patchy population* (*sensu* Harrison 1991) selon l'intensité des flux dispersifs et le degré de synchronisation démographique entre les patchs (Gilpin 2012). La dispersion influence de ce fait la contribution relative des processus démographiques locaux (e.g. survie, recrutement) et des processus régionaux (émigration, immigration) à la dynamique des populations (Hanski 1999, Freckleton & Watkinson 2002, Gilpin 2012). Du reste, elle affecte de façon plus générale la composition phénotypique des sous-populations, en particulier si la dispersion est phénotype-dépendante (Clobert et al. 2009, Cote et al. 2010a). La dispersion façonne aussi la dynamique génétique des métapopulations au travers de la modulation des flux de gènes et des modifications de composition génétique au sein et entre les sous-populations (Hanski & Gaggiotti 2004, Benton & Bowler 2012). Du reste, elle affecte aussi la dynamique évolutive des métapopulations via la régulation de la composition phénotypique et la dynamique génétique et aux travers de potentiels effets sur l'*inbreeding/outbreeding* et les adaptations locales ou à larges échelles (Saccheri & Hanski 2006, Hanski et al. 2011).

Conséquences démographiques des syndromes de dispersion

Les conséquences démographiques des syndromes de dispersion restent à ce jour assez peu étudiées (Ronce & Clobert 2012). Nous avons précédemment discuté l'existence de patrons de covariation entre les caractéristiques dispersives et des traits d'histoire de vie tels que la survie et la fécondité. En particulier, nous avons mis un accent particulier sur le fait que la dispersion constituerait une adaptation dans les environnements spatio-temporellement variables où la sélection naturelle favoriserait des stratégies de type *r* ou *fast*, ce qui conduirait à une coévolution entre les traits reliés à

la dispersion, la dispersion elle-même et les caractéristiques démographiques des populations naturelles. Néanmoins, les effets des syndromes de dispersion sur le fonctionnement des métapopulations à proprement parler restent assez spéculatifs. Sur le plan théorique, Clobert et al. (2009) ont proposé trois scénarii concernant les effets d'une dispersion phénotype-dépendante sur la dynamique d'une métapopulation (**FIGURE 3**), en imaginant un système composé de deux phénotypes (en l'occurrence des individus colonisateurs et des individus suiveurs) dans lequel la dispersion est informée (*informed dispersal*, concept selon lequel les individus accumulent et transmettent des informations avant et durant leur mouvement dans le paysage, voir par exemple Reed et al. 1999 chez les oiseaux). Dans la situation hypothétique où aucune extinction ne se produit (**FIGURE 3a**), une métapopulation composée uniquement de suiveurs peut être viable. Dans le cas plus réaliste où des extinctions locales se produisent régulièrement (**FIGURE 3b**), aucune (re)colonisation n'est possible à cause du comportement résident des suiveurs et l'existence des colonisateurs devient alors nécessaire pour la viabilité de la métapopulation (voir les simulations fournies dans le même article par Clobert et al. 2009).

Dans le troisième et dernier scénario (**FIGURE 3c**), les colonisateurs établissent les premiers de nouvelles populations, puis ces nouvelles populations sont renforcées par les suiveurs. L'immigration des suiveurs peut progressivement conduire les populations nouvellement établies à atteindre la capacité de charge maximale de l'habitat. Cette dernière situation théorique est supportée par des travaux empiriques précédemment évoqués chez le merle bleu de l'ouest (*Sialia mexicana*) (Duckworth & Badyaev 2007, Duckworth 2012) et le crapaud buffle (*Rhinella marina*) (Phillips 2009, Perkins et al. 2013). Dans les deux cas, ce syndrome du colonisateur (Baker & Stebbins 1965, Ronce et al. 2000) semble avoir substantiellement étendu les aires de répartition locale et accéléré les invasions biologiques de ces espèces, en Amérique du Nord et en Australie respectivement.

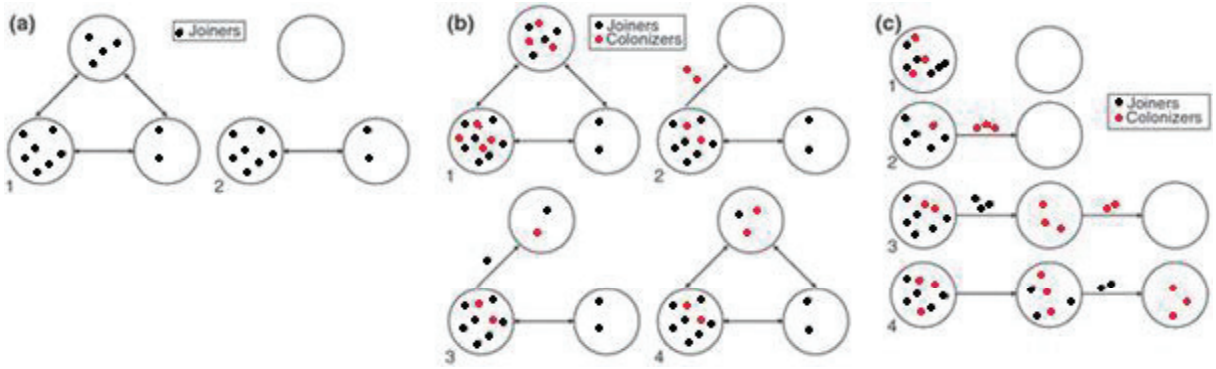

FIGURE 3. *Exemples hypothétiques des effets d'une dispersion phénotype-dépendante sur la dynamique d'une métapopulation. Dans le premier scénario où seul le phénotype suiveur est présent (a), aucune recolonisation n'est possible par les suiveurs. Dans le second scénario (b), la présence de colonisateurs permet la recolonisation de patchs éteints et la persistance de la métapopulation dans son intégralité. De la même manière, cette hétérogénéité phénotypique est susceptible de jouer un rôle critique dans les processus d'invasion biologique et d'expansion d'aire de répartition (c). Dans ce dernier scénario, les colonisateurs établissent de nouvelles populations, puis ces nouvelles populations sont renforcées par les suiveurs. L'immigration des*

suiveurs peut progressivement conduire les populations nouvellement établies à atteindre la capacité de charge maximale de l'habitat.

Conséquences génétiques et évolutives des syndromes de dispersion

De manière générale, peu d'études, tant théoriques qu'empiriques, se sont intéressées aux effets des stratégies de dispersion phénotype-dépendante sur les patrons de flux de gènes et de diversité génétique ainsi que sur les processus d'adaptation chez les populations spatialement structurées (Ronce & Clobert 2012). Théoriquement, puisque les stratégies de dispersion affectent la fréquence des phénotypes dispersants-résidents dans les populations naturelles, et par voie de conséquence les taux de dispersion entre sous-populations, il est attendu qu'elles modifient fortement les patrons de flux géniques (Clobert et al. 2004). Par ailleurs, il a été montré théoriquement et empiriquement qu'une fécondité accrue chez les immigrants due à l'hétérosis est susceptible d'augmenter les flux géniques dans les métapopulations (Whitlock et al. 2000, Ebert et al. 2002). A l'inverse, des coûts trop importants en fécondité liés à l'*outbreeding* chez les immigrants pourrait réduire les flux de gènes (Marr et al. 2002). Au travers de cette régulation de l'intensité des flux de gènes, les stratégies phénotype-dépendantes pourraient de ce fait réduire ou accentuer les phénomènes de dérive génétique et/ou moduler la diversité génétique au sein et entre les sous-populations (Benton & Bowler 2012, Ronce & Clobert 2012). Elles seraient susceptibles d'affecter le degré de divergence adaptative des populations locales en modifiant la balance entre les effets diversifiants de la sélection et les effets homogénéisants des flux de gènes (Felsenstein 1976, García-Ramos & Kirkpatrick 1997). Les stratégies phénotype-dépendantes pourraient aussi modifier le degré de divergence adaptative locale au travers d'une agrégation spatiale des individus selon leurs traits phénotypiques en fonction des caractéristiques de l'habitat (*matching habitat choice*, voir Edelaar et 2008). Chez les mésanges charbonnières (*Parus major*) par exemple, Garant et al. (2005) ont montré que des divergences adaptatives au sein d'une population résultent de différences locales en termes de qualité de l'habitat affectant les décisions d'immigration. Ils ont aussi démontré que lorsque les flux de gènes sont non-homogènes dû à une dispersion phénotype-dépendante, la différenciation évolutive peut être rapide (quelques générations) et s'effectuer à une faible échelle spatiale (moins de 4 km).

Synthèse

Les syndromes de dispersion décrivent parmi les espèces, les populations et les individus des patrons de covariation associant la dispersion à des caractéristiques morphologiques, physiologiques et des traits d'histoire de vie. Si des syndromes de dispersion ont été mis en évidence chez un grand nombre d'organismes phylogénétiquement variés, de récentes méta-analyses ont aussi montré que ces

covariations fluctuent fortement en termes de sens et d'amplitude. Le syndrome du colonisateur, associant une forte capacité dispersive, une forte fécondité et une courte durée de vie à un groupe de traits coadaptés symptomatiques des environnements spatio-temporellement variables, constitue l'un des patrons de covariation les plus communément rapportés à l'échelle interspécifique. Au niveau intraspécifique, les études ayant mis en évidence l'existence d'un tel syndrome sont plus rares. Par ailleurs, l'existence de possibles covariations entre les composantes de ce syndrome et des traits comportementaux (personnalité, type comportemental) reste spéculative. Enfin, nos connaissances concernant les conséquences de tels syndromes sur la génétique des populations spatialement structurées restent très fragmentaires.

Sélection sexuelle: bons gènes, compatibilité génétique et influence de l'environnement

Conceptions générales

Nous avons précédemment vu que les décisions individuelles, notamment en termes de dispersion, étaient susceptibles d'être influencées par la variabilité spatio-temporelle de l'environnement et que ces décisions pouvaient avoir d'importantes conséquences démographiques et évolutives. Dans cette seconde partie, nous nous intéressons plus particulièrement à l'influence des fluctuations environnementales sur les décisions individuelles en termes de choix de partenaire cette fois-ci.

Selon Darwin (1859, 1871), la sélection sexuelle résulte des différences de succès reproducteur entre les accouplements. Elle requiert de ce fait une reproduction sexuée, c'est-à-dire impliquant la combinaison de matériel génétique issu de deux parents de sexe opposé chez la progéniture. A ces deux sexes sont associées des gamètes aux propriétés contrastées, les mâles produisant des spermatozoïdes petits et mobiles, et les femelles des œufs larges et nutritifs. Selon la plupart des modèles, l'évolution de cette anisogamie repose sur deux principales pressions sélectives : accroitre la taille du zygote, ce qui en améliore sa survie, et augmenter le nombre de gamètes. Puisque les ressources sont limitées, ces pressions sélectives sont respectivement opposées et l'évolution de deux sexes différents, l'un produisant en faible nombre de larges gamètes et l'autre produisant de petits gamètes en grand nombre, constitue une solution de compromis sous-tendant l'évolution des différences inter-sexes sur les plans morphologiques et comportementaux (Parker et al. 1972, Bell 1978, Andersson 1994).

Puisqu'il est généralement considéré que la production d'ovocytes est plus énergétiquement coûteuse que celle de sperme, il est attendu que les femelles soient plus exigeantes dans leur choix de partenaires que ne le sont les mâles (Bateson 1983a, Andersson 1994 ; mais voir aussi Edward & Chapman 2011). Dans les systèmes d'accouplements dit « ressources-basés » (*resources-based mating systems*), les femelles peuvent établir leur choix d'accouplement sur la base de bénéfices directs fournis par le mâle tels que les soins parentaux, un territoire, des ressources alimentaires et une protection face aux prédateurs (Clutton-Brock 1991, Møller & Jennions 2001, Kokko et al. 2006). Parce que ces ressources améliorent la valeur sélective des jeunes, il est attendu que la sélection naturelle favorise une préférence d'accouplement basée sur l'acquisition de bénéfices directs (Møller & Jennions 2001). Néanmoins, des systèmes d'accouplement alternatifs (*nonresources-based mating systems*) existent dans lesquels les mâles ne fournissent aucun bénéfice direct et où la femelle choisit ses accouplements en fonction de bénéfices indirects, c'est-à-dire génétiques (Reynolds 1990,

Kirkpatrick & Ryan 1991, Møller & Alatalo 1999, Tregenza & Wedell 2000, Kotiaho et al. 2001, Kokko et al. 2002). Puisque les mâles diffèrent en terme de traits héritables, il est attendu que les femelles choisissent celui (ou ceux) portant les gènes qui amélioreront la qualité génétique des jeunes, laquelle est affectée par deux composantes : la variation génétique additive et la variation génétique non-additive (Mays & Hill 2004, Neff & Pitcher 2005).

Bon gènes, gènes compatibles et polyandrie adaptative

Variation génétique additive, emballement fisherien, modèle des bons gènes et principe du handicap

En 1930, Fisher (1930) propose un modèle, appelé plus tardivement modèle des *bons gènes*, prédisant que les femelles tirent un bénéfice à se reproduire avec des mâles porteurs de *bons gènes* parce que leur progéniture hérite d'allèles leur conférant un avantage sélectif supérieur à la moyenne. De ce fait, les bénéfices de valeur sélective chez les jeunes constituent une fonction de la contribution haploïde des mâles uniquement (i.e. variation génétique additive). Des études ont par la suite empiriquement confirmé le lien existant entre ces choix d'accouplement et une valeur sélective accrue chez les jeunes (voir la synthèse de Neff & Pitcher 2005) ; même si les effets positifs résultant de ces choix ont été le plus souvent mesurés chez un nombre réduit d'indicateurs de valeur sélective (Petrie 1994, Welch et al. 1998, Hine et al. 2002) et qu'ils contribuent à des variations infimes (de l'ordre de quelques pourcents) de la valeur sélective à la génération suivante (Neff & Pitcher 2005). Une seconde composante du modèle de Fisher, établie de manière verbale dans l'article de 1930, correspond à un phénomène d'emballement vis-à-vis de caractères sexuellement avantageux (i.e. *emballement fisherien*), impliquant une sélection directionnelle vers des traits sexuels exagérés et énergétiquement coûteux. Dans les années 1980, Lande (1981) a mathématiquement conforté cette idée en démontrant qu'une corrélation génétique positive entre une préférence d'accouplement et un signal attractif (e.g. ornementation, signal acoustique) constitue une conséquence inévitable du choix d'accouplement en cas de variation génétique additive. Pendant longtemps, les deux composantes du modèle de Fisher ont été perçues comme des approches dichotomiques (e.g. Møller & Pomiankowski 1993), l'*emballement fisherien* résultant simplement du bénéfice sélectif de se reproduire avec des mâles « arbitrairement » attractifs pour produire des jeunes mâles eux-mêmes sexuellement attractifs (*sexy sons*), le processus des *bons gènes* impliquant quant à lui une préférence vers des mâles avec une forte valeur reproductive et une forte viabilité. Parallèlement, Zahavi a proposé au travers de son principe du handicap (Zahavi 1975) que les femelles préfèrent des mâles présentant des « handicaps », c'est-à-dire des caractères sexuels extravagants réduisant les chances de survie fournissant à la femelle des

indicateurs honnêtes de la viabilité héritable du mâle. De ce fait, le principe de Zahavi formule donc l'hypothèse qu'il existe une interaction fonctionnelle entre les gènes responsables de la viabilité et ceux codant pour le handicap (Zahavi 1977). Plus récemment, Eshel et al. (2000) et Kokko et al. (2001, 2002, 2003) ont proposé une vision conceptuelle intégratrice en suggérant l'utilisation du terme *Fisher-Zahavi model* pour décrire l'intégralité du processus, modèle qui postule que les signaux sexuels coûteux des mâles constituent toujours des indicateurs de différentes composantes de valeur sélective (i.e. la viabilité et la valeur reproductive) avec lesquelles ils sont génétiquement corrélés.

Variation génétique non-additive et modèle des gènes compatibles

Le modèle des gènes compatibles établit que les femelles accroissent la qualité génétique (sensu Hunt et al. 2004, i.e. la valeur reproductive pour la valeur sélective totale) de leur progéniture en choisissant leurs accouplements sur base d'interactions entre leur propre génome et celui d'un partenaire sexuel potentiel (Zeh & Zeh 1996, Tregenza & Wedell 2000, Neff & Pitcher 2005, Puurtinen et al. 2009). Alors que le modèle des bons gènes prédit qu'un allèle donné augmente la valeur sélective du jeune indépendamment de l'architecture du reste du génome, le modèle des gènes compatibles postule qu'un allèle donné peut accroitre la valeur sélective du jeune lorsqu'il est associé à un homologue spécifique (phénomène de dominance ou de surdominance) ou avec un allèle particulier à un autre locus (*epistasis*) ; i.e. variation génétique non-additive. Selon les concepts de dépression de consanguinité (*inbreeding depression*) et de vigueur hybride, il est attendu que les femelles bénéficient d'un avantage sélectif à se reproduire avec des individus génétiquement non-apparentés puisqu'une progéniture hétérozygote est moins exposée à l'expression de mutations délétères récessives (dominance) et apparait sélectivement supérieur *per se* compte tenu de ses qualités hétérotiques (surdominance) (Penn et al. 2002, Kempenaers 2007, Fromhage et al. 2009, Sellis et al. 2011). Néanmoins, l'*outbreeding* peut également avoir des conséquences délétères sur la valeur sélective au travers de la perturbation maladaptative de complexes de gènes coadaptés (i.e. *outbreeding depression* ; Templeton 1986, Pusey & Wolf 1996, Kokko & Ots 2006, Frankham et al. 2011). Des études théoriques (Parker 1979, Bateson 1982, Lehmann & Perrin 2003, Kokko & Ots 2006, Puurtinen 2011) et empiriques (Bateson 1983b, Aspi 2000, LeBas 2002, Thünken et al. 2007) ont ainsi montré que la tolérance à la consanguinité est susceptible de varier entre organismes (e.g. rôle du degré d'itéroparité et des chances de rencontre de partenaires sexuels) et qu'il peut exister un avantage sélectif à se reproduire avec des individus intermédiairement apparentés.

Polyandrie adaptative et bet-hedging génétique

Le modèle de polyandrie établit que des accouplements multiples permettent d'accroitre la probabilité de fertilisation par un mâle génétiquement supérieur et/ou génétiquement compatible, ce qui améliore la valeur sélective de la progéniture (Zeh & Zeh 1996, Jennions & Petrie 2000, Cornell & Tregenza 2007, Slatyer et al. 2012). Trois principaux mécanismes sont actuellement connus. Tout d'abord, si les femelles sont capables d'évaluer la qualité ou la compatibilité génétique des mâles avant l'accouplement, celle-ci peuvent se ré-accoupler si elles rencontrent un mâle génétiquement supérieur ou compatible (Halliday 1983). Ensuite, si les femelles n'ont pas la capacité d'évaluer les caractéristiques génétiques du mâle avant la copulation, elles peuvent tirer un bénéfice sélectif de copulations multiples au travers de mécanismes post-copulatoires tels qu'un choix cryptique du sperme ou un avortement des embryons pour biaiser la paternité en faveur des meilleurs accouplements (Zeh & Zeh 1996, Zeh et al. 1998). Enfin, le modèle de bet-hedging génétique a aussi été proposé pour expliquer l'évolution d'accouplements multiples (voir la synthèse de Yasui 1998) au travers de deux principales hypothèses. Selon la première, le bet-hedging génétique constitue une stratégie permettant de réduire la probabilité que tous les œufs d'une femelle soient fertilisés par un mâle génétiquement incompatible (Jennions & Petrie, 2000, Tregenza & Wedell 2000, Zeh & Zeh 2001) ou de faible qualité génétique (Watson 1998, Yasui 1998, 2001). La seconde hypothèse postule que, dans un environnement variable, le bet-hedging génétique, au travers d'une augmentation de la diversité génétique chez la progéniture (Watson 1991, Yasui 1998, Crean & Marshall 2009), permet de réduire les chances que tous les œufs d'une femelle soient fertilisés par un mâle dont le génotype soit inadapté à l'environnement actuel (i.e. interactions génotype-environnement, pour leurs rôles dans la sélection sexuelle voir Qvarnström 2001, Greenfield & Rodriguez 2004, Ingleby et al. 2010), même si ce mâle est le meilleur accouplement possible dans d'autres conditions environnementales. Ce concept établit que, quand la valeur sélective varie au cours du temps, la moyenne de celle-ci au cours des générations est calculée en utilisant une moyenne géométrique plutôt qu'une moyenne arithmétique (Philippi & Seger 1989, Fox et al. 2003, Starrfelt & Kokko 2012) ; la première étant sensible à de fortes valeurs de variance alors que la seconde ne l'est pas. De manière générale, sous une hypothèse de bet-hedging génétique, une augmentation de variance de la valeur sélective entre les générations conduira donc à une réduction de la moyenne géométrique à long terme de la valeur sélective. Dans le cas extrême où la valeur sélective d'un génotype ou d'une lignée donnée est de zéro au cours d'une génération donnée, alors cela conduira à la complète extinction de ce génotype ou de cette lignée, même si celui-ci bénéficiait d'un avantage sélectif parmi les autres générations. En conséquence, sous l'hypothèse de bet-hedging génétique, la sélection naturelle devrait favoriser l'évolution de stratégies éliminant une forte variance intergénérationnelle de la valeur sélective (pour une discussion à propos d'un bet-hedging intragénérationnel voir Hopper et al. 2003, Sarhan & Kokko 2007).

Facteurs environnementaux et choix de partenaire

Pendant longtemps, les préférences d'accouplements des femelles ont été considérées statiques et invariables, favorisant notamment l'expression de traits sexuels exubérants (i.e. *emballement fisherien*). Cependant, un nombre grandissant d'études montrent que les règles de décision des femelles peuvent être à la fois complexes (i.e. choix multicritères) et contexte-dépendantes (Qvarnström 2001, Bussiere et al. 2008, Fricke et al. 2009). Le cadre d'études des interactions génotype-environnement prédit que, dans les environnements variables, la sélection naturelle doit favoriser une certaine plasticité dans les préférences ou la sélectivité des femelles en fonction des conditions environnementales face auxquelles seront exposés les jeunes durant leur développement. Ainsi, les préférences des femelles ne devraient pas invariablement s'orienter vers un type de mâle particulier mais plutôt dépendre de fluctuations spatiales et temporelles de l'environnement local (Edward & Gilburn 2007, Robinson et al. 2012, Grazer et al. 2014), de l'environnement social (Jann et al. 2000, Schwartz et al. 2001, Punzalan et al. 2010) ainsi que de la présence d'hétérospécifiques (Rundle et al. 2008). Par exemple, chez les femelles de gobe-mouche à collier, Robinson et al. (2012) ont montré qu'il existe de la variation génétique dans le déterminisme des préférences d'accouplement pour des mâles fortement ornementés. Par ailleurs, ils ont aussi montré que les régimes de sélection agissant sur ce choix varient en fonction des conditions environnementales : en particulier, les femelles ne bénéficient d'un avantage sélectif (i.e. augmentation du recrutement) à s'accoupler avec les mâles les plus ornementés que lors des années sèches, la tendance inverse étant observée durant les années humides. Chez des hétéroptères (*Phymata americana*), Punzalan et al. (2010) ont montré que la force et la direction de la sélection sexuelle sont susceptibles de varier durant la saison de reproduction en fonction de facteurs sociaux incluant le sexe-ratio et la densité de congénères.

Synthèse

Chez les espèces dont les mâles ne fournissent pas de ressources et de soins parentaux, les femelles choisissent leurs accouplements en fonction de bénéfices indirects permettant d'accroitre la qualité génétique et donc la valeur sélective de leur progéniture. Le modèle de Fisher-Zahavi postule que les femelles tirent bénéfice à se reproduire avec des mâles porteurs de *bons gènes* parce que leur progéniture hérite d'allèles leur conférant un avantage sélectif supérieur à la moyenne. Alternativement, le modèle des *gènes compatibles* établit que les femelles accroissent la qualité génétique de leur progéniture en choisissant leurs accouplements sur base d'interactions entre leur propre génome et celui de leur partenaire sexuel. Parallèlement, le modèle de bet-hedging génétique

établit que des accouplements multiples permettent aux femelles de réduire la probabilité que tous leurs ovocytes ne soient fertilisés par un mâle génétiquement incompatible, ou de faible qualité génétique, ou dont le génotype soit inadapté aux conditions actuelles dans un environnement spatio-temporellement variable. Pendant longtemps, les préférences d'accouplements des femelles ont été considérées statiques et invariables. Cependant, un nombre grandissant d'études montrent que les règles de décision des femelles peuvent être à la fois complexes (i.e. choix multicritères) et environnement-dépendantes. A l'heure actuelle, peu d'études se sont intéressées à l'influence de la qualité et de la variabilité spatio-temporelle de l'environnement de développement des jeunes sur le choix d'accouplement des femelles.

OBJECTIFS DE LA THESE & MODELE BIOLOGIQUE

Objectifs de la thèse

La problématique de ma thèse se focalise sur l'influence des variations spatio-temporelles de l'environnement sur les patrons de covariation entre les traits d'histoire de vie, la dispersion et les types comportementaux à l'échelle inter-populationnelle. Ma thèse s'intéresse aussi aux mécanismes démographiques permettant de limiter l'impact des fluctuations temporelles de l'environnement (e.g. climat) sur la dynamique des populations, en particulier chez des organismes exposés à des environnements hautement stochastiques. Enfin, elle examine aussi le rôle de la qualité et des variations spatio-temporelles de l'environnement sur le choix de partenaire.

Ma thèse s'articule autour de trois principaux chapitres présentés plus en détails ci-dessous. Ces questions ont été posées chez un amphibien anoure, le sonneur à ventre jaune (*Bombina variegata*, L.), dont je propose une brève présentation des traits biologiques dans la section *Modèle biologique*. Dans le premier chapitre, intégrant trois manuscrits d'article, j'ai examiné comment le degré de stochasticité interannuel de l'habitat de reproduction (réseaux de pièces d'eau) est susceptible de réguler la vitesse des rythmes de vie (*pace of life*) à l'échelle inter-populationnelle. J'ai par la suite étudié comment une accélération des rythmes de vie est susceptible d'être accompagnée d'un syndrome de dispersion (type comportemental proactif) dans les métapopulations de *B. variegata* exposées à des habitats de reproduction hautement stochastiques. J'ai ensuite examiné les conséquences génétiques de ce syndrome de dispersion dans plusieurs métapopulations exposées à des degrés contrastés de stochasticité de l'habitat reproduction. Dans le second chapitre de ma thèse, incluant trois articles publiés et un manuscrit, je me suis intéressé au rôle de la canalisation environnementale dans la stratégie d'histoire de vie de B. variegata et j'ai évalué comment diverses formes de variations climatiques (moyennes et événements climatiques extrêmes) pouvaient affecter la dynamique de différentes populations en France. Dans le troisième et dernier chapitre, incluant trois manuscrits d'article (dont deux soumis), je me suis tout d'abord intéressé au choix d'accouplement des femelles de B. variegata, en examinant successivement les hypothèses de bons gènes et de gènes compatibles puis en me focalisant sur le rôle de la qualité et de la disponibilité des sites de reproduction sur les règles de décision des femelles.

CHAPITRE I. Rythmes de vie, syndrome de dispersion et fluctuations environnementales : conséquences démographiques, génétiques et évolutives

VERROU 1 : Le concept de continuum de rythme de vie suggère l'existence de patrons de covariation récurrents entre des traits physiologiques, des traits comportementaux et des traits d'histoire de vie (Réale et al. 2010). Si ces patrons de covariation ont été relativement bien étudiés à l'échelle interspécifique (Tieleman et al. 2005, Wiersma et al. 2007, Williams et al. 2010), nos connaissances à leur propos restent fragmentaires au niveau intraspécifique. Par ailleurs, la majorité des études s'est intéressée à la prédation et la disponibilité des ressources alimentaires comme principaux agents sélectifs agissant sur la régulation des rythmes de vie à l'échelle intraspécifique (e.g. Bronikowski & Vleck 2010, Miller et al. 2011, chez Thamnophis elegans; Billerbeck et al. 2001, Lankford et al. 2001, Arnott et al. 2006, Chiba et al. 2007 chez Menidia menidia). Le rôle de facteurs tels que la fréquence des perturbations et le degré de variabilité spatio-temporelle de l'environnement sur la régulation intraspécifique des rythmes de vie reste très méconnu.

Dans cette première partie, j'ai tout d'abord examiné comment des degrés contrastés de stochasticité de l'habitat sont susceptibles d'entrainer des changements de position des populations le long du continuum de rythme de vie. Pour ce faire, j'ai développé une approche comparative impliquant différentes métapopulations exposées à deux types d'environnements distincts : des environnements dits *imprévisibles*, dans lequel les ressources nécessaires à la reproduction (site d'oviposition) apparaissent et disparaissent annuellement de façon stochastique dans le paysage ; des environnements dits *prévisibles*, dans lesquels les ressources de reproduction restent disponibles à l'échelle de plusieurs générations sans gains ni pertes. Nous avons postulé que les changements de position des métapopulations le long du continuum de rythme de vie pouvaient à la fois s'opérer au travers modifications de la moyenne et de la variance temporelle de trois principaux traits d'histoire de vie : la survie annuelle (à différents stades ontogénétiques), les probabilités individuelles de reproduction annuelle et la fécondité des femelles. Puisque la théorie prédit que la sélection naturelle favorise des stratégies de type *r* ou *fast* dans les environnements spatio-temporellement variables (Pianka 1970, Stearns 1992), nous avons prédit une accélération et un ralentissement des rythmes de vie dans les métapopulations exposées respectivement à un environnement *imprévisible* et *prévisible*.

VERROU 2 : Les syndromes de dispersion décrivent parmi les espèces, les populations et les individus des patrons de covariation associant la dispersion à des caractéristiques morphologiques, physiologiques et des traits d'histoire de vie (Cote et al. 2010a, Ronce & Clobert 2012). Si des syndromes de dispersion ont été mis en évidence chez un grand nombre d'organismes phylogénétiquement variés, une récente méta-analyse a aussi montré que ces covariations fluctuent fortement en termes de sens et de magnitude (Stevens et al. 2014). Le syndrome du colonisateur (sensu Baker & Stebbins 1965), associant une forte capacité dispersive, une forte fécondité et une courte durée de vie à un groupe de traits coadaptés symptomatiques des environnements spatio-temporellement variables, constitue l'un des patrons de covariation les plus communément rapportés à l'échelle interspécifique (Baker & Stebbins 1965, Ronce et al. 2000, Stevens et al. 2012). Au niveau intraspécifique, les études ayant mis en évidence l'existence d'un tel syndrome sont plus rares (Melitaea cinxia : Hanski et al. 2006, Saastamoinen 2007; Rhinella marina : Phillips 2009). Par ailleurs, l'existence de possibles covariations entre les composantes de ce syndrome et des traits comportementaux (personnalité, type comportemental) reste putative. Enfin, nos connaissances concernant les conséquences de tels syndromes sur la génétique des populations spatialement structurées restent très fragmentaires.

Des modèles théoriques prédisent que la variabilité spatio-temporelle de l'environnement (McPeek & Holt 1992, Paradis 1998, Travis & Dytham 1999, Reigada et al. 2015) constitue une importante force sélective agissant sur l'évolution de la dispersion dans les populations naturelles. A partir de cette base théorique, j'ai examiné si une accélération du rythme de vie est aussi accompagnée d'un syndrome de dispersion dans les métapopulations de sonneur à ventre jaune exposées à un environnement *imprévisible*. Au travers d'une approche *en common garden*, j'ai tout d'abord testé l'hypothèse que les individus issus de métapopulations exposées aux deux types d'environnement diffèrent en termes de type comportemental. En particulier, j'ai testé la prédiction que les individus provenant d'un environnement *imprévisible* présentent un type comportemental proactif tandis que ceux issus d'un environnement *prévisible* ont un type comportemental réactif, ceci résultant d'une transmission transgénérationnelle. Ensuite, à l'aide de données de capture-recapture, j'ai examiné l'hypothèse que les taux de dispersion démographique (entre sous-populations) sont supérieurs dans les métapopulations exposées à des environnements *imprévisibles*. Enfin, j'ai examiné comment les variations des taux de dispersion, fonctionnellement associés à des différences de vitesse des rythmes de vie dans notre système d'étude, affectent les flux de gènes et la diversité génétique dans les métapopulations de chaque type d'environnement.

CHAPITRE II. Canalisation des traits d'histoire de vie et fluctuations environnementales : impact des variations climatiques sur la dynamique des populations

VERROU 3 : Parce que la variabilité environnementale affecte négativement les taux d'accroissement démographiques (Haldane & Jayakar 1963, Cohen 1966, Bulmer 1985, Lande & Orzack 1988, Boyce et al. 2006), il est attendu que les composantes de valeur sélective dont les variations ont le plus fort impact sur le taux d'accroissement démographique (la survie adulte chez les espèces longévives ; Gaillard et al. 1998, Sæther & Bakke 2000) bénéficient d'une pression de sélection pour l'évolution de traits phénotypiques limitant l'amplitude de leurs fluctuations temporelles. Ce mécanisme évolutif est connu sous le nom de canalisation environnementale (*sensu* Gaillard & Yoccoz 2003). Chez les espèces longévives, le comportement de saut de reproduction constitue l'un des traits phénotypiques susceptibles de limiter les variations de survie adulte (Cubaynes et al. 2011, Rideout & Tomkiewicz 2011), par exemple lorsque des conditions météorologiques stressantes interviennent pendant la période de reproduction (Church et al. 2007). De fortes variations des probabilités de reproduction, résultant des effets combinés de facteurs internes et environnementaux (McNamara & Houston 1996), doivent *ipso facto* conduire à de fortes fluctuations annuelles du recrutement. A l'heure actuelle, peu d'études ont examiné comment des facteurs externes tels que des variations de paramètres météorologiques ou l'occurrence d'événements climatiques extrêmes (sécheresses, crues) peuvent simultanément affecter la survie à différents stades ontogénétiques, les probabilités de reproduction annuelle ainsi que le recrutement dans plusieurs populations distinctes.

Dans ce deuxième chapitre, à l'aide de données de capture-recapture collectées dans différentes populations, j'ai cherché à mettre en évidence l'existence d'un processus de canalisation environnementale permettant une réduction de la variance temporelle de certains traits démographiques chez le sonneur à ventre jaune. Comme attendu chez les espèces longévives, j'ai examiné l'hypothèse que la moyenne de la survie augmente avec l'âge tandis que sa variance temporelle décroit. J'ai du reste testé l'hypothèse que les probabilités de reproduction sont condition-dépendantes (i.e. dépendantes de l'état reproducteur de l'individu au cours de la saison précédente) et varient fortement d'une année à l'autre, entrainant une forte variance temporelle de la fécondité réalisée. Enfin, j'ai examiné comment des facteurs météorologiques tels que la quantité de précipitations et la température moyenne durant la saison de reproduction (deux facteurs affectant généralement la dynamique des populations d'amphibiens, voir TABLEAU 1) affectent simultanément la survie à différents stades ontogénétiques, les probabilités de reproduction annuelle et le recrutement dans plusieurs populations distinctes. Compte tenu des différences inter-populationnelles mises en évidence dans le précédent chapitre, j'ai fait l'hypothèse que l'impact de ces

facteurs météorologiques sur la dynamique des populations devait être fortement contexte-dépendant. Enfin, j'ai cherché à prédire l'impact de ces fluctuations météorologiques sur le taux d'accroissement démographique à long terme.

TABLEAU 1. Synthèse bibliographique concernant les effets climatiques sur les traits démographiques des amphibiens

FACTEUR	SAISON	ESPECE	STADE	TRAIT	EFFET
température	hiver	*Bufo bufo*	adulte	condition maternelle	Negative[1]
			adulte	survie des femelles	Negative[1]
			adulte	fécondité	Negative[1]
précipitations	été-automne-hiver	*Triturus cristatus*	adulte	survie	Negative[2]
température	hiver	*Triturus cristatus*	adulte	survie	Negative[2]
sécheresse	automne-hiver-printemps	*Ambystoma tigrinum*	adulte	probabilité de reproduction	Negative[3]
			adulte	survie	Negative[3]
sécheresse	hiver-printemps	*Rana sevosa*	adulte	probabilité de reproduction	Negative[4]
			larve	succès de métamorphose	Negative[4]
sécheresse	hiver-printemps	*Ambystoma opacum*	larve	succès de métamorphose	Negative[5]
	automne	*Gyrinophilus porphyriticus*	juvénile	survie	Negative[6]
température	hiver	*Rana sylvatica*	adulte	fécondité	Negative[7]
précipitations	hiver	*Rana sylvatica*	adulte	fécondité	Positive[7]

Reading 2007[1], Griffiths et al. 2010[2], Church et al. 2007[3], Richter et al. 2003[4], Taylor et al. 2006[5], Lowe 2012[6], Benard 2015[7]

CHAPITRE III. Sélection sexuelle et fluctuations environnementales : bons gènes, gènes compatibles et qualité de l'habitat

VERROU 4 : Chez les espèces dont les mâles ne fournissent pas de ressources et de soins parentaux, les femelles choisissent leurs accouplements en fonction de bénéfices indirects permettant d'accroitre la qualité génétique et donc la valeur sélective de leur progéniture. Le modèle de Fisher-Zahavi (Eshel et al. 2000) postule que les femelles tirent bénéfice à se reproduire avec des mâles porteurs de bons gènes parce que leur progéniture hérite d'allèles leur conférant un avantage sélectif supérieur à la moyenne (Neff & Pitcher 2005). Alternativement, le modèle des gènes compatibles établit que les femelles accroissent la qualité génétique de leur progéniture en choisissant leurs accouplements sur la base d'interactions entre leur propre génome et celui de leur partenaire sexuel (Tregenza & Wedell 2000, Neff & Pitcher 2005). Parallèlement, le modèle de bet-hedging génétique établit que des accouplements multiples permettent aux femelles de réduire la probabilité que tous leurs ovocytes soient fertilisés par un mâle génétiquement incompatible, ou de faible qualité génétique, ou dont le génotype est inadapté aux conditions actuelles de l'environnement (Yasui 1998, 2001). Pendant longtemps, les préférences d'accouplements des femelles ont été considérées statiques et invariables. Cependant, un nombre grandissant d'études montrent que les règles de décision des femelles peuvent être à la fois complexes (i.e. choix multicritères) et environnement-dépendantes (Qvarnström 2001, Bussiere et al. 2008, Fricke et al. 2009). A l'heure actuelle, peu d'étude se sont intéressées à l'influence de la qualité et de la variabilité spatio-temporelle de l'environnement de développement des jeunes sur le choix d'accouplement des femelles.

Dans ce troisième chapitre, nous examinons comment, sous l'hypothèse des bons gènes, la qualité génétique des mâles est susceptible d'affecter le choix d'accouplement des femelles. Au travers d'expériences en enclos, j'ai testé l'hypothèse que la condition physique des mâles, généralement positivement corrélée aux performances de chant (Castellano et al. 2009, Humfeld 2013), au statut de santé et à la viabilité des individus chez les anoures (Brodeur et al. 2011, Janin et al. 2011, Hegde & Krishnamurthy 2014), influence le succès reproducteur des mâles.

Ensuite, dans une autre série d'expériences, j'ai testé l'hypothèse que, à taille et condition physique égale, de forts taux de testostérone circulante, un paramètre physiologique généralement positivement corrélés aux performances de chant, à la réactivité sociale et à la territorialité chez les amphibiens (Orchinik et al. 1988, Marler & Ryan 1996, Emerson & Hess 2001, Moore et al. 2005, de Assis et al. 2012) affectent positivement le succès reproducteur des mâles. J'ai ensuite examiné comment la comptabilité génétique entre partenaire sexuel est susceptible d'affecter le choix des femelles. A taille et condition physique égale chez les mâles, j'ai testé l'hypothèse que le degré d'apparentement

génétique, évalué à l'aide de métriques de coancestralité (Wang 2011), pouvait affecter le choix des femelles, positivement ou négativement. Parallèlement, sous l'hypothèse d'un bet-hedging génétique, j'ai examiné si, à taille et condition physique égale des mâles, les femelles avaient tendance à minimiser les risques d'une fertilisation de tous leurs ovocytes par un mâle génétiquement incompatible, ou de faible qualité génétique.

Enfin, au travers d'une dernière série d'expérience, j'ai testé comment des différences de qualité des sites de reproduction sont susceptibles d'affecter les décisions d'accouplement des femelles. En m'appuyant sur les résultats des précédentes expériences et en manipulant la présence de compétiteurs larvaires dans les enclos expérimentaux, j'ai testé la prédiction que le choix d'accouplement des femelles est contexte-dépendant et que celles-ci hiérarchisent leur choix en fonction de la qualité génétique du mâle (condition physique et fréquence fondamentale du chant) et des risques de compétition intraspécifique auxquelles sera exposée la progéniture.

Modèle biologique

Phylogénie des lignées étudiées

Le sonneur à ventre jaune (*Bombina variegata*) est un anoure de la famille de *Bombinatoridae* (voir **FIGURE 1A)**, laquelle rassemble les représentants de très anciennes lignées étroitement apparentées aux premiers anoures (e.g. genres *Callobatrachus* et *Eodiscoglossus*) du Jurassique inférieur (Roček 2000, 2013, Wang et al. 2000). Une forte différenciation mitochondriale (à l'échelle du génome mitochondrial complet, voir Pabijan et al. 2008, 2013) au sein de cette espèce confirme l'existence de différentes lignées de *B. variegata* s'étant différenciées dans trois refuges glaciaires majeurs (voir **FIGURE 1A** et **1B)** : *B. v. scabra* dans le sud des Carpates, *B. v. pachypus* dans les Apennins, et *B. v. variegata* dans les Balkans. Les populations étudiées dans ma thèse correspondent à la lignée *B. v. variegata*.

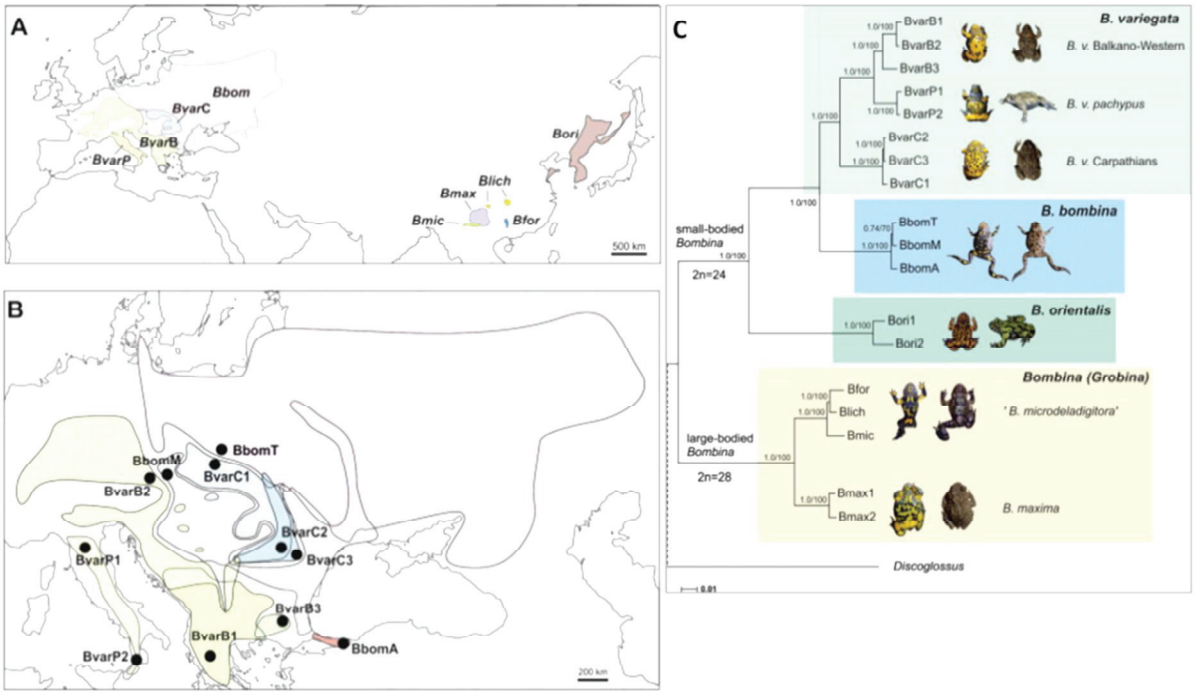

FIGURE 4. *Distribution des espèces actuelles du genre Bombina (Bombinatoridae) dans le Paléarctique (A) et les principales lignées mitochondriales d'Europe centrale [B, d'après Hofman et al. (2007) et Fijarczyk et al. (2011)]. Les codes utilisés dans (A) et (B) pour désigner chacune des lignées correspondent à ceux utilisés dans les analyses du génome mitochondrial (C) effectuées chez le genre Bombina par Pabijan et al. (2013) : Bbom – B. bombina, Bfor – B. (Grobina) fortinuptialis, Blich – B. (Grobina) lichuanensis, Bmax – B. (Grobina) maxima, Bmic – B. (Grobina) microdeladigitora, Bori – B. orientalis, BvarB – B. variegata Balkano-Western haplogroup, BvarC – B. variegata Carpathian haplogroup, BvarP – B. variegata pachypus. La figure 1C montre un phylogramme résultant d'analyses bayésiennes effectuées sur 18 génomes mitochondriaux complets [voir le détail des analyses dans Pabijan et al. (2013)].*

Régimes de prévisibilité intra- et interannuel de l'habitat de reproduction

Classiquement, la richesse spécifique des amphibiens peut être modélisée comme une fonction quadratique du gradient d'hydropériode–surface des pièces d'eau potentiellement utilisable pour la reproduction (Werner et al. 2007). En d'autres termes, un maximum d'espèces semblent préférentiellement se reproduire dans des pièces d'eau situées autour de la position médiane du gradient d'hydropériode–surface. Cette relation résulte d'un compromis entre les risques d'assèchement d'une part et le risque de prédation d'autre part (Welborn et al. 1996, Urban 2004, Chase 2007). A l'extrémité inférieure de ce gradient, la forte imprévisibilité des conditions de mise en eau et de fréquent assecs entrainent des échecs réguliers de la reproduction et une forte variance du recrutement (Cayuela et al. 2012, Anderson et al. 2015). A l'inverse, à l'extrémité supérieure du gradient, une forte diversité de prédateurs, en particulier des poissons carnassiers (Hecnar & M'Closkey 1997, Adams 2000), influencent très négativement le succès reproducteur chez les amphibiens dont les larves ne présentent pas de stratégies anti-prédatrices efficaces (e.g. forte plasticité morphologique et comportementale, sécrétion de répulsifs chimiques ; Relyea & Werner 1999, Lardner 2000, Van Buskirk 2002).

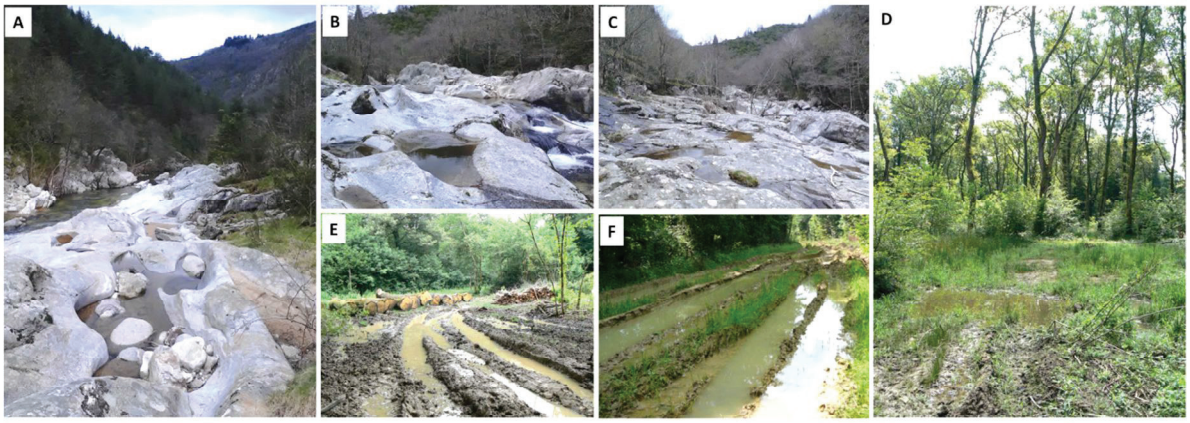

FIGURE 5. *Deux types d'habitats de reproduction du sonneur à ventre jaune (Bombina variegata) en Europe de l'ouest. A l'échelle intra-annuelle, ces deux types d'habitat présentent des conditions de mise en eau stochastiques, dépendantes des précipitations et des crues. A l'échelle interannuelle, le degré de prévisibilité de ces deux habitats varie fortement : dans les environnements A-B-C (Ardèche), les ressources de reproduction (i.e. mares cupulaires rocheuses) restent disponibles à l'échelle de plusieurs générations sans gains ni pertes annuelles (environnements dits « prévisibles » dans ma thèse) ; dans les environnements D-E-F (Ain, Meuse), les ressources de reproduction (i.e. ornières, fossés) apparaissent et disparaissent annuellement de façon stochastique dans le paysage au grès des exploitations forestières (environnements dits « imprévisibles »).*

Le sonneur à ventre jaune utilise pour la reproduction des habitats aquatiques situés dans la partie inférieure de ce gradient d'hydropériode–surface (Joly & Morand 1994, MacCallum et al. 1995, Yanchukov et al. 2006, Hartel et al. 2007), dans lesquelles le degré de compétition interspécifique et la pression de prédation sont relativement faibles **(FIGURE 5)**. En Europe de l'ouest, l'espèce est

susceptible de se reproduire dans deux grands types d'habitat : i) des mares cupulaires de rivière (principalement dans le massif central et les Préalpes ; voir Cayuela et al. 2011, 2013) et des habitats semi-naturels (e.g. ornières, fossés ; voir Hartel 2008, Canessa et al. 2013). A l'échelle intra-annuelle, ces deux types habitats aquatiques présentent des conditions de mise en eau hautement instables dépendantes de la fréquence et de l'intensité des précipitations et des crues. A l'échelle interannuelle, le degré de prévisibilité de ces types d'habitat est fortement contrasté. Dans les environnements de mares cupulaires rocheuses (dits « prévisibles » dans ma thèse), les ressources de reproduction restent quantitativement et qualitativement prévisibles et disponibles à l'échelle de plusieurs générations. Dans les environnements de pièces d'eau semi-naturelles (dits « imprévisibles »), les ressources de reproduction apparaissent et disparaissent annuellement de façon stochastique dans le paysage, au grès des exploitations forestières et agricoles (environnements dits « imprévisibles »).

TABLEAU 2. *Synthèse bibliographique des traits d'histoire de vie du sonneur à ventre jaune (Bombina variegata) aux stades larvaire et post-métamorphique. T = température en degrés Celsius, D = densité d'individus par litre d'eau, NPOP = nombre de populations.*

TRAITS D'HISTOIRE DE VIE	CARACTERISTIQUES
Stade larvaire	
Vitesse de développement (jours)	40.2 (37.3 – 43), (T = 17-19° C, D = 13 ind/L) [1]
	65 (34 – 128), (T = 27° C, D = 12 ind/L) [2]
	106 (87 – 131), (T = 15° C, D = 12 ind/L) [2]
Taille à la métamorphose (mm)	25 (14 – 48), (T = 27° C, D = 12 ind/L) [2]
	25 (8 – 39), (T = 15° C, D = 12 ind/L) [2]
	(T = 17-19° C, D = 13 ind/L) [1]
Taux de métamorphose	0.7 – 0.13 [3]
Stade post-métamorphique	
Taux de survie annuel des juvéniles†	0.29 – 0.77 (NPOP = 5) [4]
Taux de survie annuel des subadultes‡	0.46 – 0.88 (NPOP = 5) [4]
Taux de survie annuel des adultes*	0.71 – 0.92 (NPOP = 5) [4]
Espérance de vie moyenne	2.43 – 11.5 ans (NPOP = 5) [4]
Age à la maturité sexuelle	2 – 3 ans [5]
Fécondité : nombre d'œufs/femelle/ponte	150 (3 – 339) [1]
	100 (41 – 186) [6]
Nombre de ponte/femelle/an	4 (1 – 8) [9]
Fécondité : taille de l'œuf	103 (4 – 228) [9]
	1.99 (1.6 – 2.7) [1]
	2.25 [7]
	1.9 (1.7 – 2.2) [8]

[1]Rafinska 1991, [2]Morand et al. 1997, [3]Beshkov & Jameson 1980, [4]Cayuela et al. *in press*, [5]Plytycz & Bigaj 1993, [6]Cayuela données non-publiées, [7]Morand 1997, Barandun 1995, Buschmann 2002

Une stratégie d'histoire de vie adaptée à l'imprévisibilité de l'habitat de reproduction

Le sonneur à ventre jaune présente un certain nombre de traits d'histoire de vie ayant probablement évolué en réponse à la forte stochasticité des conditions de mise en eau de ses sites de reproduction (Rafinska 1991, Barandun et al. 1997) (voir **TABLEAU 2, FIGURE 6**). Au stade post-métamorphique, l'espèce présente une durée de vie relativement longue résultant, au moins

partiellement, d'une stratégie anti-prédateur incluant un grand nombre de glandes granulaires relâchant des sécrétions cutanée toxiques riches en peptides, protéines et alcaloïdes (Anastasi 1971, Chen & Shaw 2003, König & Bininda-Emonds 2011, König et al. 2015), des colorations aposématiques (Bajger 1980) et des réponses comportementales telle que la lordose lombaire (*unken reflex*, voir Toledo et al. 2011). Une durée de vie relativement longue permet au sonneur à ventre jaune un fort degré d'itéroparité, constituant vraisemblablement une réponse adaptative à l'incertitude du succès reproducteur.

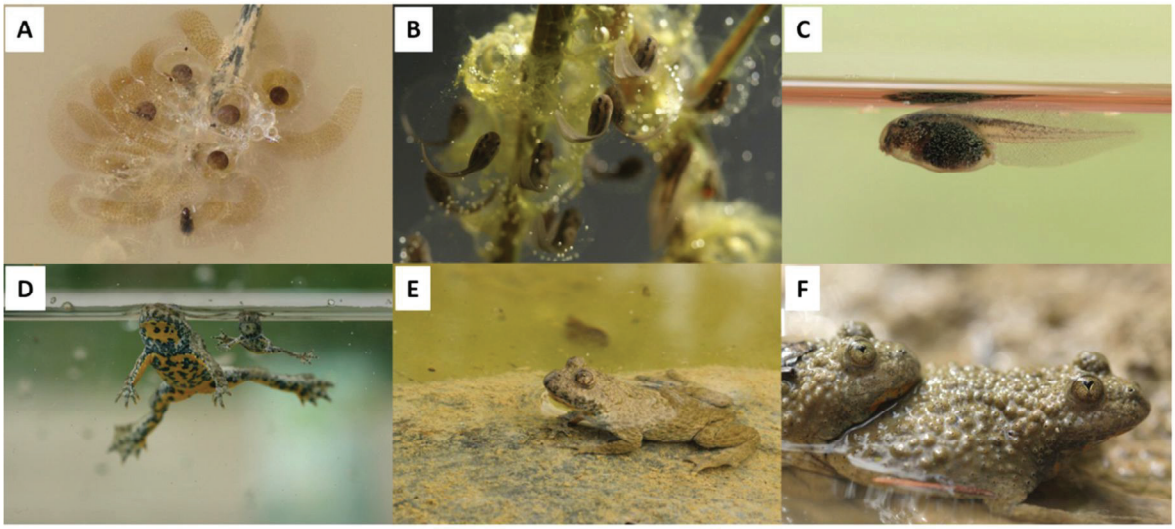

FIGURE 6. *Le sonneur à ventre jaune est un organisme à cycle de vie complexe présentant trois principaux stades de développement : embryonnaire (A, ponte accompagnée d'œufs de chironome), larvaire (stade 22-25 de Gosner, B ; stade 26-30, C) et métamorphosé (D et E). La reproduction est sexuée, la fécondation est externe et l'amplexus est lombaire (F). Crédits : B-C-D-E-F, Yves Fol.*

A l'échelle interannuelle, l'investissement reproducteur des femelles semble résulter d'interactions complexes entre des facteurs internes (taille, quantité de ressources énergétiques disponibles) et environnementaux (e.g. le régime de précipitation) (Rafinska 1991, Barandun et al. 1997), conduisant les femelles à ne se reproduire que tous les deux voire trois ans (Beshkov & Jameson 1980). Le fort risque d'assèchement des pièces d'eau durant le développement larvaire ainsi qu'une mortalité taille-dépendante chez les jeunes métamorphosés constituent très probablement deux forces évolutives couplées conduisant à la sélection de gros œufs chez cette espèce. Des œufs de grandes de taille permettent à la fois un raccourcissement de la période développement larvaire et une augmentation de la taille à la métamorphose (Rafinska 1991), sachant qu'il existe classiquement un compromis entre ceux composantes de valeur sélective chez les amphibiens (Werner 1986). Rafinska (1991) a par ailleurs montré qu'il existe une relation positive entre la taille des œufs et la taille de la femelle, suggérant l'existence d'effets maternels susceptibles d'impacter la valeur sélective des jeunes avant et après la métamorphose. A l'échelle intra-annuelle, les femelles sont capables de fractionner leur capital d'ovocytes en plusieurs séquences (jusqu'à 8 ; Buschmann 2002) d'oviposition

successives effectuées dans différentes pièces d'eau (Mirabile et al. 2009). Ce comportement a été confirmé par la présence de follicules post-copulatoires dans les ovaires (Guarino et al. 1998). Il est généralement considéré comme une tactique de répartition des risques face à l'imprévisibilité des conditions de mise en eau de son habitat de reproduction (Buschmann 2002). Au stade larvaire, une période de développement relativement courte et une forte plasticité phénotypique permettent de limiter la mortalité causée par les prédateurs (les odonates en particulier) et l'asséchement des pièces d'eau (Rafinska 1991, Vorndran et al. 2002).

Du sexe dans un environnement imprévisible

Le sonneur à ventre jaune présente les quatre critères d'un lek ressource-basé (*ressource-based lek*, voir Höglund & Alatalo 2014): i) les mares constituent une ressource de reproduction utilisée par les femelles qu'occupent les mâles et qui agit comme une arène ou un lek dans lequel la majorité des accouplements s'effectuent (Wells 2010), ii) les mâles ne fournissent pas de soins parentaux (Barandun et al. 1996), iii) les mâles défendent activement des places de chant qui ne constituent pas des territoires susceptibles de fournir un bénéfice direct à la femelle (Schneider & Eichelberg 1974, Schneider et al. 1986, Sanderson et al. 1992), iv) les performances de fertilisation constituent les seuls bénéfices directs susceptibles d'être fournis par les mâles, v) les mâles fournissent vraisemblablement des bénéfices indirects, c'est-à-dire génétiques. Les mâles rentrent en compétition pour l'accès aux femelles en émettant des signaux acoustiques nuptiaux, en utilisant des signaux hydrodynamiques (i.e. *wave communication* ; Seidel 1999, Seidel et al. 2001) servant à la délimitation des places de chants (d'un rayon de 30 cm environ) et en montrant des comportements agonistiques dans le cas d'une trop grande proximité d'un compétiteur (Schneider et al. 1986). A l'instar d'autres amphibiens se reproduisant dans des environnements hydriquement instables et présentant de faibles ressources trophiques, les risques d'assèchement et de compétition larvaire devraient influencer le choix de la ressource de reproduction chez les deux sexes et affecter en conséquence les patrons d'appariement (Wells 2010).

CHAPITRE I. Rythmes de vie, syndrome de dispersion et fluctuations environnementales : conséquences démographiques, génétiques et évolutives

ARTICLE 1. Cayuela Hugo, Arsovski Dragan, Thirion Jean-Marc, Bonnaire Eric, Pichenot Julian, Boitaud Sylvain, Brison Anne-Lise, Miaud Claude, Joly Pierre, Besnard Aurélien. Contrasting patterns of environmental fluctuation contribute to divergent life histories among amphibian populations. Ecology 97:980-991. DOI: 10.1890/15-0693.1

ARTICLE 2. Cayuela Hugo, Boualit Laurent, Arsovski Dragan, Bonnaire Eric, Pichenot Julien, Bellec Arnaud, Miaud Claude, Léna Jean-Paul, Joly Pierre, Besnard Aurélien. Do contrasting levels of habitat unpredictability promote the evolution of a colonizer syndrome in amphibian metapopulations ?. Ecology, 97:2658-2670. DOI: 10.1002/ecy.1489

ARTICLE 3. Cayuela Hugo, Joly Pierre, Besnard Aurélien, Lengagne Thierry, Kaufmann Bernard, Bonnaire Eric, Pichenot Julian, Konecny Lara, Grolet Odile, Bellec Arnaud, Léna Jean-Paul. Habitat unpredictability shapes dispersal behavioral syndromes, dispersal dynamics and population genetic differentiation. *In Prep.*

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Contrasting patterns of environmental fluctuation contribute to divergent life histories among amphibian populations

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Abstract. Because it modulates the fitness returns of possible options of energy expenditure at each ontogenetic stage, environmental stochasticity is usually considered a selective force in driving or constraining possible life histories. Divergent regimes of environmental fluctuation experienced by populations are expected to generate differences in the resource allocation schedule between survival and reproductive effort and outputs. To our knowledge, no study has previously examined how different regimes of stochastic variation in environmental conditions could result in changes in both the temporal variation and mean of demographic parameters, which could then lead to intraspecific variation along the slow–fast continuum of life history tactics. To investigate these issues, we used capture–recapture data collected on five populations of a long-lived amphibian (*Bombina variegata*) experiencing two distinct levels of stochastic environmental variation: (1) constant availability of breeding sites in space and time (predictable environment), and (2) variable spatio-temporal availability of breeding sites (unpredictable environment). We found that female breeding propensity varied more from year to year in unpredictable than in predictable environments. Although females in unpredictable environments produced on average more viable offspring per year, offspring production was more variable between years. Survival at each ontogenetic stage was slightly lower and varied significantly more from year to year in unpredictable environments. Taken together, these results confirm that increased environmental stochasticity can modify the resource allocation schedule between survival and reproductive effort and outputs and may lead to intraspecific variation along the slow–fast continuum of life history tactics.

Key words: amphibian; Bombina variegata; *demography; environmental predictability; life history; multievent capture-recapture models; slow–fast continuum.*

Introduction

Identifying the rules that shape life history evolution is a crucial challenge for evolutionary biology. According to life history theory, ontogenesis involves a sequence of developmental events that are ordered to optimize survival and reproductive outputs (Stearns 1992). Over a lifetime, energy and trophic resources are allocated between growth, somatic maintenance, and reproductive effort (Pianka 1976). Growth and somatic maintenance include investments that contribute to longevity, whereas reproductive effort includes investments in offspring production and assistance that contribute to fecundity. Because it modulates the fitness returns of possible options of energy expenditure at each ontogenetic stage, stochastic environmental variation is usually considered a selective force in driving or constraining possible life histories (Levins 1968, Schaffer 1974, Tuljapurkar et al. 2009).

When environmental fluctuation generates strong variation in adult mortality, natural selection favors a short lifespan, early maturity, and large reproductive outputs (characteristics of "fast" life histories along a "slow–fast continuum;" e.g., Kraus et al. 2005). In contrast, when environmental fluctuation affects birth rate and juvenile mortality, it contributes to the selection for a longer lifespan, later maturity, and smaller reproductive outputs (characteristics of "slow" life histories; e.g., Morris et al. 2008). For species with long lifespans, selective forces drive the evolution of traits that favor a canalization process (*sensu* Gaillard and Yoccoz 2003) of adult survival, since this demographic parameter has the highest impact on fitness. Such a reduction of variation in adult survival may initially be achieved by tradeoffs between vital rates (Stearns 1992, Shaw

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and Levin 2011). In particular, adults may modulate their yearly breeding investment or may temporarily cease to breed at any age to increase longevity (Warner 1998, Rideout et al. 2005, Ruf et al. 2006). Reduced variation in adult survival may also result from behavioral or physiological processes that buffer the impact of environmental fluctuation. This can be seen in adaptive behavioral mechanisms such as the wing-fanning and shade-seeking of endotherms that allow individuals to maintain their body temperature in increasing ambient temperatures, which may drastically reduce adult survival variation due to temperature fluctuation (Welbergen et al. 2008).

By constraining the availability and quality of resources that could be used by an iteroparous organism over its lifetime, environmental fluctuation also regulates the spread of reproductive effort over time (Tuljapurkar et al. 2009). An organism's ability to reproduce strongly depends on a combination of environmental and physiological factors (McNamara and Houston 1996), which include its fat reserves, foraging skills, parasite load, and the responsiveness of its immune system. Given these constraints, at each breeding opportunity an iteroparous organism has to make a decision whether or not to breed, and if it does breed, it must modulate its breeding investment in accordance with its lifetime fitness gain (Reznick and Yang 1993, Muths et al. 2010, Souchay et al. 2014). Variation in food availability due to environmental fluctuation (e.g., yearly weather variation) may lead to insufficient energy accumulation for initiating oocyte development in females, which therefore skip reproduction (Jenouvrier et al. 2003). Moreover, environmental fluctuation also regulates the availability and quality of resources required by offspring during their development, which may lead organisms to modulate breeding investment accordingly. Breeding females may respond to fluctuation in food availability by delaying oocyte production, which increases their fitness, as this produces offspring with higher fat content, which can better survive and grow in low-food environments (Reznick and Yang 1993).

As is predicted at the interspecific level (Stearns 1992), divergent regimes of environmental conditions experienced among populations are expected to generate differences in the resource allocation schedule between survival and reproductive effort and outputs at the intraspecific level, as well (Van Tienderen 2000). For instance, a population of *Capreolus capreolus* submitted to the harsh environmental conditions generated by the co-occurrence of high hunting pressure and predation by lynx exhibited a slower life history cycle than that of a population in less harsh conditions (Nilsen et al. 2009). Conversely, an acceleration of the life history cycle has been reported in *Sarcophilus harrisii*; the population responded to increased adult mortality caused by a pathogen by increasing reproductive effort at an earlier age, which suggested an abrupt transition from iteroparity to semelparity (Jones et al. 2008). These studies provide an interesting overview on how contrasting environmental conditions can impact – sometimes very quickly – the tradeoff between mean survival and reproductive effort and outputs, and in turn affect the speed of the life history cycle at an intraspecific level. No previous study, however, has yet examined how different regimes of stochastic variation in environmental conditions could result in changes in both the temporal variation and mean of demographic parameters, which could then lead to intraspecific variation along the slow–fast continuum of life history tactics.

The aim of this study was to test whether contrasting levels of environmental fluctuation contribute to divergent life histories among free-ranging populations of a long-lived amphibian, the yellow-bellied toad (*Bombina variegata*). We conducted a study on five populations of *B. variegata* including two levels of stochastic environmental variation: (1) constant availability of breeding sites in space and time (called hereafter "predictable environments," as breeding site availability was predictable from one year to another); and (2) stochastic spatio-temporal availability of breeding sites, which were randomly created or destroyed each year by human activity (called hereafter "unpredictable environments," as breeding site availability was not predictable from year to year). In each population studied, we considered the following key parameters: (1) age-dependent survival, (2) female breeding propensity, (3) offspring productivity per female per year (a proxy for female fitness), and (4) temporal variation of these vital rates. Using capture–recapture data collected in both predictable and unpredictable environments, we specifically tested the hypothesis that survival would be lower on average and more variable from year to year in unpredictable environments, whatever the ontogenetic stage considered (juvenile, subadult, or adult); increased mortality was expected to result from human activity (e.g., through pollution or habitat alteration) (Mann et al. 2009, Semlitsch et al. 2009) and/or from the cost induced by moving from an aging rut network to a more recent one (Bonte et al. 2012). We also tested the hypothesis that a female could modify its schedule of resource allocation to reproduction according to the degree of environmental fluctuation. In particular, we predicted that breeding propensity would be more variable from year to year in unpredictable environments. In parallel, we hypothesized that offspring productivity would also be more variable from year to year but would be higher on average in unpredictable environments. Accordingly, we expected that enhanced environmental stochasticity could result in an accelerated life history cycle.

Methods

Biological model

Bombina variegata is a long-lived anuran. The life expectancy ranges from 4 to 10 yr in natural

conditions given the estimated survival rate of 0.7–0.9 (Beshkov and Jameson 1980, Cayuela et al. 2014, 2015*b* and the present study); some individuals reach an age of >20 yr in the wild and almost 30 yr in captivity (Smirina 1994). This species breeds in small water bodies characterized by stochastic water level variation. Its long lifespan and iteroparity are assumed to be a response to habitat uncertainty (Joly and Morand 1994, Morand and Joly 1995, Cayuela et al. 2014). Furthermore, females display risk-spreading tactics such as egg clutch fractionation over space and time (Buschmann 2002). The flexibility of the ovarian functioning of bombinatorids allows the continuous production or resorption of oocytes over the course of the breeding season (Guarino et al. 1998).

In Western Europe, *Bombina variegata* populations occupy both natural (Cayuela et al. 2011, 2013) and artificial environments (Cayuela et al. 2014, 2015*a*). In natural environments such as riverbanks (usually considered as ancestral habitats), these toads breed in rocky pools and natural depressions filled by floodwater or rainwater. The availability of natural breeding sites depends on long-term spatio-temporal changes in waterbed morphology; on the scale of a toad's lifetime, natural breeding site availability is therefore highly predictable (predictable environment). In contrast, *B. variegata* individuals that occupy artificial environments, such as woodlands exploited for logging or agricultural areas, breed in artificial water bodies such as ruts, ditches, and residual puddles created by skidders or farming equipment. Thus the interannual predictability of potential breeding sites depends on short-term spatio-temporal variation driven by logging or farming operations. In exploited woodlands, for instance, rut networks are created during logging operations (Cayuela et al. 2015*a*) and are filled in at the end of the exploitation of the forest patch or in the following 2 yr; on the scale of an individual's lifespan, the availability of breeding sites is therefore highly stochastic in artificial environments (unpredictable environment).

Surveyed populations and fieldwork

As in most studies that compare intraspecific and interspecific life history strategies (e.g., Gaillard and Yoccoz 2003, Nilsen et al. 2009, Miller et al. 2011, but also see Lawson et al. 2015 and Barraquand and Yoccoz 2013), we indirectly assessed environmental stochasticity through variations in demographic rates. No specific measures of environmental predictability (e.g., pond duration) were available for the studied populations. The study was conducted on five *B. variegata* populations in France (Table 1, see also in Appendix S1 for a map and details concerning environmental characteristics): three in unpredictable environments and two in predictable environments. The three unpredictable environment populations (hereafter POP1, POP2 and POP3) were located in the Ardennes, Meuse, and Charente departments, respectively. In these areas, the species reproduces in networks of water bodies resulting from logging and farming operations (e.g., ruts, ditches, and residual puddles); these are distributed in a landscape matrix consisting of managed woodlands and agricultural areas (Cayuela et al. 2015*a*). The two predictable environment populations were located in two distinct watersheds in the Ardèche department. Here the species breeds in networks of rocky pools and natural depressions filled by floodwater or rainwater in the vicinity of river channels (Cayuela et al. 2011, 2013). In these areas, the surrounding landscape mainly consists of nonmanaged woodlands.

The five populations were monitored using capture–recapture methods during survey periods varying from 5 to 10 yr between 2000 and 2014 (see Table 1). The capture–recapture (CR) survey design has previously been described in published studies (POP1, Pichenot 2008, POP2, Cayuela et al. 2014); a similar design was used for POP3, POP4, and POP5 (details concerning the survey design are provided in Appendix S1, Table S1–S6). It consisted of capturing the toads by hand or with a dip net during daylight hours (09:00–19:00). Capture sessions were carried out during the breeding season from late May to July. The entire study area was carefully checked every year in order to census all available water bodies. The yellow-bellied toads were captured in all distinct water-body networks (ranging from three networks in POP5 to 80 networks in POP2), which comprised a range of two water bodies (POP2, POP4, and POP5) to more than 100 water

Table 1. Survey design characteristics for the five populations investigated in the study: study period, survey duration, number of capture sessions performed during the survey period, total number of captures, and number of individuals identified during the survey.

	Study period	Survey duration	Capture sessions	Number of captures	Number of individuals
POP1	2000–2008	9 yr	45	953	581
POP2	2008–2014	7 yr	23	12 300	9418
POP3	2005–2014	10 yr	111	1053	456
POP4	2010–2014	5 yr	40	3053	1154
POP5	2010–2014	5 yr	37	2086	758

bodies (e.g., in POP4 and POP5). At each capture session, we sampled all water bodies in all networks. The time required to sample the entire study area in a single session varied from one (POP3) to 15 d (POP2). We considered three age classes: juveniles (captured after their first overwintering), subadults (captured after their second overwintering), and sexually mature adults (captured after at least three overwinterings). Although one study has considered that individuals can be sexually mature at age 2 (Barandun et al. 1997), four others consider the sexual maturity of this species to be age 3 (Kapfberger 1982, 1984, Rafinska 1991, Plytycz and Bigaj 1993). In any case, even if gonads may already be producing viable gametes at age 2, we assumed that individuals would be only marginally involved in breeding before age 3 because male reproductive success and female fecundity often increases with size/age in amphibians (Wells 1977, 2010, Arak 1983, Woolbright 1983). Therefore, we have assumed that yellow-bellied toads become sexually mature at age 3. The size (snout–vent length) of juveniles ranged from 22–29 mm, the size of subadults ranged from 30–34 m and individuals become sexually mature with a mean body length of 35 mm in males and 36 mm in females. We identified gender on the basis of forearm size and the presence of nuptial pads in males (Kyriakopoulou-Sklavounou et al. 2012). We identified each individual by the specific pattern of black and yellow mottles on its belly, which were recorded by photographs. To minimize misidentification errors, multiple comparisons of individual patterns were performed using the pattern-matching software Extract Compare (Hiby and Lovell 1990).

Multievent model design

The CR data was modeled using a re-parameterized version of the robust design proposed by Cayuela et al. (2014). The model follows the typical structure of "standard" robust design (Nichols et al. 1994, Kendall et al. 1997, 2012), i.e., made up of two nested levels of capture occasions. "Secondary sessions" encompass several field sessions performed over the same year. Sampling sessions were also conducted over successive years: "primary periods" correspond to yearly sessions. During a primary period (i.e., between secondary sessions), we assumed that the state of an individual was fixed and transitions between states were thus allowed between primary periods only.

The model was conditional on the occasion of first capture and an "unborn individual" state was included, which allowed us to model the probability of being recruited as a juvenile between two primary periods. After being recruited, individuals could successively transition between three ontogenetic stages, i.e., juvenile, subadult, and adult, given they survived. As is typical in a capture–recapture framework, survival estimates include both death and permanent emigration, i.e., apparent survival: see Schmidt et al. (2007) for a discussion on this point in amphibians. We assumed that sexually mature *Bombina variegata* individuals could breed or skip breeding each year (see Cayuela et al. 2014). Since individuals were captured in aquatic breeding sites only, non-breeding toads were considered as not available for capture (Church et al. 2007, Muths et al. 2010). Skipping breeding in a given year was thus equivalent to becoming a temporary emigrant and shifting to an unobservable state (Kendall and Nichols 2002). In the model, transitions between breeding/non-breeding states were assumed to obey a Markov chain process.

We specified our states as conditional on the occasion of first capture (Table 2). Because gender is not identifiable in juveniles or subadults, we used a multievent CR approach (Pradel 2005) to model uncertainty in gender assignment; gender was thus coded as a state instead of as a group as is usual in CR data modeling. Individuals could occupy one of the eleven distinct states: (UM) unborn male; (UF) unborn female; (JM) alive juvenile male; (JF) alive juvenile female; (SM) alive subadult male; (SF) alive subadult female; (BM) breeding male; (BF) breeding female; (NBM) non-breeding adult male; (NBF) non-breeding adult female; (†) dead individual. Ten state transitions were possible for the recruitment and age transition probabilities between two primary periods (Fig. 1, matrix A). Given that we examined recruitment without accounting for gender dependency, A^{JM}/A^{JF} were constrained to be equal (the parameter is hereafter quoted A). Moreover, age transition probabilities $\beta^{JM}/\beta^{JF}/\beta^{SM}/\beta^{SF}$ were fixed at 1 between secondary sessions and at 0 between primary periods. For the survival probability between two primary periods, ten state transitions were possible (Fig. 1, matrix Φ). Given that the parameters Φ^{BNM} and Φ^{BNF} were not identifiable, Φ^{BM}/Φ^{BNM} and Φ^{BF}/Φ^{BNF} were constrained to be equal in the model. Survival transition probabilities were fixed at

TABLE 2. Definition of parameters estimated in the capture–recapture multi-event model.

Parameter	Definition
A	Probability that a newly metamorphosed individual is recruited (Fig. 1, matrix A)
β	Probability that an individual does not reach the next ontogenetic stage (Fig. 1, matrix A)
Φ	Probability that an individual survives (Fig. 1, matrix Φ)
γ^{B}	Probability that a sexually individual bred at time t, given it has bred at $t-1$ (Fig. 1, matrix Y)
γ^{NB}	Probability that a sexually mature individual skipped a breeding opportunity at time t, given it skipped breeding at $t-1$ (Fig. 1, matrix Y)
P	Probability that an individual was recaptured during a secondary session (Fig. 1, matrix P)

matrix A (recruitment and age transition)

$$
\begin{array}{c}
 \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ \mathrm{NBM} \\ NBF \\ \dagger
\end{array}
\begin{array}{c}
\begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\
\begin{pmatrix}
1-\alpha^{JM} & 0 & \alpha^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1-\alpha^{JF} & 0 & \alpha^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \beta^{JM} & 0 & 1-\beta^{JM} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \beta^{JF} & 0 & 1-\beta^{JF} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \beta^{SM} & 0 & 1-\beta^{SM} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \beta^{SF} & 0 & 1-\beta^{SF} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\end{array}
$$

matrix Φ (survival transition)

$$
\begin{array}{c}
 \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger
\end{array}
\begin{array}{c}
\begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \phi^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{JM} \\
0 & 0 & 0 & \phi^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{JF} \\
0 & 0 & 0 & 0 & \phi^{SM} & 0 & 0 & 0 & 0 & 0 & 1-\phi^{SM} \\
0 & 0 & 0 & 0 & 0 & \phi^{SF} & 0 & 0 & 0 & 0 & 1-\phi^{SF} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi^{BM} & 0 & 0 & 0 & 1-\phi^{BM} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{BF} & 0 & 0 & 1-\phi^{BF} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBM} & 0 & 1-\phi^{NBM} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBF} & 1-\phi^{NBF} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\end{array}
$$

matrix Y (breeder/non-breeder transition)

$$
\begin{array}{c}
 \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger
\end{array}
\begin{array}{c}
\begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BM} & 0 & 1-\gamma^{BM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BF} & 0 & 1-\gamma^{BF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBM} & 0 & \gamma^{NBM} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBF} & 0 & \gamma^{NBF} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
\end{array}
$$

matrix *P* (recapture)

$$
\begin{array}{c}
 \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger
\end{array}
\begin{array}{c}
\begin{array}{ccccc} NS & J & S & M & F \end{array} \\
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1-p^{JM} & p^{JM} & 0 & 0 & 0 \\
1-p^{JF} & p^{JF} & 0 & 0 & 0 \\
1-p^{SM} & 0 & p^{SM} & 0 & 0 \\
1-p^{SF} & 0 & p^{SF} & 0 & 0 \\
1-p^{BM} & 0 & 0 & p^{BM} & 0 \\
1-p^{BF} & 0 & 0 & 0 & p^{BF} \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0
\end{pmatrix}
\end{array}
$$

FIG. 1. Elementary matrices for state–state and events transitions: UM, unborn male; UF, unborn female; JM, juvenile male; JF, juvenile female; SM, subadult male; SF, subadult female; BM, breeding male; BF, breeding female; NBM, non-breeding male; NBF, non-breeding female; †, dead; NS, not seen; J, seen juvenile, S, seen subadult; M, seen sexually mature male; F, seen sexually mature female.

1 between secondary sessions. For breeder/non-breeder transitions between two primary periods, four state transitions were possible (Fig. 1, matrix Y). 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* multi-event modeling formulation, six observation probabilities were considered (Fig. 1, matrix *P*). Note that as non-breeding individuals were not available for recapture, their recapture probability was fixed at 0.

Building biological scenarios

The parameterization was implemented in the E-SURGE program (Choquet et al. 2009), which provides robust tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters.

The datasets from the five populations differ markedly in terms of the number of study years and capture sessions per year (Appendix S1, Table S2–S6), and we did not expect any identical parameters in the different populations. Thus the expected benefit in terms of precision or statistical power of simultaneously analyzing the five datasets would be rather small or null, whereas the cost in terms of computation would be high. As a result, we separately analyzed the five datasets and then compared the mean and variance of vital rates provided by the best-fitted model for each population.

For each population, competing models were ranked through a model-selection procedure using Akaike information criteria adjusted for a small sample size (AICc) and AICc relative weights (Burnham and Anderson 2002). We tested our hypotheses concerning recapture and state transition probabilities from the general model [A (YEAR), Φ(YEAR × AGE), γ(YEAR × SEX), *P*(YEAR + AGE + SEX)]. Variation in survival between ontogenetic stages (AGE) was tested by specifying state transition differences between the three stages coded as states in the model. Since we were interested in investigating female breeding investment, we accounted for gender-dependent variation (SEX) in breeding probability by considering state transition differences between genders coded as states in the model. Initial state probability was held to be different between ontogenetic stages and gender. Furthermore, recruitment probability A was held to be different among years (YEAR).

From the general model, we successively modeled field observation, breeding probability and survival probability. We used a downward testing procedure by removing the effects one by one and retained the best linear combination at each step. First, we tested whether recapture probability *P* varied between years (YEAR), as well as between ontogenetic stages (AGE) and gender in sexually mature adults (SEX). For the last hypothesis, p^{JM}/p^{JF}, p^{SM}/p^{SF} and p^{BM}/p^{BF} were held to be different. Since we aimed at investigating the yearly breeding propensity of females, we then considered gender-specific differences in breeding probability and tested whether breeder/non-breeder transitions γ varied between years (YEAR). For this last hypothesis, the pair of transitions was held to be different γ^{BM}/γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$. We then tested whether survival probability Φ differed (1) between years (YEAR) and (2) between ontogenetic stages (AGE).

For the third hypothesis, Φ^{JM}/Φ^{JF}, Φ^{SM}/Φ^{SF} and Φ^{SM}/Φ^{SF} were constrained to be equal.

Because the violation of the closure assumption may bias survival estimates in robust design models (Kendall 1999), we assessed the robustness of our analysis by removing secondary sessions in which only a few individuals were encountered. Within a primary period, the secondary session resulting in the maximum number of encountered toads has been retained as the reference session for this year. For each primary period, we removed all secondary sessions in which the number of captured toads was <50% of the number of toads encountered during this reference session. This led to the exclusion of between 5 and 10 sessions (detailed in Appendix S2, Table S1) depending on the population and the year (mainly early or late secondary sessions during the breeding season). Then we fitted to these reduced datasets the best-supported model from our model selection procedure for each population. The comparisons of mean and temporal survival variance with and without the removal of these secondary sessions are provided in the appendix (Appendix S2, Fig. S1 and Fig. S2). Only marginal discrepancies were detected, so the potential violation of the closure assumption is not an issue in our analysis. Moreover, unlike many other amphibians (Ranids, Bufonids, and Hylids), the yellow-bellied toad has a lateral line as well as complete interdigital webs (Seidel et al. 2001), which are adaptations for an extended aquatic breeding period. Prolonged spermiation and the presence of post-vitellogenic follicles (Guarino et al. 1998) throughout the period of breeding activity allow this species of toad to reproduce from April to August (Di Cerbo and Biancardi 2004), which makes individuals available for capture during this relatively long period. Taken together, these factors suggest that the closure assumption may hold in our study.

Quantifying temporal variation in survival and breeding propensity

We built models with yearly variation in survival and breeding transition for all five populations [A (YEAR), Φ(AGE × YEAR), γ(AGE × YEAR), *P*(CST)] in order to obtain annual estimates of survival rates along with their estimated variance and covariance. Using the methods proposed in Gould and Nichols (1998), we estimated the temporal variance in survival of all age classes by removing the effects of sampling variance from the estimated total variance in survival. We used these calculated standard deviations resulting from the yearly variation in survival probability as indicators of variation in survival of a certain age class over time, which was in turn a proxy for estimating the presence of canalization of the given trait. We then used the method proposed by Gaillard and Yoccoz (2003) to compare the temporal variation variance of survival rates between ontogenetic stages and populations. This method compares the maximum variance of survival we can expect (from the observed mean survival rate) with the observed variance in juvenile, subadult, and adult survival. This maximum variance is $s \times (1 - s)$, where s is the mean survival rate. Between the observed variance and the maximum variance, we then obtained the ratio of possible variation (called "temporal variation ratio" hereafter, following the terminology used by Gaillard and Yoccoz 2003) and compared this between ontogenetic stages and populations. In order to provide uncertainty measures of the temporal variation ratio of survival (and breeding) rates, we bootstrapped in the individual capture–recapture histories. Because E-surge does not provide an automatic procedure for bootstrapping CMR-histories, we had to perform this manually. We thus limited our approach to 50 bootstraps per population. For each bootstrap of each population, we fitted the best model we obtained from the model selection procedure and applied the Gould and Nichols (1998) method. This allowed us to obtain a variance for the 50 bootstraps, from which we derived the 95% CI of the temporal variation ratio of survival rate. We then used the overlap of the 95% CIs to discuss the statistical differences between the variation estimates. Temporal variation ratios of breeding propensity were calculated using the same procedure.

Quantifying annual offspring production and its temporal variance

From the same model, annual offspring production was estimated as the number of newly recruited juvenile females at t per number of breeding females at $t - 1$. The number of recruited juvenile females at time t (*NRJ*) and the number of annual breeding females at $t - 1$ (NBF) were derived (1) from the number of juveniles captured at t and breeding females captured at $t - 1$, (2) from their capture probability estimates at a given secondary session (CPJ: the capture probability of juveniles at a secondary session of year t; *CPBF*: the capture probability of breeding females at a secondary session of year $t - 1$), (3) from the best supported model, and (4) from the number of secondary sessions at t (K) and $t - 1$ (L). Annual offspring production was thus expressed as: $(\mathrm{NRJ} / (1 - (1 - \mathrm{CP})^{K})) / (\mathrm{NBF}/(1 - (1 - \mathrm{CPBF})^{L}))$. The variance and covariance of annual fecundity was estimated using the methods as described for survival probability.

Results

The model selection procedure and best-supported model for each population are provided in Table 3. We did not detect differences in the average breeding propensity of females (breeding vs. skipping reproduction during two consecutive years) between unpredictable and predictable environments (Fig. 2). Small overlaps in the 95% CI of the temporal variation ratios (Fig. 2) indicated that breeding propensity was more variable over time in unpredictable than in predictable environments,

TABLE 3. Model selection procedure showing the competing models run for each population: r = model rank, k = number of parameters, Dev. = residual deviance, AICc = Akaike information criteria adjusted for a small sample size and their derivate quantities, w = AICc relative weight.

	Model definition							
r	Survival	Breeding	Recruitment	Recapture	k	Dev.	AICc	w
POP1 (Unpredictable)								
1	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	59	11942.87	12064.39	1.00
2	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	50	11973.54	12076.38	0.00
3	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	75	11929.29	12085.74	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	YEAR	72	11954.25	12104.19	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	64	12006.38	12139.06	0.00
6	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	61	12100.12	12226.37	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	67	12556.51	12705.64	0.00
POP2 (Unpredictable)								
1	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	61	127315.07	127437.49	0.92
2	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	49	127331.91	127430.19	0.08
3	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	44	127364.50	127452.73	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	YEAR	58	127603.53	127719.91	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	50	128088.70	128188.98	0.00
6	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	47	128126.73	128220.98	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	55	128228.80	128339.15	0.00
POP3 (Unpredictable)								
1	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	67	19925.58	20062.09	0.58
2	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	85	19888.94	20062.98	0.42
3	AGE × YEAR	SEX × YEAR	YEAR	YEAR	83	19908.03	20077.88	0.00
4	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	70	19946.22	20088.96	0.00
5	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	64	19986.76	20117.05	0.00
6	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	56	20010.99	20124.74	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	76	20730.38	20885.61	0.00
POP4 (Predictable)								
1	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	34	40734.24	40802.44	1.00
2	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	35	41777.84	41848.05	0.00
3	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	35	42156.09	42226.3	0.00
4	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	43	42149.91	42236.23	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	36	42183.84	42256.06	0.00
6	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	39	42323.67	42401.93	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	YEAR	40	42412.86	42493.13	0.00
POP5 (Predictable)								
1	AGE × YEAR	SEX	YEAR	AGE × SEX + YEAR	34	25874.07	25942.37	1.00
2	AGE	SEX × YEAR	YEAR	AGE × SEX + YEAR	34	26963.43	27031.73	0.00
3	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	43	26995.75	27082.23	0.00
4	AGE × YEAR	YEAR	YEAR	AGE × SEX + YEAR	35	27019.16	27089.48	0.00
5	YEAR	SEX × YEAR	YEAR	AGE × SEX + YEAR	36	27049.63	27121.97	0.00
6	AGE × YEAR	SEX × YEAR	YEAR	YEAR	49	27199.63	27298.25	0.00
7	AGE × YEAR	SEX × YEAR	YEAR	AGE × SEX	38	27255.67	27332.05	0.00

however. Furthermore, although breeding females in unpredictable environments annually produced more offspring on average, offspring production was more variable over time (small overlaps in the 95% CI, see Fig. 3).

In the five populations, survival differed between ontogenetic stages (juvenile, subadult, and adult) and increased with age (Fig. 4). At the three ontogenetic stages, survival was lower in unpredictable environments. Small overlaps in the 95% CI of the temporal variation ratios indicated that the survival of juveniles and subadults was more variable in unpredictable environments, whereas large overlaps in the 95% CI suggested that temporal variability of adult survival was similar in both environments (Fig. 4).

DISCUSSION

Comparing the population dynamics in unpredictable environments (variable spatio-temporal availability of breeding sites created by human activity) and predictable environments (persistent availability of natural breeding sites) reveals divergent life history tactics in *B. variegata*.

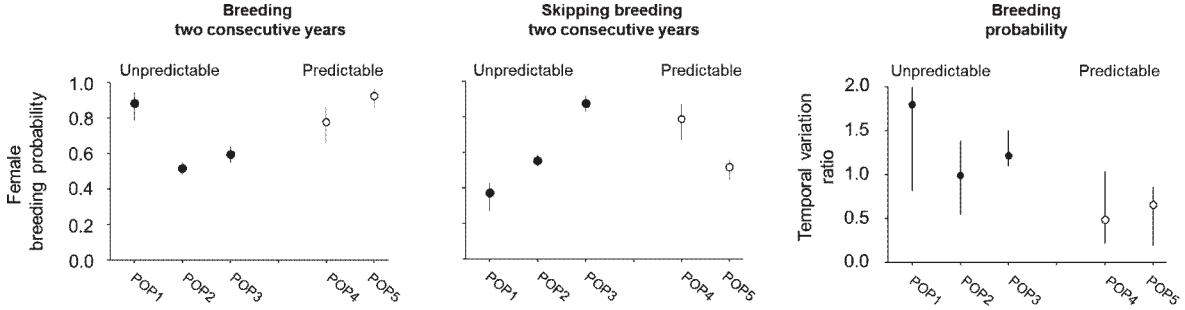

FIG. 2. Conditional breeding probability (breeding or skipping breeding during two consecutive years) and temporal variation ratio of breeding propensity of *B. variegata* females studied in France over the 2000–2014 period. The 95% CI is shown using error bars.

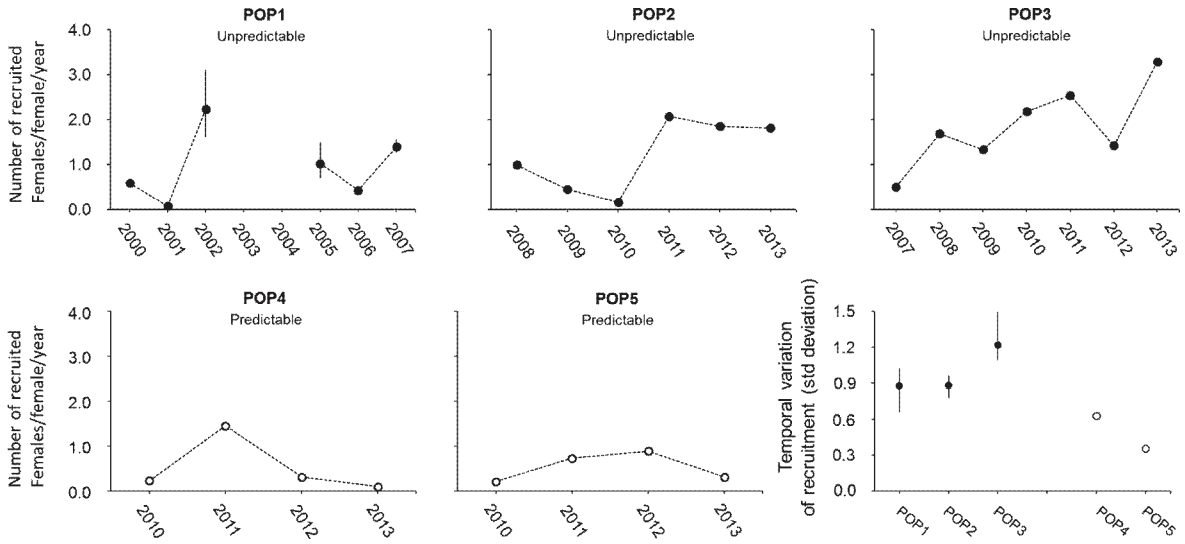

FIG. 3. Annual offspring productivity (number of recruited females per female per year) and temporal variation (standard deviation) in five populations of *B. variegata* studied in France over the 2000–2014 period. The 95% CI is shown using error bars.

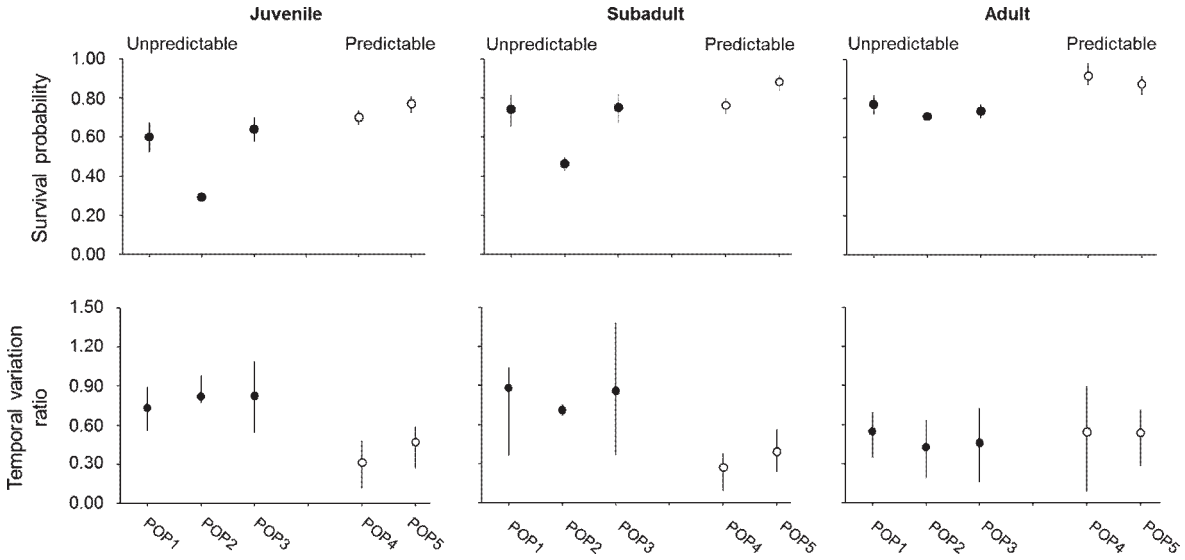

FIG. 4. Mean annual survival at three ontogenetic stages (juvenile, subadult and adult) and temporal variation ratios in five populations of *B. variegata* studied in France over the 2000–2014 period. The 95% CI is shown using error bars.

While on average female breeding propensity did not differ between environments, our results demonstrated that it was more variable from year to year in unpredictable than in predictable environments. In addition, although females produced on average more viable offspring per year in unpredictable environments, offspring production was more variable from year to year. Survival at the three ontogenetic stages was slightly lower and more variable (except in adults) from year to year in unpredictable environments. Taken together, the differences recorded in vital rates indicate that populations in unpredictable environments respond to increased overall mortality by increasing offspring production, which leads to an acceleration of the life history cycle.

Alternative hypothesis

It is possible that alternative mechanisms – for example, differences in weather, predation, or competition regimes – might have caused the observed pattern in demographic rate mean and variation. Weather is often considered the most important environmental driver of amphibian vital rates (reviewed in Walls et al. 2013). Yet in our studied populations, the strongest yearly weather variations were recorded for populations in which the spatial configuration of ponds was most stable over time and in which vital rates were the least variable (Appendix S1, Table S1). This suggests that the differences of mean and variance in vital rates in our findings did not result from local differences in weather variability. Another possible factor could be local differences in the occurrence of predators. This seems rather unlikely, however, because predation has been found to have a small effect on tadpole survival of *B. variegata* compared to drought risks (Morand 1997). In addition, after metamorphosis, *B. variegata* displays anti-predator strategies (described in Bajger 1980) involving numerous venom glands that produce a noxious secretion (König and Bininda-Emonds 2011) as well as behavioral responses such as defensive postures (the "unken reflex," see Toledo et al. 2011) in which toads exhibit their aposematic coloration. A third possible factor could be local differences in the presence of competitors. *B. variegata* breeds in highly temporary water bodies that are avoided by most other amphibians (Morand and Joly 1995, Morand 1997), however, so local differences in the amphibian community are not likely to have an impact on the demographic rate of *B. variegata.*

Contrasting patterns of environmental fluctuation influence female breeding propensity and offspring productivity

Our results indicate that female breeding propensity was on average similar in the two environments, but was more variable from year to year in unpredictable environments. In *B. variegata*, the decision to reproduce depends on a variety of external factors (e.g., water deficit) and the physiological state of the female during the current breeding opportunity (Cayuela et al. 2014), in line with the concept of "state-based life history" (McNamara and Houston 1996). In females, the energetic costs of breeding are usually related to three factors: the storage of lipids in body fat ("capital breeder tactic;" Fitzpatrick 1976, Bonnet et al. 1998), internal sexual mechanisms (especially oogenesis dynamics), and escaping unwanted sexual attention and possible injury inflicted by males during attempts at amplexus (Wells 2010). These costs are likely to be enhanced by spatio-temporal unpredictability of breeding sites. In managed woodlands in particular, breeding sites are created by logging operations that leave deep ruts that fill with rainwater (Cayuela et al. 2015*a*) and typically remain attractive for toads for 2 yr. This type of water body creation generates strong local stochasticity of available breeding sites. As a result, the interannual fidelity of females to breeding sites is lower and more variable in unpredictable than in predictable environments (Pichenot 2008, H. Cayuela et al. *in prep*). Breeding propensity that is more variable over time in unpredictable environments could thus be a result of the costs induced by moving from an aging rut network to a more recent one. These costs could be indirect, due to lost metabolic energy in movement, or direct, due to the time invested in movement (Bonte et al. 2012) that may prevent a female from breeding during a reproduction opportunity.

Differences in annual offspring productivity between the two types of environment indicate contrasting lifetime schedules of resource allocation to breeding. Risk-spreading tactics, including bet-hedging and adaptive coin-flipping (see Philippi and Seger 1989, Wilbur and Rudolf 2006), have been highlighted in various organisms (Veening et al. 2008, Childs et al. 2010, Nevoux et al. 2010, Gamelon et al. 2013). In *B. variegata*, risk-spreading tactics (e.g., egg clutch fractionation over space and time) usually allow females to cope with reproductive success uncertainty caused by high desiccation risk in oviposition sites (Buschmann 2002). In predictable environments, our results indicate that the interannual predictability of breeding site availability allows females to more consistently spread their breeding effort over multiple reproduction opportunities in a year. Since female breeding investment in a given reproduction period depends on past breeding status (Cayuela et al. 2014), subsequent fitness gains (number of offspring) are therefore annually lower but more constant over time in predictable environments. In contrast, in unpredictable environments, the interannual unpredictability of breeding site availability and localization constrains the allocation of breeding investment over time. Since egg resorption allows females to recover energetic resources that can be reinvested later, yearly fitness gains are higher on average, but less constant from year to year. Our results show that contrasting

patterns of environmental fluctuation could regulate risk-spreading tactics among populations by shaping the trade-off between mean and variance of breeding investment and subsequent fitness gains.

Contrasting patterns of environmental fluctuation influence survival across ontogenetic stages

Our results show that mean survival increases with age while temporal variation decreases, which is in line with the environmental canalization paradigm of "slow species" (Yoccoz and Gaillard 2003). The survival estimates of adults in our study are congruent with those found in previous studies (Φ = 0.80 in Plytycz and Bigaj 1993, Φ = 0.74 in Cayuela et al. 2014). In amphibians, post-metamorphosis survival is positively correlated with age and size (Altwegg and Reyer 2003, Garner et al. 2011, Schmidt et al. 2012). Compared to most anurans, recorded *B. variegata* survival rates and longevity (Smirina 1994) are high when corrected for allometry (see the HAGR website: http://genomics.senescence.info). This is likely due to anti-predator and anti-microbial strategies – specific and unique families of antimicrobial peptides in bombinatorid skin secretions protect them against invasion by pathogenic microorganisms and also play a role in protecting the animal from ingestion by predators (Conlon 2011, König and Bininda-Emonds 2011).

At each ontogenetic stage, survival was slightly lower and more variable in unpredictable environments. In these environments, the interannual unpredictability of breeding sites may result in high dispersal propensity, thus reducing apparent survival (in amphibians, see Perret et al. 2003, Schmidt et al. 2007); in capture–recapture approaches, apparent survival estimates include both death and permanent emigration (Nichols et al. 1994, Kendall et al. 1997). The lower survival rate may also be the result of dispersal costs in unpredictable environments. For example, increased mortality may result from logging if operations are carried out in the spring. Logging activities near breeding ponds may also negatively impact survival due to changes in the surface temperature of the soil and loss of moisture (Semlitsch et al. 2009). Moreover, rut filling resulting from path restoration during reproduction activity could lead to catastrophic mortality in breeding adults. Finally, in agricultural areas, prolonged exposure to pesticides can alter growth before and after metamorphosis by inhibiting normal thyroid activity and/or increase susceptibility to disease through the suppression of the humoral response (Mann et al. 2009).

Conclusion

Taken together, the differences recorded in *B. variegata* vital rates in unpredictable and predictable environments demonstrate that different regimes of stochastic variation in environmental conditions may contribute to intraspecific variation of life history tactics along the slow–fast continuum. An increase in offspring productivity as well as increased variation in adult survival (leading to a decrease in average annual adult survival) results in an acceleration of the life history cycle in populations in unpredictable artificial environments. Habitat anthropization modifies the spatio-temporal availability of breeding sites and contributes to divergent selection gradients at intraspecific scales. Because of this new selective pressure, *B. variegata* colonization of human-impacted habitats may lead to local adaptations that could minimize to some extent the fitness costs induced by changes in the regime of environmental fluctuation. Understanding the processes of this adaptation (plasticity vs. selection) requires further investigation based on experimental and/or translocation approaches.

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Supporting Information

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Does habitat unpredictability promote the evolution of a colonizer syndrome in amphibian metapopulations?

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Abstract. Dispersal is a central component of life history evolution. An increasing number of studies suggest that spatiotemporally variable environments may promote the evolution of "dispersal syndromes," consisting of covariation patterns between dispersal and morphological, physiological, behavioral, and life history traits. At the interspecific scale, the "colonizer syndrome" appears to be one of the most frequently recorded associations between dispersal and life history traits, linking a high dispersal rate, high fecundity, and a short lifespan as systematically combined adaptations in spatiotemporally varying environments. However, few studies have highlighted the existence of a "colonizer syndrome" at the intraspecific scale, and none have investigated how different degrees of habitat stochasticity might shape covariation patterns between dispersal and life history traits. In this study, we examined this issue in free-ranging metapopulations of the yellow-bellied toad (*Bombina variegata*) using capture–recapture data. Combining the results of this study with another recent study, we found that a high dispersal rate, high fecundity, and a short lifespan are associated in metapopulations experiencing unpredictable environments. In contrast, a very low dispersal rate (close to zero), low fecundity and a long lifespan are associated in metapopulations occupying predictable environments. We discuss these results as well as their demographic and evolutionary consequences.

Key words: amphibian; Bombina variegata; *colonizer syndrome; demography; dispersal; environmental predictability; life history; multievent capture–recapture models.*

Introduction

Dispersal is a central component of life history evolution and is usually defined as the movement of an individual from its natal or previous breeding site to another site (Ronce 2007). Since dispersal results in the movement of individuals and genes among populations, it has wide-ranging consequences on population dynamics and viability, genetic structure, and local adaptation (Clobert et al. 2009, Cote et al. 2010). When a habitat is homogeneous and stable over time, the avoidance of inbreeding and competition among kin are usually the main selective forces acting on dispersal evolution (Matthysen 2012). However, when a habitat is heterogeneous and unstable over time, theoretical models predict that the spatiotemporal variability of the environment is the strongest evolutionary force shaping dispersal evolution and favors dispersal polymorphism within and between populations (McPeek and Holt 1992, Paradis 1998, Travis and Dytham 1999, Reigada et al. 2015).

An increasing number of studies suggest that spatiotemporally variable environments may promote the evolution of "dispersal syndromes" (reviewed in Duckworth 2012, Ronce and Clobert 2012), consisting of covariation patterns between dispersal and morphological (Denno et al. 1996, Zera and Denno 1997), physiological (Haag et al. 2005, Zera et al. 2007), and behavioral traits (Dingemanse et al. 2003, Cote et al. 2010). Other studies have also suggested the existence of dispersal syndromes that involve covariation between dispersal propensity and life history traits such as survival, fecundity, breeding decision, and age at maturity (Ronce and Clobert 2012, Stevens et al. 2013). However, the direction and magnitude of these associations seem to vary broadly at intra- and interspecific scales, precluding any general conclusions regarding the covariation patterns between dispersal and demographic traits (Stevens et al. 2014). The "colonizer syndrome" (Baker and Stebbins 1965) appears to be one of the most frequently recorded associations between dispersal and life history traits, linking high dispersal ability, high fecundity, and a short lifespan as systematically combined adaptations in spatiotemporally varying environments. High dispersal ability is therefore associated with "fast" life history strategies (Ronce and Olivieri 2004). According to the "fast-slow continuum" concept (sensu Sæther 1987), life history traits of species show covariation patterns that allow them to be classified on a continuum from fast to slow (Gaillard et al. 1998, Bielby et al. 2007); a fast life history

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is characterized by early reproduction, short generation time, short lifespan, and high fecundity. At interspecific scale, one of the best empirical examples of the colonizer syndrome has been provided by two studies that focus on the covariation pattern between dispersal and demographic traits in 142 butterfly species (Stevens et al. 2012, 2013). These studies confirm that high dispersal is associated with "fast" strategies in species occupying spatiotemporally varying environments, and that dispersal is likely to be a tactic for temporally escaping from unsuitable environmental conditions.

As has been demonstrated at interspecific level, colonizer syndrome has also been reported at intraspecific level. Particularly in range-shifting populations (e.g., invasive species), individuals from populations located at the edge of the colonization range have been found to have greater dispersal capacities, associated with a fast life history strategy (Phillips et al. 2010, Chuang and Peterson 2015). For example, in their invasive Australian range, cane toads (*Rhinella marinus*) occupying recently colonized areas show higher dispersal propensity and grow more quickly than toads from older, long-established populations, even when raised under similar environmental conditions (Phillips 2009). Similarly, Glanville fritillaries (*Melitaea cinxia*) in recently colonized environments tend not only to be highly dispersive, but also to invest more in reproduction (Hanski et al. 2006, Saastamoinen 2007). These studies provide an interesting overview on how the age of a population may result in life history shifts from slow to fast tactics, which further accelerate the rate of population spread and biological invasions (also reviewed in Chuang and Peterson 2015). Yet no previous study has examined how different regimes of habitat unpredictability (i.e., stochastic variation of habitat availability in space and time), an environmental factor that usually promotes dispersal polymorphism in populations, might shape covariation patterns between dispersal and life history traits among natural populations.

In this study, we examined whether contrasting levels of habitat predictability contribute to divergent dispersal patterns in free-ranging metapopulations (i.e., a spatially structured population in the broad sense) of an amphibian: the yellow-bellied toad (*Bombina variegata*). We compared dispersal rates in four metapopulations of yellow-bellied toads experiencing two levels of habitat predictability: (1) constant availability of breeding pond networks in space and time (called hereafter "predictable environments" as pond networks availability was predictable from one year to another) and (2) stochastic spatiotemporal availability of breeding pond networks, which were randomly created or destroyed each year by human activity (called hereafter "unpredictable environments" as pond network availability was not predictable from year to year). In a recent study (Cayuela et al. 2016*a*), we found that demographic traits differ between metapopulations occupying these two environments, with an acceleration of the life history cycle in metapopulations located in unpredictable semi-natural environments (Table 1). Indeed, individuals from metapopulations occupying unpredictable environments displayed lower and more variable survival rates before and after sexual maturity than individuals occupying predictable environments. In addition, female breeding frequency was more variable from year to year, and offspring production was on average higher and annually more variable in unpredictable environments than in predictable ones.

Using recently developed multi-event capture–recapture (CR) models (Lagrange et al. 2014), we tested the hypothesis that both intra- and interannual dispersal rates between pond networks were higher in metapopulations

Table 1. Life history characteristics (life span, adult survival, and female fecundity; see Cayuela et al. 2016*a*, *b*) and survey design (present study) for the four metapopulations of *Bombina variegata* considered in this study.

	Unpredictable environment		Predictable environment	
Characteristics	POP1	POP2	POP3	POP4
Life history (Cayuela et al. 2016*a*, *b*)				
Life history tactic	fast	fast	slow	slow
Life span (yr)	3.16	2.44	11.5	7.33
Adult survival	0.76 (0.91)	0.71 (0.71)	0.92 (0.91)	0.88 (0.89)
Female fecundity	1.21 (0.71)	0.96 (0.81)	0.52 (0.62)	0.53 (0.32)
Survey design (present study)				
Study period	2000–2007	2012–2014	2010–2014	2010–2014
Survey duration (yr)	6	3	5	5
Capture sessions	45	9	15	15
Number of captures	953	4587	4475	2982
Number of individuals	581	2532	479	814
Number of pond networks	28	64	14	8

Notes: Female fecundity is expressed as the mean annual number of females produced per breeding female per year. Life span after adulthood has been calculated using the adult survival rates (s) provided in Cayuela et al. (2016*a*, *b*) as follows: $s/(1 - s)$. Temporal variance ratios of demographic parameters are given in brackets. Concerning the survey design, the following information is provided: study period, survey duration, number of capture sessions performed during the survey period, total number of captures, number of individuals identified during the survey, and the number of pond networks sampled during the study period.

with fast life history strategies that experience unpredictable environments. In these metapopulations, we expected that dispersal rates would show higher inter-annual variation due to stochastic spatiotemporal fluctuation in pond networks availability.

Methods

Biological model

The life history characteristics of *B. variegata* in metapopulations experiencing unpredictable and predictable environments are provided in Table 1. *B. variegata* breeds in small, highly temporary waterbodies avoided by most other amphibians (Morand and Joly 1995, Morand 1997). To cope with uncertainty in breeding success resulting from pond desiccation, females use risk-spreading tactics such as egg clutch fractionation over space and time (Barandun et al. 1997, Buschmann 2002). The flexibility of the ovarian functioning of bombinatorids allows the continuous production or resorption of oocytes over the course of the breeding season (Guarino et al. 1998).

In Western Europe, *B. variegata* occurs in both natural (Cayuela et al. 2013) and seminatural environments (Barandun 1990, Cayuela et al. 2015). Metapopulations usually occupy a set of pond networks (i.e., group of spatially aggregated water bodies), which were located in our study case in a matrix dominated by woodland; the dispersal cost in this habitat is usually expected to be low in amphibians (see Cushman 2006). Subpopulations occupy distinct pond networks (Tables 1 and 2) between which dispersal may occur. The delineation of pond network was established using ArcGis 10.1 (ArcGis 10.1, Environmental Systems Research Institute, Redlands, California, USA) by creating polygons connecting the water bodies located on the boundary of the network (i.e., approach named "Minimum Convex Polygon"; see White and Garrott 1991). As previously done in *B. variegata* (see Pichenot 2008), pond networks were assumed to be different when the minimal distance separating the boundary of polygons exceeded 100 m; this distance has been fixed because the between pond movement distances are usually <100 m in this species (Beshkov and Jameson 1980, Hartel 2008). Within metapopulations, pond networks varies in terms of size (i.e., the mean number of water bodies per network; Table 2) and isolation (i.e., the mean distance separating two pond networks in each metapopulation; Table 2). The surface covered by the different networks widely varied from 18 m^2 to almost 2,500 m^2.

In natural environments such as riverbanks (usually considered as ancestral habitats; see Cayuela et al. 2011), the species breeds in networks of rocky pools filled by floodwater or rainwater (see pictures in Appendix S1). At the intra-annual scale, the water level of the rocky pools is highly stochastic and the number of pools within the networks can thus strongly fluctuate over the breeding season. At the inter-annual scale, however, the availability of these networks depends on long-term spatiotemporal changes in waterbed morphology, so, on the scale of a toad's lifetime, pond network availability is highly predictable from one year to another (i.e., "predictable environments"). The annual rates of network appearance/disappearance are null in these systems (Table 2). In these habitats, the surrounding landscape consists mainly of non-managed woodlands (Fig. 1). Yellow-bellied toads may also occur in seminatural environments, such as woodlands exploited for logging. In these systems, toads breed in networks of semi-natural waterbodies such as ruts, ditches, and residual puddles created by skidders during logging operations (see pictures Appendix S1); these are naturally filled with soil in the following years or at the end of the exploitation of the forest plot to restore the pathways. At the intra-annual scale, the water level of these semi-natural waterbodies strongly varies according to rainfall, leading to large fluctuation in the number of breeding ponds within the networks. At the inter-annual scale, the rate of network appearance varies from 0.20 to 0.50 in POP1 and from 0.24 to 0.25 in POP2 (Table 2). Simultaneously, the annual rate of network disappearance varies from 0.05 to 0.17 in POP1 and from 0.09 to 0.21 in POP2. Thus, on the scale of a toad's lifespan, this high

Table 2. Environmental characteristics of the four studied populations: pond network origin, logging vs. natural erosion; number of pond networks over a 3-yr period of reference, 2006–2008 in POP1 and 2012–2014 in POP2, POP3, and POP4; probability of pond network appearance and disappearance over the 3-yr period; pond network isolation, i.e., mean distance between two pond networks and their coefficients of variation; and pond network size, i.e., mean number of ponds within a pond network and their coefficient of variation.

Population	Pond network origin	No. pond networks	Rate of pond network appearance	Rate of pond network disappearance	Pond network isolation	Pond network size
POP1 unpredictable	Logging	2006, 18; 2007, 23; 2008, 25	2006, 0.50; 2007, 0.39; 2008, 0.20	2006, 0.05; 2007, 0.17; 2008, 0.12	2,864.50 (57%)	3.70 (70%)
POP2 unpredictable	Logging	2012, 60; 2013, 66; 2014, 71	2012, NA; 2013, 0.24; 2014, 0.25	2012, NA; 2013, 0.09; 2014, 0.21	4,424.64 (53%)	5.64 (88%)
POP3 predictable	Erosion	2012, 14; 2013, 14; 2014, 14	2012, 0.00; 2013, 0.00; 2014, 0.00	2012, 0.00; 2013, 0.00; 2014, 0.00	676.57 (61%)	4.52 (105%)
POP4 predictable	Erosion	2012, 8; 2013, 8; 2014, 8	2012, 0.00; 2013, 0.00; 2014, 0.00	2012, 0.00; 2013, 0.00; 2014, 0.00	501.62 (61%)	4.71 (93%)

Note: NA is unavailable data.

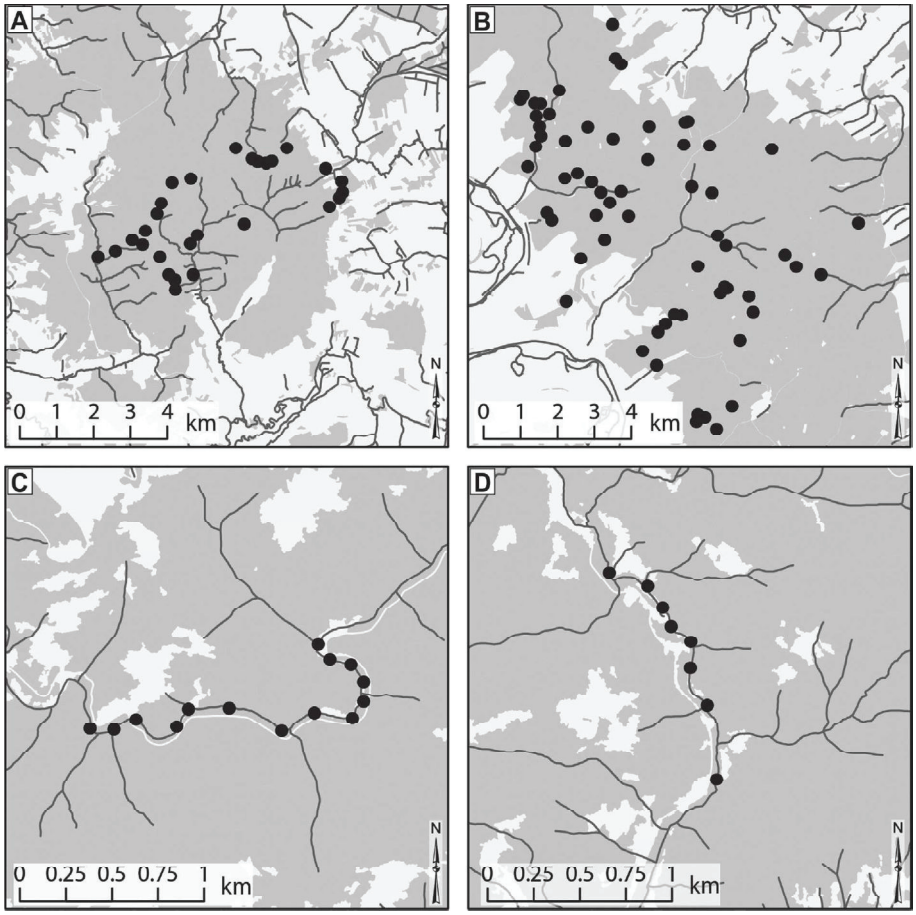

FIG. 1. Map of the four studied metapopulations of *Bombina variegata* occupying (A, B) unpredictable and (C, D) predictable environments. The black dots show the pond networks used by *B. variegata* for breeding. The forest is shown in gray and the rivers in black lines.

turn-over rate makes the availability of pond networks highly stochastic (i.e., "unpredictable environments"). In these semi-natural systems, toads occupying disappeared pond networks are thus constrained to move and may settle in an existing pond network or colonize a newly available one. At the same time, toads occupying remaining pond networks may also disperse between available networks or may colonize newly created ones.

Surveyed metapopulations and fieldwork

The study was conducted on four metapopulations of *B. variegata* in France (see Table 1 and Appendix S1 for details concerning survey design): two in unpredictable environments (hereafter, POP1 and POP2) and two in predictable environments (hereafter, POP3 and POP4). The two unpredictable environment metapopulations were located in the Ardennes (POP1, Boult-au-Bois forest, 4°48′00.0″ E, 49°25′44.6″ N, and altitude 220 m) and Meuse (POP2, Verdun forest, 5°24′00.5″ E, 49°16′14.5″ N, and altitude 337 m) regions. The two predictable environment metapopulations (POP3, Gluèyre river, 4°32′08.4″ E, 44°49′39.2″ N, and altitude 368 m; and POP4, Bourge river, 4°15′54.8″ E, 44°42′22.5″ N, and altitude 399 m) were located in two distinct watersheds in the Ardèche region. These four metapopulations are well isolated; the distance separating them from the nearest metapopulation is always higher than the maximal dispersal distance recorded in this species (i.e., 3.8 km, see Pichenot 2008): 20 km for POP1, 6.2 km for POP2, 5.5 km for POP3 and 4.2 km for POP4.

Details concerning the characteristics of the pond networks within the four surveyed metapopulations are provided in Table 2. The four metapopulations were monitored using capture–recapture methods over periods varying from 3 to 7 yr between 2000 and 2014. The toads were captured by hand or with a dip net during daylight hours (09:00–19:00) in capture sessions carried out during the breeding season (late May–August). The entire study area was carefully checked each year to census all pond networks. At each capture session, we sampled all waterbodies in all networks. The time required to sample the entire study area in a single session varied from 1 d (POP3) to 15 d (POP2). We assumed that toads became

sexually mature at 3 yr old (Cayuela et al. 2016*b*), with a minimal body length (snout–vent length) of 35 mm; smaller individuals were excluded from the analysis as we focused only on adults in this study. We identified gender on the basis of strong forearms and the presence of nuptial pads in males. We identified each individual by the specific pattern of black and yellow mottles on its belly, which were recorded by photographs. To minimize misidentification errors, multiple comparisons of individual patterns were performed using the pattern-matching software ExtractCompare (Hiby and Lovell 1990). ExtractCompare provides similarity scores between patterns scanned from photographs showing ventral patterns. During a visual confirmation step, the observer then validates the automatic matching returned by two algorithms, which further minimizes the risk of false rejection.

Designing multi-event CR models

For the purpose of our study, we extended the CR multi-event model recently proposed by Lagrange et al. (2014) that allows dispersal to be estimated for numerous recapture locations (from eight to 64 pond networks per population in our study case) while accounting for mortality and imperfect detection. Since yellow-bellied toads may skip breeding opportunities, we modified the model parameterization to include breeder/non-breeder transition as done in Cayuela et al. (2014). Accordingly, the model follows the typical structure of "standard" robust design (Kendall et al. 1997), i.e., made up of two nested levels of capture occasions. "Secondary sessions" encompass several field sessions performed over the same year. "Primary periods" correspond to yearly sessions during which we assumed that the breeder state of an individual was fixed; breeder/non-breeder transitions were thus allowed between primary periods only and were assumed to obey a Markov chain process. Furthermore, because heterogeneity of capture probability is usually a critical issue in amphibians and especially in the yellow-bellied toad (Cayuela et al. 2014), we included heterogeneity-level states in the CR models. To avoid problems of parameter estimation and numerical convergence issues, we only considered two-class mixture models, which are usually robust to detect inter-individual variation of demographic and recapture rates (see for instance Péron et al. 2010, Cubaynes et al. 2012).

We considered 15 states (Fig. 2) that combine information about the individual's dispersal status, namely whether it occupied the same pond network as on the previous capture occasion (H for here) or not (E for elsewhere), and information concerning its capture status (detected or undetected) at $t - 1$ and t. We conserved the syntax used in Lagrange et al. (2014) to describe the composite states; the dispersal status (H or E) is prefixed by the previous capture status (+ if detected or o if not detected) and suffixed by the current capture status (same notation). H or E is followed by a prime (′) to designate the states of the second group of recapture heterogeneity. Four successive transition steps were considered, which update, in a stepwise fashion, the state (survival, breeding, dispersal, and recapture) taking place between times $t - 1$ and t. At the initial state of departure, the dispersal status of an individual is unknown while its current and previous capture statuses are known. Therefore, individuals can enter the data set in three different states (Fig. 3): oH+, oE+, and oH′+. Then, at the first transition step, the survival status (D) is updated (in bold) as an individual can survive or not (Fig. 3). At the second step, the breeder/non-breeder status (T) is in turn updated as an individual can "decide" to breed or to skip the current breeding opportunity (Fig. 3). Note that skipping breeding in a given year is equivalent to becoming a temporary emigrant and shifting to an unobservable state (for the use of unobservable states, see Kendall and Nichols 2002). In the third step, dispersal status is updated as an individual that has survived and "decided" to breed can go back to the pond network (H, Here) it had previously occupied at $t - 1$ or move to another one (E, Elsewhere; Fig. 3). In the fourth step, we updated recapture status as an individual can be recaptured at time t given it has survived and made the choice to breed (Fig. 3). The last component of multi-event CR models links events to states (Fig. 3). In this model, each state corresponds to only one possible event (but one event can correspond to several states), making the event probabilities trivial.

Building biological scenarios and assessing temporal variation of dispersal rates

The parameterization was implemented in the E-surge program (Choquet et al. 2009), which provides robust tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters. Because the data sets from the four metapopulations differ markedly in terms of the number of study years and capture sessions per year, we separately analyzed the four data sets and then compared the mean and variance of vital rates provided by the best-fitted model for each metapopulation; nevertheless additional analyses were also carried out on a reduced data set to directly test in a single model the hypothesis that dispersal varies between populations and according to the degree of environmental unpredictability (see Appendix S2). For each metapopulation, competing models were ranked through a model-selection procedure using Akaike information criteria adjusted for a small sample size (AIC_c) and AIC_c relative weights. We tested our hypotheses concerning survival (φ), breeding decision (γ), dispersal (ψ) and recapture (p) from the general model [φ(YEAR × SEX), γ(YEAR × SEX), ψ(YEAR × SEX), p(HET + YEAR)]. We tested whether survival, breeding and dispersal probabilities may be constant (CST) or varied between year (YEAR) and sex (SEX). We also tested whether recapture probabilities varied according to capture heterogeneity level (i.e., two heterogeneity mixtures: highly capturable

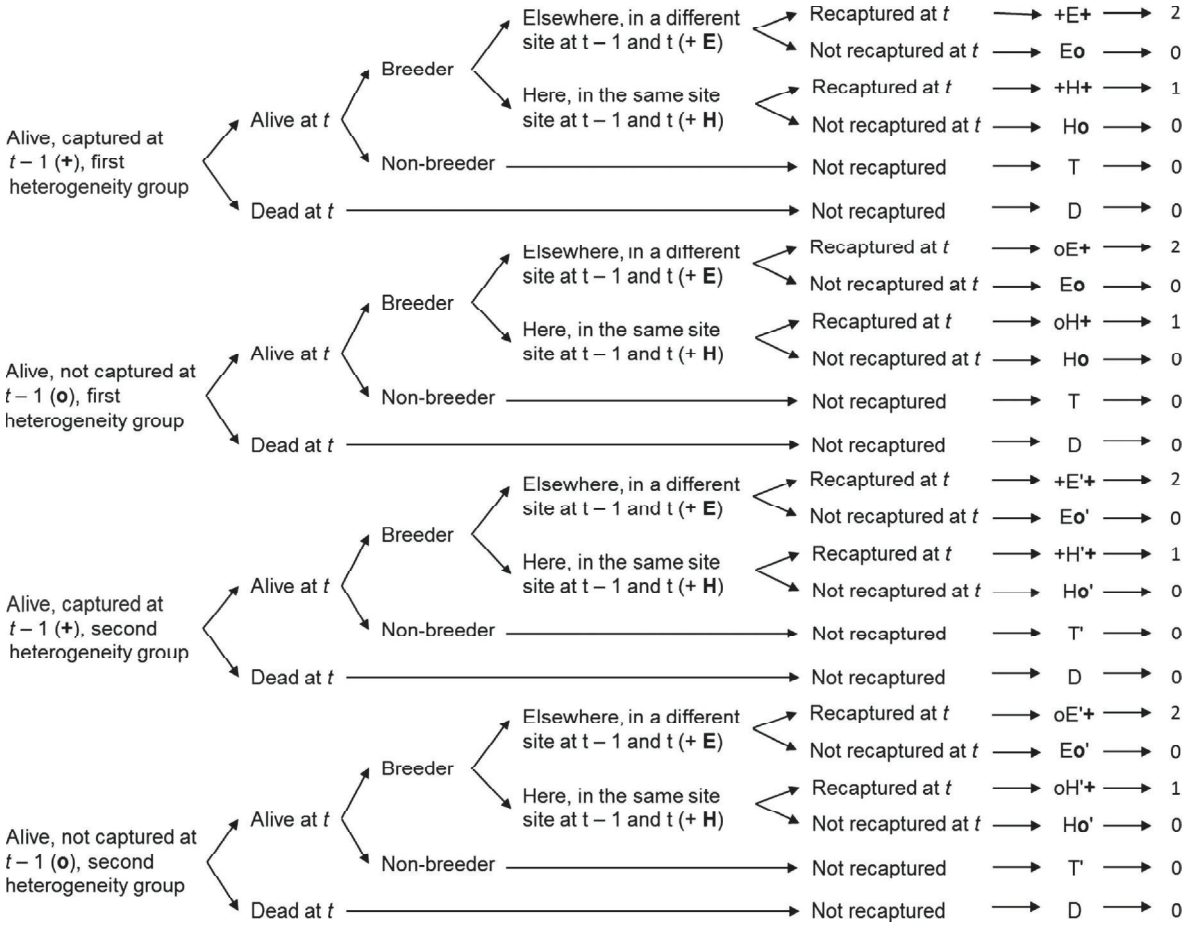

FIG. 2. Transition steps of an individual from $t-1$ to t, underlying states and field observations (i.e., events). The diagram shows the steps and associated transitions leading to the field observation at $t-1$ and t of an individual: survival (alive or dead, D), breeding (breeder or non-breeder, T), dispersal (Here, H; Elsewhere, E) and recapture (recaptured, +; or not, letter o). At each step, updated information appears in bold. In the last step, we provide the 15 states that can generate the four events (numbered 0, 1, 2, 3) considered in our model: Elsewhere, in the first capture heterogeneity level and captured at $t-1$ and t, +E+; Elsewhere, in the first capture heterogeneity level, and not captured at t (whatever the capture status at $t-1$), Eo; Here, in the first capture heterogeneity level and captured at $t-1$ and t, +H+; Here, in the first capture heterogeneity level and not captured at t (whatever the capture status at $t-1$), Ho; Elsewhere, in the first capture heterogeneity level and captured at t but not at $t-1$, oE+; Here, in the first capture heterogeneity level and captured at t but not at $t-1$, oH+; Non-breeder (and therefore not available for capture at t) and in the first capture heterogeneity level, T; Elsewhere, in the second capture heterogeneity level and captured at $t-1$ and t, +E′+; Elsewhere, in the second capture heterogeneity level, and not captured at t (whatever the capture status at $t-1$), Eo′; Here, in the second capture heterogeneity level and captured at $t-1$ and t, +H′+; Here, in the second capture heterogeneity level and not captured at t (whatever the capture status at $t-1$), Ho′; Elsewhere, in the second capture heterogeneity level and captured at t but not at $t-1$, oE′+; Here, in the second capture heterogeneity level and captured at t but not at $t-1$, oH′+; Non-breeder (and therefore not available for capture at t) and in the second capture heterogeneity level, T′; Dead. Events are not recaptured at t, recaptured at t and not recaptured at $t-1$, recaptured at t in the same site as at $t-1$, recaptured at t in another site as at $t-1$.

vs. lowly capturable individuals) and year. We tested all the possible linear combinations.

Next, we aimed at comparing the range of variation of dispersal between populations while accounting for potential differences in the mean dispersal rate between populations. For that purpose, we built models with yearly variation in dispersal rates for all four metapopulations [φ(YEAR × SEX), γ(YEAR × SEX), ψ(YEAR) p(HET + YEAR)] in order to obtain annual estimates of dispersal rates (both within a year and between years) along with their estimated variance and covariance. Using the methods proposed in Gould and Nichols (1998), we estimated the temporal variance of dispersal by removing the effects of sampling variance from the estimated total variance in dispersal. We then used the method proposed by Gaillard and Yoccoz (2003) to compare the temporal variation of dispersal rates between metapopulations. This method compares the maximum variance of dispersal we can expect (from the observed mean dispersal rate) with the observed variance. This maximum variance is $d \times (1-d)$, where d is the mean dispersal rate. Between the observed variance and the maximum variance, we then obtained the ratio of possible variation (hereafter called "temporal variation ratio," following the terminology

Initial states of departure

$$\begin{array}{cccccccccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{Ho'} & \text{oH'+} & \text{+H'+} & \text{Eo'} & \text{oE'+} & \text{+E'+} & \text{T} & \text{T'} \\ (0 & I & 0 & 0 & I & 0 & 0 & I & 0 & 0 & 1-I & 0 & 0 & 0) \end{array}$$

Step 1: Survival

$$\begin{array}{c|ccccccccccccccc} & \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{Ho'} & \text{oH'+} & \text{+H'+} & \text{Eo'} & \text{oE'+} & \text{+E'+} & \text{T} & \text{T'} & \mathbf{D} \\ \hline \text{Ho} & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oH+} & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+H+} & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{Eo} & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oE+} & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+E+} & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{Ho'} & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oH'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+H'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{Eo'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oE'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 1-\phi \\ \text{+E'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 1-\phi \\ \text{T} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 1-\phi \\ \text{T'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 1-\phi \\ \mathbf{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Step 2: Breeder/non-breeder

$$\begin{array}{c|ccccccccccccccc} & \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{Ho'} & \text{oH'+} & \text{+H'+} & \text{Eo'} & \text{oE'+} & \text{+E'+} & \mathbf{T} & \mathbf{T'} & \text{D} \\ \hline \text{Ho} & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{oH+} & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{+H+} & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{Eo} & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{oE+} & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{+E+} & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \text{Ho'} & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 \\ \text{oH'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 \\ \text{+H'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 1-\gamma & 0 \\ \text{Eo'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 1-\gamma & 0 \\ \text{oE'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 1-\gamma & 0 \\ \text{+E'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 1-\gamma & 0 \\ \mathbf{T} & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma & 0 & 0 \\ \mathbf{T'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma & 0 & 0 & 0 & 1-\gamma & 0 \\ \text{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Step 3: Dispersal

$$\begin{array}{c|ccccccccccccccc} & \mathbf{Ho} & \mathbf{oH+} & \mathbf{+H+} & \mathbf{Eo} & \mathbf{oE+} & \mathbf{+E+} & \mathbf{Ho'} & \mathbf{oH'+} & \mathbf{+H'+} & \mathbf{Eo'} & \mathbf{oE'+} & \mathbf{+E'+} & \mathbf{T} & \mathbf{T'} & \mathbf{D} \\ \hline \text{Ho} & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{oH+} & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{+H+} & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{Eo} & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{oE+} & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{+E+} & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{Ho'} & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 \\ \text{oH'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 \\ \text{+H'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 \\ \text{Eo'} & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 & 0 \\ \text{oE'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 & 0 \\ \text{+E'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\psi & 0 & 0 & \psi & 0 & 0 & 0 \\ \text{T} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ \text{T'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ \text{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Step 4: Recapture

$$\begin{array}{c|ccccccccccccccc} & \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{Ho'} & \text{oH'+} & \text{+H'+} & \text{Eo'} & \text{oE'+} & \text{+E'+} & \text{T} & \text{T'} & \text{D} \\ \hline \mathbf{Ho} & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{oH+} & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{+H+} & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{Eo} & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{oE+} & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{+E+} & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{Ho'} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{oH'+} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{+H'+} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{Eo'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 \\ \mathbf{oE'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 \\ \mathbf{+E'+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 \\ \mathbf{T} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ \mathbf{T'} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ \mathbf{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Events

$$\begin{array}{c|cccc} & \mathbf{0} & \mathbf{1} & \mathbf{2} & \mathbf{3} \\ \hline \text{Ho} & 1 & 0 & 0 & 0 \\ \text{oH+} & 0 & 0 & 0 & 1 \\ \text{+H+} & 0 & 1 & 0 & 0 \\ \text{Eo} & 1 & 0 & 0 & 0 \\ \text{oE+} & 0 & 0 & 0 & 1 \\ \text{+E+} & 0 & 0 & 1 & 0 \\ \text{Ho'} & 1 & 0 & 0 & 0 \\ \text{oH'+} & 0 & 0 & 0 & 1 \\ \text{+H'+} & 0 & 1 & 0 & 0 \\ \text{Eo'} & 1 & 0 & 0 & 0 \\ \text{oE'+} & 0 & 0 & 0 & 1 \\ \text{+E'+} & 0 & 0 & 1 & 0 \\ \text{T} & 1 & 0 & 0 & 0 \\ \text{T'} & 1 & 0 & 0 & 0 \\ \mathbf{D} & 1 & 0 & 0 & 0 \end{array}$$

FIG. 3. Matrices of state–state transitions (one for each of the four steps considered in our model) and events. As proposed in Lagrange et al. (2014), the updated information at each step is shown in boldface type.

used by Gaillard and Yoccoz 2003) and compared these values between metapopulations. In order to provide uncertainty measures of the temporal variation ratio of dispersal rates, we bootstrapped in the individual capture–recapture histories. Because E-surge does not provide an automatic procedure for bootstrapping CR-histories, we had to perform this manually. We thus limited our approach to 50 bootstraps per metapopulation. For each bootstrap of each metapopulation, we fitted the model [φ(YEAR × SEX), γ(YEAR × SEX), ψ(YEAR) p(HET + YEAR)] and applied the Gould and Nichols (1998) method. This allowed us to obtain a variance for the 50 bootstraps, from which we derived the 95% CI of the temporal variation ratio of the demographic parameters. We then used the overlap of the 95% CIs to analyze the statistical differences between the temporal variation estimates of dispersal.

RESULTS

In unpredictable environments, 74 and 76 dispersal events between two consecutive capture sessions were directly observed in POP1 and POP2, respectively. In predictable environments, 11 and nine were detected in POP3 and POP4, respectively.

The competitive models of each metapopulation are provided in Table 3. In both metapopulations occurring in predictable environments, the best-supported model was [φ(CST), γ(YEAR + SEX), ψ(CST), p(HET + YEAR)]. In this model, survival was constant between years and did

TABLE 3. Model selection procedure showing the five best-supported models for the four studied populations of yellow-bellied toads; the complete model selection is provided in Appendix S1.

r	Model definition	*k*	Dev.	*w*	AICc
	POP1 "Unpredictable environment"				
1	φ(CST), γ(YEAR + SEX), ψ(YEAR), p(HET + YEAR)	49	4,961.87	0.87	5,063.31
2	φ(CST), γ(YEAR + SEX), ψ(SEX), p(HET + YEAR)	41	4,983.44	0.09	5,067.84
3	φ(CST), γ(YEAR + SEX), ψ(YEAR + SEX), p(HET + YEAR)	61	4,942.92	0.03	5,070.25
4	φ(CST), γ(YEAR + SEX), ψ(CST), p(HET + YEAR)	39	4,991.31	0.01	5,071.47
5	φ(CST), γ(CST), ψ(YEAR), p(HET + YEAR)	27	5,032.03	0.00	5,087.07
	POP2 "Unpredictable environment"				
1	φ(CST), γ(YEAR + SEX), ψ(YEAR), p(HET + YEAR)	16	10,312.92	0.24	10,345.04
2	φ(CST), γ(CST), ψ(YEAR), p(HET + YEAR)	12	10,321.07	0.23	10,345.13
3	φ(CST), γ(YEAR + SEX), ψ(CST), p(HET + YEAR)	13	10,319.20	0.22	10,345.28
4	φ(CST), γ(CST), ψ(CST), p(HET + YEAR)	9	10,327.35	0.20	10,345.39
5	φ(YEAR + SEX), γ(CST), ψ(YEAR), p(HET + YEAR)	15	10,316.67	0.10	10,346.77
	POP3 "Predictable environment"				
1	φ(CST), γ(YEAR + SEX), ψ(CST), p(HET + YEAR)	27	4,757.28	0.60	4,811.79
2	φ(CST), γ(YEAR + SEX), ψ(SEX), p(HET + YEAR)	29	4,754.10	0.38	4,812.69
3	φ(CST), γ(YEAR + SEX), ψ(YEAR), p(HET + YEAR)	34	4,751.16	0.02	4,819.97
4	φ(CST), γ(YEAR + SEX), ψ(YEAR + SEX), p(HET + YEAR)	43	4,738.79	0.00	4,826.08
5	φ(YEAR + SEX), γ(CST), ψ(CST), p(HET + YEAR)	19	4,800.75	0.00	4,839.01
	POP4 "Predictable environment"				
1	φ(CST), γ(YEAR + SEX), ψ(CST), p(HET + YEAR)	27	7,617.91	0.58	7,676.30
2	φ(CST), γ(YEAR + SEX), ψ(SEX), p(HET + YEAR)	29	7,622.83	0.38	7,677.17
3	φ(CST), γ(YEAR + SEX), ψ(YEAR), p(HET + YEAR)	34	7,613.35	0.04	7,681.89
4	φ(CST), γ(YEAR + SEX), ψ(YEAR + SEX), p(HET + YEAR)	43	7,598.93	0.00	7,685.79
5	φ(YEAR + SEX), γ(CST), ψ(SEX), p(HET + YEAR)	21	7,679.09	0.00	7,741.30

Notes: Parameters are *r*, model rank; *k,* number of parameters; Dev., residual deviance; AIC_c, Akaike information criteria adjusted for a small sample size; *w*, AIC_c weights. Four effects (CST, constant; YEAR, year effect; SEX, sex effect; HET, capture heterogeneity effect) were examined on survival φ, breeding γ, and ψ dispersal probabilities.

not differ between sexes. Breeding probability varied between sexes and years, while recapture probability depended on capture heterogeneity level and year. Model-averaged estimates indicate that dispersal probability marginally varied between years and sexes (Fig. 4). In both metapopulations facing unpredictable environments, the best-supported model was [φ(CST), γ(YEAR + SEX), ψ(YEAR) p(HET + YEAR)]. In this model, survival was also constant between years and sexes. Breeding probability also differed between sexes and years, while recapture probability depended on capture heterogeneity level and year. Model-averaged estimates indicate that dispersal probability was constant between sexes, but substantially varied between years (Fig. 4).

Importantly, our results showed that dispersal rates were drastically higher in unpredictable environments than in predictable ones (Fig. 4; see also the additional analyses provided in Appendix S2). In unpredictable environments, the mean dispersal rate ranged from 0.17 (95% CI 0.11–0.26) in POP1 to 0.14 (95% CI 0.10–0.20) in POP2 on an interannual scale and from 0.11 (95% CI 0.08–0.14) in POP1 to 0.05 (95% CI 0.04–0.06) in POP2 on an intra-annual scale. In contrast, in predictable environments, mean dispersal rates were close to 0 on an interannual scale and ranged from 0.01 (95% CI 0.00–0.02) in POP3 to 0.02 (95% CI 0.01–0.03) in POP4 on an intra-annual scale. Temporal variance ratios also showed that intra-annual and inter-annual dispersal rates were much more variable between years in unpredictable environments than in predictable ones (Fig. 4). In unpredictable environments, temporal variance ratios ranged from 0.21 (95% CI 0.12–0.27) in POP1 to 0.17 (95% CI 0.0.09–0.25) in POP2 on an interannual scale and from 0.06 (95% CI 0.03–0.10) in POP1 to 0.04 (95% CI 0.03–0.08) in POP2 on an intra-annual scale. In contrast, in predictable environments they were close to 0 on both inter-annual and intra-annual scales.

DISCUSSION

The results of our study show that *B. variegata* survival is lower in unpredictable environments than in predictable ones, and that breeding rates vary according to sex and year; these contrasting patterns have been discussed in detail in a previous paper (Cayuela et al. 2016*a*) in which the influence of the level of habitat unpredictability on the

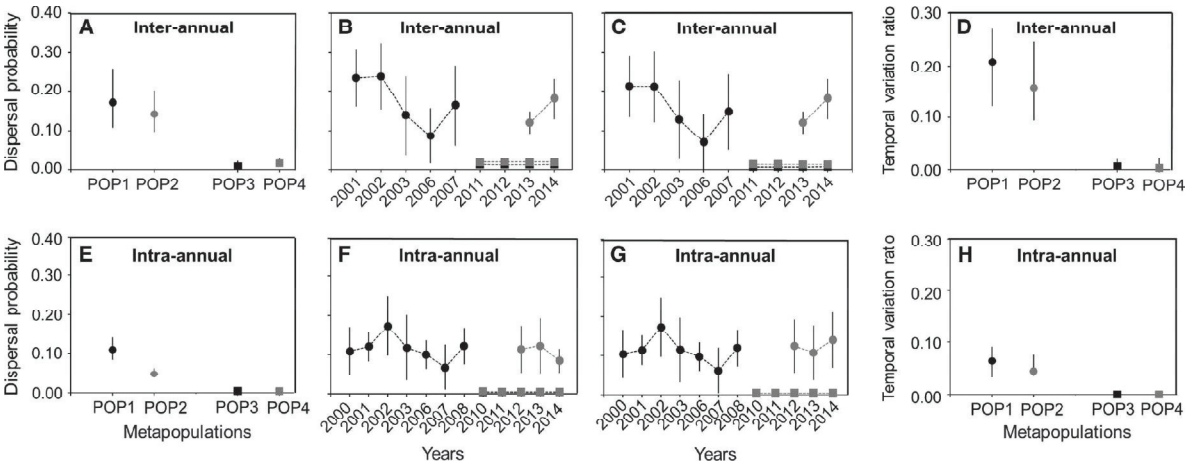

FIG. 4. Inter-annual and intra-annual dispersal probabilities and their temporal variation in four *B. variegata* metapopulations experiencing unpredictable (POP1, black dots; and POP2, gray dots) and predictable environments (POP3, black squares; and POP4, gray squares). Mean estimates of inter-annual and intra-annual dispersal are provided in panels A and E; temporal variation ratios are provided in panels D and H. Model-averaged estimates of dispersal and their associated standard errors are provided for both sexes (female, panels B and F; male, panels C and G); the years correspond to the survey period during which dispersal rates were estimated in each populations.

speed of the life history cycle has been highlighted. More importantly, our results also provide evidence that intra- and interannual dispersal rates are much higher on average and more annually variable in unpredictable environments than in predictable ones. Interannual dispersal rates are more than 10 times higher in unpredictable environments (close to 20%) than in predictable ones (<2%), regardless of sex. This strongly suggests that the accelerated life histories (short lifespan and high fecundity) occurring in unpredictable environments is also associated to a higher dispersal rate. We discuss these findings in the light of the colonizer syndrome hypothesis.

Is dispersal rate actually related to environmental predictability?

In a previous study (Cayuela et al. 2016*a*), we put forward that the differences in life history tactics that we found were related to the degree of pond network unpredictability, but not linked to other environmental factors such as weather variation, predation or competition. Although these conclusions also apply to the dispersal patterns reported in the present study, one might object that several other environmental factors could also explain the pattern in dispersal rate mean and variation we observed. In particular, differences in pond network density or isolation as well as different landscape matrixes between the studied metapopulations we compared could result in differing dispersal rates. Indeed, it has been previously suggested that pond network size and isolation affect amphibian dispersal patterns (Marsh and Trenham 2001, Smith and Green 2005). Yet in our study, pond network size (i.e., the mean number of ponds per network) is comparable among metapopulations (Table 2). Moreover, although the total number of pond networks is larger in unpredictable environments, the pond network density remains similar among the metapopulations we compared (Fig. 1). Furthermore, the degree of pond isolation (i.e., the mean Euclidian distance between each pair of pond networks) is drastically higher in unpredictable environments (Table 2), where dispersal rates were found to be substantially higher. One would expect to observe the opposite dispersal pattern in compared metapopulations if the cause was differing pond network size or isolation. Landscape fragmentation and more generally the composition and configuration of the landscape matrix can also strongly influence animal movement (Fahrig 2003). This landscape effect is thought to be particularly important in biphasic and ground-dwelling animals such as amphibians (Cushman 2006). But in our study, all the sampled metapopulations were located in relatively homogenous landscape matrixes composed mainly of woodland. This habitat is usually considered highly favorable for the movement of most amphibian species (Rothermel and Semlitsch 2002) and is also the ancestral terrestrial habitat inhabited by *B. variegata* (Cayuela et al. 2015). Another objection might be that in predictable environments, the river along which pond networks occur could constrain toad dispersal. However, small rivers are usually thought to facilitate dispersal in *B. variegata*, and genetic data suggests that individuals preferentially move between pond networks along the river stream (H. Cayuela, *unpublished data*). Finally, one could object that the difference in the dispersal rate observed between metapopulations might result from a methodological bias inherent to capture–recapture approaches. Indeed, it is well known that apparent survival estimates include both death and definitive emigration (Kendall et al. 1997, Pradel et al. 1997), resulting in negatively biased estimates for both dispersal and

survival. Although we cannot rule out such a bias in our study, its severity should be higher in unpredictable environments given the lower apparent survival estimated in these. Thus, if our estimates were biased, this would likely result in an underestimation of the dispersal rate difference rather than an overestimation. This makes us confident that the differences we found in dispersal rates are more likely to be related to the degree of pond network unpredictability prevailing among the metapopulations rather than to variation in other environmental factors or to methodological issues.

Does a high level of habitat unpredictability lead to a colonizer syndrome?

Given the low spatial turnover of ponds, pond-breeding amphibians are usually expected to show high breeding site fidelity, and conversely low breeding dispersal (Sinsch 1997, Smith and Green 2005, Semlitsch 2008). Indeed, most research directly investigating dispersal has reported very low breeding dispersal (Gill 1978, Berven and Grudzien 1990, Sinsch 1997, Smith and Green 2006, Gamble et al. 2007, Grant et al. 2010, but see Breden 1987, Trenham et al. 2001). Usually, dispersal is thought to take place at the early stages of the life cycle, and the rare studies that have investigated juvenile dispersal in amphibians indeed reveal such a trend (Sinsch 1997, Grant et al. 2010, Griffiths et al. 2010). Our study, investigating adults, clearly indicates that dispersal during breeding can be substantial (i.e., 20%) and strongly suggests it correlates to the predictability of breeding resources: in unpredictable environments, intra- and interannual dispersal rates are much higher on average and more annually variable than in predictable ones. Our results did not show evidence of sex-biased dispersal in any of the studied metapopulations. Taken together, these results are in accordance with theoretical studies stating that spatiotemporal environmental variation should favor dispersal in highly stochastic environments (McPeek and Holt 1992, Paradis 1998, Travis and Dytham 1999, Reigada et al. 2015). Our results are also congruent with empirical data showing that, in organisms displaying dispersal polymorphism, the more dispersive phenotype usually predominates in unstable and unpredictable environments, while the resident phenotype is more prone to occur in stable and predictable environments (Ronce and Olivieri 2004, Ronce 2007, Clobert et al. 2009). Our study provides direct evidence that pond network fidelity and breeding dispersal are strongly related to the predictability of breeding resources, as recently suggested by Chan and Zamudio (2009) and Mims et al. (2015) on the basis of indirect measurements of dispersal (i.e., through genetic differentiation) at the interspecific level.

This pattern might result from plastic behavioral responses to environmental cues indicating pond network disappearance or creation (i.e., pond drying out or the presence of newly created water bodies in recently exploited forest patches). Indeed, amphibians are well known to select ponds according to their breeding value on the basis of environmental cues (Resetarits and Wilbur 1989, Rieger et al. 2004, Resetarits 2005). Beside the pond networks turn over, seasonal fluctuation of pond quality (e.g., risk of larval competition; see Jasieński 1988) could also explain the high breeding dispersal we observed within and between years in unpredictable environments. However, one should expect a similar pattern in predictable environments because the pond quality also greatly fluctuates during the breeding season in riverine pond networks (Cayuela et al. 2011). It seems therefore likely that the difference of dispersal pattern we observed between environments results, at least partly, from local adaptation. In particular, one could expect that pond network unpredictability could have selected for a dispersal syndrome, which often includes complex combinations between morphological, behavioral and life history traits associated with different phases of the dispersal process, i.e., departure, transience, and settlement (Ronce and Clobert 2012). In our case, an increased dispersal could thus result from the combined effects of both phenotypic plasticity and genetic factors. For instance, toad sensitivity to pond network characteristics associated to departure/settlement decisions might be modulated by genetic factors; in metapopulations experiencing unpredictable environments, one could expect a higher sensitivity to environmental cues, leading to a higher dispersal propensity.

As outlined above, we found that there is covariation between dispersal and life history traits among metapopulations of yellow-bellied toads according to environmental predictability. In unpredictable environments, high dispersal rates are linked to accelerated life histories; conversely, in predictable environments, low dispersal rates are linked to decelerated life histories. In unpredictable environments, this association is congruent with the colonizer syndrome stating that a high dispersal rate, high fecundity and a short life span constitute a set of adapted traits in organisms occupying stochastic habitats (Baker and Stebbins 1965, Ronce and Olivieri 2004, Stevens et al. 2013). This covariation pattern might be explained in one of two ways: first, lower survival rates may be the result of increased costs during the transfer phase of the dispersal process in unpredictable environments (Bonte et al. 2012, Clobert et al. 2012). A shorter life span could then be compensated by higher fecundity, leading to an acceleration of the life history cycle as shown in other vertebrates (Jones et al. 2008, Lachish et al. 2009). A second possibility is that this covariation pattern may not result from a trade-off between dispersal and life history traits, but might be indirectly associated with a trade-off between survival and fecundity (Pianka 1976, Stearns 1992).

Conclusion

This study provides evidence of the existence of a colonizer syndrome among *B. variegata* metapopulations.

Nevertheless, additional researches are needed to investigate both the proximal and ultimate drivers of such a syndrome. In particular, it is still not clear whether the higher breeding dispersal observed in unpredictable environments is the result of a selected phenotype or of phenotypic plasticity. For this purpose, current investigations are in progress to examine whether this pattern also occurs in natal dispersal and whether it correlates with a dispersal phenotype combining traits such as behavioral type and locomotion performance.

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Supporting Information

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Habitat unpredictability shapes dispersal behavioral syndromes, dispersal dynamics and population genetic differentiation

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Abstract

INTRODUCTION

Dispersal is a key process in ecology and evolution, corresponding to the movement of an individual from its natal site to a breeding site or between sites successively (Matthysen 2012). Dispersal is usually thought as a multicausal process involving the combination of multiple ultimal factors (Starrfelt & Kokko 2012, Clobert et al. 2012). In particular, the avoidance of inbreeding and kin competition has been reported to be the main selective forces acting on dispersal when the environment is relatively spatio-temporally stable (Gandon 1999, Szulkin & Sheldon 2008, Cote & Clobert 2010). However, most of the natural systems are actually dynamics and both theoretical models and empirical data indicate that spatio-temporal variation of the environment shapes dispersal rates and may promote dispersal polymorphism within and between populations (McPeek & Holt 1992, Paradis 1998, Blanquart & Gandon 2011). In particular, it is widely reported that, in organisms displaying dispersal polymorphism, the more dispersive phenotype predominates in unstable and unpredictable environments while the resident phenotype is more prone to occur in stable and predictable ones (Ronce 2007).

An increasingly growing number of studies suggest that dispersive and resident phenotypes differ in terms of life history, morphological, physiological and behavioral traits (Clobert et al. 2009, Ronce & Clobert 2012); these associations between dispersal and phenotypic traits are termed 'dispersal syndromes'. In particular, dispersal propensity appears to be positively correlated with behavioral traits as boldness, explorative behavior and aggressiveness in various organisms (birds: Dingemanse et al. 2006, reptiles: Cote & Clobert 2012, fishes: Chapman et al. 2011, amphibians: Lindström et al. 2013). These individual differences in behavioral characteristics can be either displayed only when the decision to disperse is about to be made or can be stable over ontogeny or across situations (i.e. personality, behavioral type, coping style). Whather the consistency of these traits over individual lifetime, such 'dispersal behavioral syndromes' (Cote et al. 2010) can have important, novel implications for the dynamics and the genetics of spatially structured populations (Ronce & Clobert 2012, Wolf & Weissing 2012). At the demographic level, Clobert et al. (2009) have postulated that, in a theoretical metapopulation composed of joiners and dispersers that experience frequent local extinction events, colonization might not be feasible due to the settlement behavior of joiners and the existence of colonizers is then critical to metapopulation viability. In the case where dispersal polymorphism is genetically based on morphological, physiological or behavioral adaptations (e.g. Hanski & Mononen 2011, Duckworth 2012, Rollins et al. 2015), the coexistence of colonizers and joiners would most probably depend on extinction rate, such that the potential for colonization might be very weak in stable and predictable habitats (Clobert et al. 2009). By regulating dispersal rates between patches within the metapopulations, 'dispersal behavioral syndromes' are also expected to affect gene flow and population genetic differentiation (Edelaar & Bolnick 2012). Even if this link still remains speculative in the absence of empirical validation, few studies seems to suggest that habitat

instability and unpredictability may select for low site fidelity and high propensity for dispersal and should increase gene flow and reduce fine-scale population genetic structuring (Chan & Zamudio 2009, Mims et al. 2015).

Surprisingly, although the 'behavioral dispersal syndromes' have received a considerable attention during the last decade (reviewed in Ronce & Clobert 2012), their demographic and genetic consequences remain largely unexplored. In this paper, we thus aimed at demonstrating that the prevalence of dispersive and resident phenotypes depends on the level of habitat unpredictability experienced by metapopulation and that these two phenotypes differ in terms of behavioral traits, leading to the emergence of a dispersal behavioral syndrome. We then examined the demographic and genetic consequences of that syndrome by showing that inter-patches dispersal rates differ between metapopulations according the level of habitat unpredictability, which then affects genetic population structuring. We challenged these questions in an amphibian, the yellow-bellied toad (*Bombina variegata*) that breeds in archipelagoes of small temporary water bodies (Barandun & Reyer 1997, Cayuela et al. 2011). This species displays two distinct ecotypes with divergent life history tactics, experiencing two contrasting levels of habitat predictability (Cayuela et al. in press): (i) a first ecotype with a 'slow' life history tactic, including a relatively long life span and a reduced fecundity, that use breeding ponds whose the availability is constant in space and time (called hereafter 'predictable environments' as the availability of pond archipelagoes is predictable from one year to another); (ii) a second ecotype with a 'fast' life history tactic, including a relatively short life span and an increased fecundity, that reproduces in breeding ponds randomly created or destroyed each year by human activity (called hereafter 'unpredictable environments' the availability of pond archipelagoes is not predictable from year to year). First, using common garden experiments, we tested the hypothesis that the dispersive phenotype predominates in the metapopulations experiencing unpredictable environments and that individuals displayed a high boldness and exploration tendency. In opposite, we expected that the resident phenotype is more prone to occur in the metapopulations occupying predictable environments and that individual are relatively shy and displayed a lower exploration propensity. Then, using capture-recapture data intensively collected in almost 3000 yellow-bellied toads, we tested the prediction that inter-patches dispersal rates at both intra-annual and inter-annual scales are higher within metapopulations experiencing unpredictable environments than in metapopulations occurring in predictable ones. Lastly, using genetic data collected in different metapopulations, we tested the hypothesis that genetic structuring between pond archipelagoes is lower in metapopulations experiencing unpredictable environments than predictable ones.

MATERIAL AND METHODS

Characterizing dispersal behavioral syndrome in metapopulations

First, we aimed at demonstrating that behavioral type varies according to the degree of environmental unpredictability. For that purpose, eggs were collected from three metapopulations experiencing unpredictable environments and three other metapopulations occurring predictable environments. All these populations are situated in Eastern France and the distance separating each other varies from 20 km to 500 km. Between May and June, 9-15 egg clutches (i.e. families) were randomly sampled from each population. The samples were transported gently to the laboratory where they were individually placed in 32×17 cm aquariums with 2 L of aged tape water equipped with an oxygen pump. Aquariums were placed in a climatic room with a light/dark cycle of 19:6, corresponding to the natural light/dark cycle in the area, with an ambient temperature varying from 21.5 to 23.5° C. The embryo development ended from 2 to 5 days after eggs clutches arrival at the laboratory. After hatchling, when tadpoles reached Gosner stage 24-25 (active swimming, external gill atrophy) (Gosner 1960), five siblings per family were randomly chosen and placed individually into plastic containers (14×8.5 cm, height 13.5 cm) filled with 0.5 L of tap water previously aged and aerated in a tank. The plastic containers were distributed in a predetermined random pattern in the climatically controlled room. The tadpoles were fed, and the water was replaced every three day. The tadpoles were fed every day with 150 mg of cooked salad; this represents an ad libitum situation for the tadpoles. At Gosner stage 44-45 (tail atrophy, mouth posterior to eyes), feeding was terminated, the water was drained and replaced with a dampened sponge placed in the bottom of the plastic container. The sponge and the wall box were sprayed by means of age taped water every two day. Individual were kept until their complete metamorphosis (Gosner stage 46) and then experienced behavioral trials.

As previously done in amphibians (Brodin et al. 2013, Maes et al. 2013, Gifford et al. 2014), each toadlet was subjected to an open-field behavioral trial in a novel environment to quantify both boldness exploratory behavior: an arena of 70 cm diameter made of polyethylene terephthalate. At the center of the arena, a removable, cylindrical (9 cm diameter, height 90 cm), opaque, covered refuge chamber was placed. The cylinder had a circular opening (diameter = 3 cm), covered by a lid. Around the interior edge of the arena, we installed a pit with a width of 10 cm and a depth of 0.3 cm, filled with a desiccating mixture of sand and powdered highly-active silica gel in a weight ratio of 0.8:0.2. Over its entire circumference, arena wall included 12 doors placed at regular interval. The arena was confined to an enclosed chamber (150×17 cm, height, 175 cm) made of an iron support on which a dark opaque sheet was placed to limit potential acoustic and visual interferences during behavioral trials. To estimate boldness and exploration in toadlets, a toadlet was added gently to the refuge chamber, accompanied by the dampened sponge previously placed in its own individual plastic container; the sponge was considered as a familiar object. After 5 minutes (300 s), we remotely opened the lid of the refuge chamber, allowing toadlet accessing to the experimental arena while digital cameras recorded behavior. The operator left the room during the rest of the trial, which ended after 25 min (1.500 s). At the end of the trial, refuge chamber interior, as well as the bottom of the arena, was cleaned with a dry rag.

Boldness was estimated as the actual latency for toadlets to exit the refuge chamber (called thereafter BOLD); as assumed in previous studies (Brodin et al. 2013, Maes et al. 2013), shorter latency to exit indicates higher boldness and conversely higher shyness. We used a generalized linear mixed model to test whether juvenile' boldness varies according to the environmental unpredictability experienced at the meta-population of origin. More specifically, the time latency to exit the refuge (BOLD) was treated as the dependent variable using a Poisson distribution. The habitat unpredictability status of the meta-populations (Environmental unpredictability) was introduced as an explanatory term in the fixed part of the model. We also introduced individual body size and its interactive effect with the habitat status as adjustment covariates in the fixed part of the model since both locomotion performance and exploration can vary according to the size of post-metamorphic animals (Beck & Congdon 2000, Gomez-Mestre et al. 2010, Brodin et al. 2013). The meta-population of origin was treated as a random effect, and juveniles belonging from a same family were treated as repeated measurements (i.e. family effect). The body size was standardized before introduction in the model as recommended (Nakagawa & Schielzeth 2010). The parameter were estimated using the restricted likelihood optimization and the significance of each explanatory term was examined with a non-sequential F test based on the Kenward-Roger method to approximate the denominator *df* (Littel et al. 2006). Non-significant terms were successively removed to obtain the final model. Least squares means were used to estimate the difference of latency to exit the refuge according to the environmental predictability status experienced at the meta-population of origin.

As proposed by previous studies in amphibians (Brodin et al. 2013, Maes et al. 2013), exploration tendency is measured using individual behavior in the arena following the exit from the refuge chamber. Toadlet exploratory propensity was inferred from the latency to cross the desiccating obstacle and exit the arena onset refuge chamber departure (called thereafter EXPL); shorter latencies indicate high exploration propensity. Since this variable is right censored, we used a random proportional hazards model (i.e. a frailty model based on a Cox model) enabling such a feature (PHREG procedure, SAS 9.3) to test whether juveniles originating from unpredictable environment are more prone to exit the arena than the other ones. It was not possible to introduce multiple random factors; we therefore take into account only the family effect. The environmental unpredictability, the body size and their interactive effect were introduced as explanatory terms. Parameters were estimated using partial likelihood estimation and the significance of explanatory terms was assessed using non sequential chi-square tests (SAS 9.3).

Estimating dispersal within metapopulations using capture-recapture data

Second, we aimed at demonstrating that dispersal between pond archipelagoes at adult stage varies according to the level of habitat unpredictability. For that purpose, we used capture-recapture data

collected during three consecutive years in two metapopulations of *B. variegata* experiencing unpredictable environments (VE and BO) and two other metapopulations (BG and GL) occurring in predictable environments (a detailed description of the four sampled metapopulations and the survey design is provided in **Appendix 1**). We surveyed 3873 individuals and performed 9859 captures. The method used to survey toads on the field was similar in the four metapopulations: three capture sessions (the time interval between each session is one month) were carried out during toad activity period (from May to July). During a capture session, each water body of the surveyed pond archipelagoes where sampled. Each individual was identified by the specific pattern of black and yellow mottles on its belly, recorded by photographs. Multiple comparisons of patterns were performed using a robust computing tool to minimize misidentification error (Extract Compare, Hiby & Lovel 1990).

We used the multievent capture-recapture model developed by Lagrange et al. (2014) to test the hypothesis that dispersal within metapopulations depends on the level of habitat unpredictability. This model allows to simultaneously estimating survival and dispersal probabilities among a large number of sites while accounting to recapture probabilities. Since heterogeneity of recapture probability has been already detected in previous studies on *B. variegata* (Cayuela et al. 2014), we modified the parameterization of Lagrange's model by including heterogeneity level states (see for instance Péron et al. 2010) to deal with this problem (the modified matrix of state-state transition and events are provided in **Appendix 2**). This new parameterization was then entered into 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 (AICc) and AICc relative weights (Burnham & Anderson 2002). Parameters were then model-averaged if the AICc difference of the two best-supported models was less than 2 points and if the AICc weight of the best-supported is less than 0.90. Based on the findings of previous studies on *B. variegata* (Cayuela et al. 2014, 2015a), recapture probabilities has been modeled as a function of inter-individual heterogeneity (quoted HET) and variation among recapture sessions (TIME). While systematically applying these two explanatory terms on recapture probabilities, we then tested the hypotheses that apparent survival as well as intra-annual and inter-annual dispersal rates may be : i) constant (CST) or ii) differ between metapopulations (POP), or metapopulation status (experiencing unpredictable environments vs predictable environments, STATUS).

Quantifying genetic differentiation within metapopulations

Lastly, we tested the hypothesis that genetic divergence between pond archipelagoes is lower in metapopulations experiencing unpredictable environments than predictable ones. For that purpose we collected DNA samples in two metapopulations of *B. variegata* experiencing unpredictable environments (DA and BL) and two other metapopulation (BG and GL) occurring in predictable

environments. Each metapopulation was composed of different pond archipelagoes used by toads for reproducing. The number of pond archipelagoes surveyed per metapopulation ranged from 13 to 43. From 1 to 41 DNA samples were collected per pond archipelago depending on local toad abundance. A detailed description of the metapopulations and the sampling design, see **Appendix 3**). DNA samples were collected using a non-invasive way, namely buccal swab. DNA was extracted from buccal swabs following standard digestion (proteinase K [75 µg] + 200 µl of TNES buffer [0.05 M Tris, 0.1 M NaCl, 0.01 M EDTA, 0.5% SDS]) and salt-chloroform purification (adapted from Nürnberger et al. 2003). We genotyped all the individuals sampled in the four metapopulations using 15 polymorphic microsatellites loci (Bv11.7, Bv11.2, Bv24.12, Nürnberger et al. 2003; Bobom5F, Bobom8A, Bobom9H, Bobom10F, Bobom12F, Hauswaldt et al. 2007; Bomvar_DLWD0, Bomvar_Cons470, Bomvar_CUSGH, Bomvar_DORC3, Bomvar_DM3QM, Bomvar_4EMX7J, Bomvar_CWL3Z, Bomvar_4EGYJ3 Cayuela et al. submitted), following the protocol described in Cayuela et al. (submitted). For each locus, alleles were scored independently by two operators with GENEMARKER v.1.95 (SoftGenetics), using GS600 LIZ size standard (Applied Biosystems).

First, we examined basic assumptions (i.e. detection of null alleles, Hardy-Weinberg equilibrium) and descriptive statistics of the genetic diversity (i) within the four studied metapopulations. Then, both an overlay method (ii) and a correlative approach (ii) developed in landscape genetic (Manel et al. 2003) were used to investigate the spatial genetic structuring in relation to the environmental unpredictability experienced by the metapopulations.

(i) Because of an unbalanced number of DNA samples per pond archipelagoes resulting from wide spatial variation in toad abundance, the heterozygosity metrics were only Observed and expected heterozygosity were calculated using GENALEX (Peakall & Smouse 2006). The inbreeding coefficient Fis and the deviation of Hardy-Weinberg were assessed with GENEPOP 4.1 (Rousset 2008). The detection of null alleles as performed using the program MICRO-CHECKER 2.2.3 (Oosterhout et al. 2004). All these descriptive characteristics for the complete set of 15 loci and the four metapopulations of *B. variegata* are provided in **Appendix 3**.

(ii) Then, we described the genetic structure among pond archipelagoes within each metapopulation using an assignation method based on the Bayesian clustering algorithm implemented in the software STRUCTURE (Pritchard et al. 2000). More precisely, we estimated the most likely number of genetic clusters (*K*) contained in each metapopulation and we applied overlaying of spatial genetic cluster. STRUCTURE program was run with the admixture model, a burn-in period of 100,000, and 100,000 subsequent MCMC repetitions. *K* values were tested ranging from 1 to 10 and repeated analyses for each value 10 times. We used STRUCTURE HARVESTER (Earl 2012) to summarize the results and the optimal *K* value was determined using both log-likelihood plots and the delta *K* statistic (Evanno et al. 2005). We followed the hierarchical approach proposed by Coulon et al. (2008) to test for additional population substructure within clusters. Accordingly, these analyses were then repeated for each inferred population cluster separately the optimal *K* value was 1 (meaning that no additional

structure was found within clusters). To map the spatial distribution of the different clusters, the individual ancestry values were averaged across the ten STRUCTURE runs using software CLUMMP (Jakobsson & Rosenberg 2007). Using the 'greedy' algorithm implemented CLUMMP program, the individuals were assigned to the cluster in which they showed highest Q-values.

(ii) Lastly, we used a correlative approach based on linear mixed models to test whether individual pairwise genetic distances between pond archipelagoes and controlled for the landscape distance, are lower within metapopulations facing environmental unpredictability than within the other ones. Inter-individual genetic distances were based on the Bray-Curtis percentage dissimilarity measure (Cushman et al. 2006, Cushman & Landguth 2010, Legendre & Legendre 2012, Castillo et al. 2014). All selected metapopulations are located in relatively homogenous landscapes mostly composed of woodland actually (see **Appendix 1)**, one of the two metapopulation facing unpredictable environment is situated in a more fragmented landscape than the other ones, given the presence of crop and meadows). Since forested area is usually considered as highly favorable for the movement of most amphibian species (Rothermel & Semlitsch 2002, Cushman 2006, Popescu & Hunter 2011, Janin et al 2012) and is also the terrestrial habitat inhabited by *B. variegata* (Cayuela et al. 2015b), we therefore discarded the cover type to control for the landscape distance in these analyses. Rather, we focused on the landscape process generating the spatial organization of pond archipelagoes. In particular, pond archipelagoes results from linear landscape elements whatever the metapopulation: those located in the predicable environment correspond to the natural stream networks while those located in the unpredictable environment results from the skidding places spread over the man-made clearance path networks. While in the latter the path networks may have little effect on movements between pond archipelagoes (Pichenot 2008), this could not be the case in the case of stream network that could act as hydrological and topological corridors for dispersing animals. We therefore considered two alternative hypotheses concerning the landscape resistance to toad movements: the movement between two pond archipelagoes depends only on the Euclidian distance separating both archipelagoes whatever the metapopulation; the movement further depends on the hydrological distance imposed by the dendritic organization of the stream network in the case of the metapopulations facing predictable environment. In order to improve interpretability of alternative hypotheses, both the Euclidian and hydrological distance were based on the topological distance. Mixed models were then constructed to estimate the relationship between the individual genetic distances treated as the dependent variable. The environmental unpredictability experienced by the metapopulation (metapopulation status) was introduced in the model as an explanatory term, and either alternative landscape distances as well as its interactive effect with the metapopulation status were introduced as two adjustment covariates. Two distinct models were thus constructed according to the landscape variable used as the adjustment covariate, and the landscape variable was standardized before introduction in the model. The non-independency among pairwise distances was taken into account though the covariance structure of the model. More specifically, we used the method proposed by Clarke et al. (2002) (see Selkoe et al. 2010,

van Strien et al. 2012 for application on pairwise *Fst* distances) using a Toeplitz(1) as a covariance structure to specify the non-independence of pairwise genetic distance according to the demes of origin. In brief, this method allows to include both demes as additive random effects in the estimation of each pairwise genetic distance with the constraint that these random effects follow a $N(0, \sigma_\tau^2)$ distribution. This method was also compared to the usual Mantel test by Prunier et al. (2013). In our case, using *Fst* distance could be misleading since the number of toads sampled is not well balanced between archipelagoes, furthermore, using inter-individual genetic distance is more powerful than using summarized pairwise genetic distance as Fst distance (Prunier et al. 2013). We therefore extended this method to the nested sample design of metapopulation use of individual pairwise genetic distance. Since we would the inter-deme variance $(i.e. \sigma_\tau^2)$ to be independently estimated according to the river of origin, we also used a modified version allowing this task.

The relative support of each landscape alternative hypotheses (i.e. including or not the effect of the stream network on the genetic distance between individuals) was evaluated according to the corresponding model AIC. As stream networks only occur within metapopulation facing predictable environment, we also conduced partial analyses to investigate this effect (i.e. same analyses as above but discarding all but metapopulation located in stream networks). Given the best-supported model, the parameters were estimated using the restricted likelihood optimization, and the significance of the explanatory terms was tested with a non-sequential F statistic. The Kenward-Roger method was not practicable for this task, we therefore fixed the denominator *df* to the number of sampled archipelagoes, which is more conservative.

RESULTS

Characterizing dispersal behavioral syndrome in metapopulations

The latency to exit the refuge chamber was significantly affected by the environmental unpredictability status experienced by the metapopulation of origin but neither by the body size of the toadlet nor its interactive effect (N=295, respectively for the environmental unpredictability, the body size, and their interactive effect: $F_{1dnf,2.718\ ddf}$=29.64, P=0.0157; $F_{1dnf,18.75ddf}$=0.03, non-significant; $F_{1df,18.75dnf}$<0.01, non-significant). The mean time departure from the refuge chamber was 2.077+-0.24 time higher for toadlets from predictable environments compared to the ones from unpredictable environments (respectively 9.58+-0.72' and 4.67+-0.41', see Fig.2). Similar results were observed on the latency time to exit the arena onset the departure of the refuge chamber. The latency was significantly affected by the environmental unpredictability status experienced at the metapopulation of origin but neither by the toadlet body size nor its interactive effect (N=295, χ^2_{1df}=81.34, P <.0001; respectively for the Environmental unpredictability, the body size, and their interactive effect: χ^2_{1df}=81.34, P <.0001; χ^2_{1df}=0.04, non-significant; χ^2_{1df}=0.71, non-significant). The latency to exit the

arena was 7.14 time higher for toadlets from predictable environments compared to the ones from unpredictable environment.

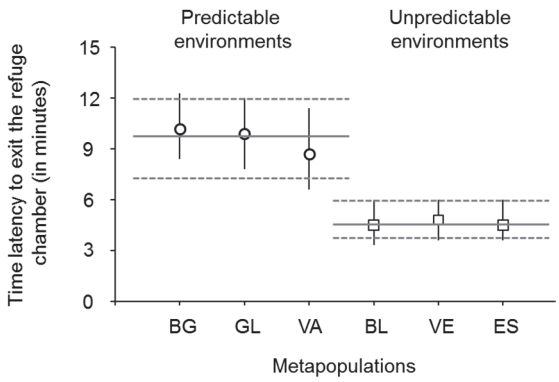

Fig.1. *Differences in behavioral traits related to dispersal measured in toadlets from six metapopulations of Bombina variegata experiencing predictable (metapopulations BG, GL and VA) and unpredictable environments (metapopulations BL, VE and ES). Estimates (circle and squares) and their associated 95% confidence intervals (bars) are provided for each metapopulations. The mean estimates for the metapopulations of each environmental status (continuous line) and their 95% confidence intervals (broken line) are also shown.*

Estimating dispersal within metapopulations using capture-recapture data

Table 1. *Estimating dispersal within metapopulations using capture-recapture data, model selection procedure. In the multi-events capture-recapture models, recapture probabilities always depend on an interaction between heterogeneity groups (HET) and time variation (TIME). Survival and dispersal probabilities can be constant (CST) or may vary between metapopulations (POP) and according to the level of environmental unpredictability (STATUS). Models are ranked according to AICc and relative AICc weights (w). The number of model parameters (k) and the model deviance are provided.*

r	Model	*k*	Deviance	*w*	*AICc*
1	$S_{(POP)}, D_{(STATUS)}, P_{(HET \times TIME)}$	25	19633.18	0.68	19683.31
2	$S_{(POP)}, D_{(POP)}, P_{(HET \times TIME)}$	29	19626.65	0.32	19684.83
3	$S_{(STATUS)}, D_{(STATUS)}, P_{(HET \times TIME)}$	23	19683.75	0.00	19729.86
4	$S_{(STATUS)}, D_{(POP)}, P_{(HET \times TIME)}$	27	19677.23	0.00	19731.38
5	$S_{(POP)}, D_{(CST)}, P_{(HET \times TIME)}$	23	19782.67	0.00	19828.78
6	$S_{(STATUS)}, D_{(CST)}, P_{(HET \times TIME)}$	21	19833.25	0.00	19875.34
7	$S_{(CST)}, D_{(STATUS)}, P_{(HET \times TIME)}$	22	20100.14	0.00	20144.25
8	$S_{(CST)}, D_{(POP)}, P_{(HET \times TIME)}$	26	20093.62	0.00	20145.76
9	$S_{(CST)}, D_{(CST)}, P_{(HET \times TIME)}$	20	20249.64	0.00	20289.72

Since the AICc difference between the two best-supported models was less than 2 and the AICc weight of best-supported model was less than 0.90 (Table 1), survival and dispersal rates were model-

averaged (the details of the model-averaging procedure are provided in **Appendix 2**). Our results indicate that apparent survival was significantly lower in metapopulations exposed to unpredictable environments than in predictable ones (Fig. 2A). Furthermore, both intra-annual and inter-annual dispersal rates were drastically higher in unpredictable environments than in predictable ones (Fig. 2B and 2C).

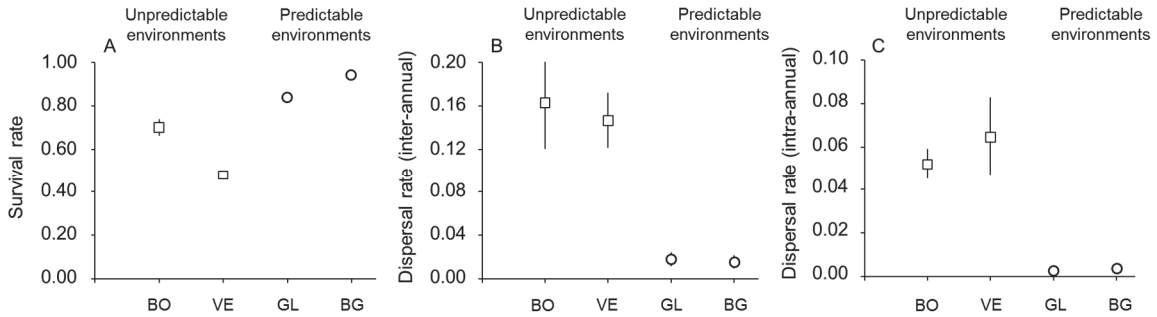

Fig.2. *Model-averaged survival and dispersal rates (and their associated standard errors) in four metapopulations of Bombina variegata experiencing unpredictable (BO and VE, squares) and predictable environments (GL and BG, circles).*

Quantifying genetic differentiation within metapopulations

First, regardless of the sample size in each metapopulation, the unbiased expected heterozygosity (uHE) was higher in 87% of the loci in the metapopulations experiencing unpredictable environments than those occurring in predictable ones (see **Appendix 3)**. Equally, inbreeding coefficients (*Fis*) were lower in 87% of the loci in the metapopulation exposed unpredictable environments. Furthermore, in predictable environments, deviation from Hardy-Weinberg equilibrium was significant for 75% and 45% of the loci in metapopulations BG and GL respectively. Conversely, in unpredictable environments, deviation from Hardy-Weinberg equilibrium was significant in 18% and 0% of the loci in metapopulations BL and BG respectively.

Second, we examined the genetic structure within each metapopulation using hierarchical STRUCTURE analyses. Within the two metapopulations experiencing unpredictable environments (DA and BL), STRUTURE have only detected a single genetic group (K = 1), suggesting the absence of genetic structuring (Fig.3). In opposite, in metapopulations occurring in predictable environments (BG and GL), complex hierarchized genetic structure has been found (Fig. 3; see also **Appendix 3** for detailed STRUCTURE outputs). In metapopulation BG, two genetic clusters were initially inferred (K = 2) and hierarchical analysis revealed further genetic substructure for cluster 3-A in which two nested clusters were inferred (K = 2), i.e. 3-AA and 3-ABB. In metapopulation GL, two clusters (K = 2) were initially identified, i.e. cluster 4-A and 4-B, and hierarchical analysis then highlighted further substructure within cluster 4-B (K = 2), i.e. 4-BA and 4-BB. Further genetic substructure was then

identified within the cluster 4-BA (K = 3) and three new clusters were thus inferred, i.e. 4-BAA, 4-BAB and 4-BAC.

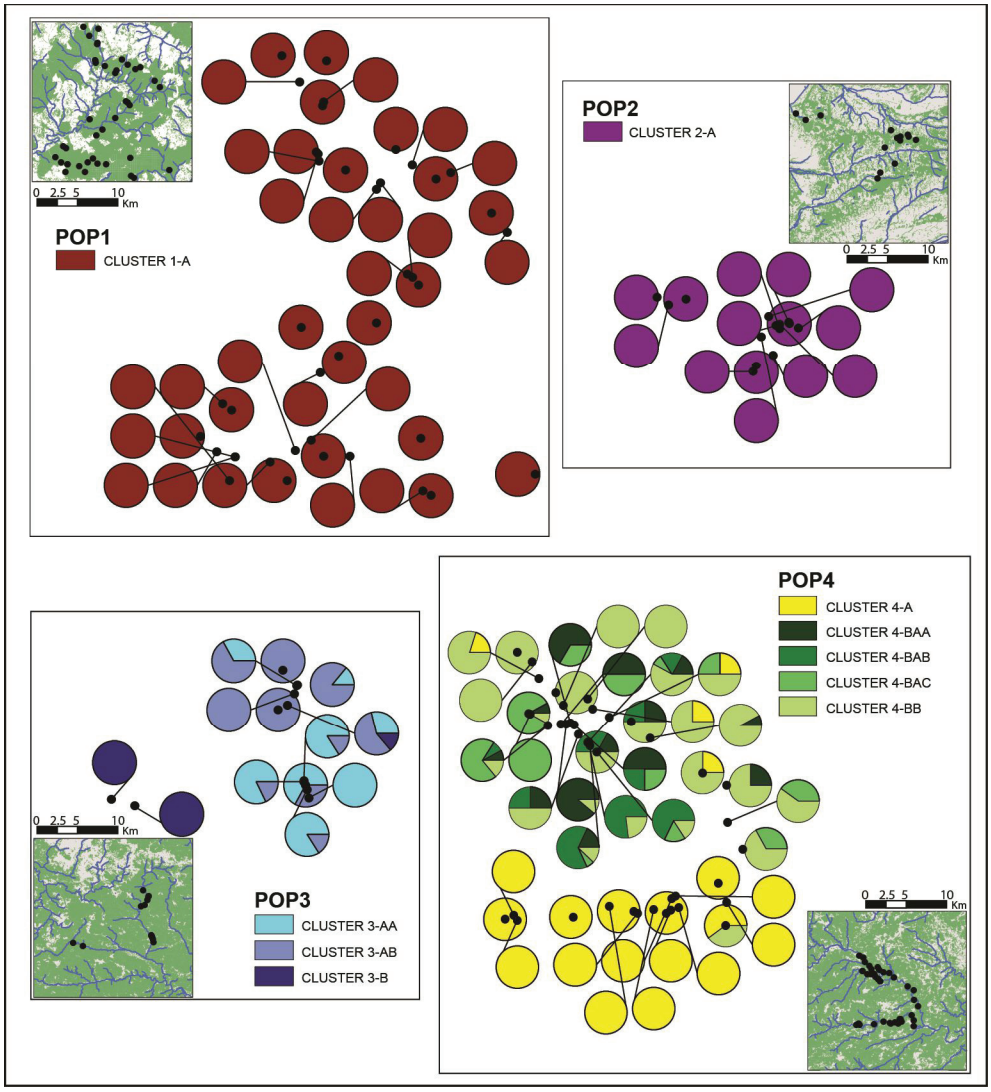

Fig.3. Mapping the spatial distribution of the different genetic clusters inferred by hierarchical STRUCTURE in the four studied metapopulations. In the metapopulation exposed to unpredictable environments (POP1 = DA, POP2 = BL), no genetic structuring was detected. In opposite, in metapopulations occurring in predictable environments (POP3 = BG, and POP4 = GL), complex hierarchized genetic structure has been found. In metapopulation BG, the hierarchical analysis revealed the existence of two initial genetic clusters, i.e. 3-A and 3-B, and genetic substructure within cluster 3-A where two nested clusters were inferred, i.e. 3-AA and 3-ABB. In metapopulation GL, the hierarchical analysis highlighted the presence of two initial genetic clusters, i.e. cluster 4-A and 4-B, and further substructure was detected within cluster 4-B, i.e. 4-BA and 4-BB. Further genetic substructure was then identified within the cluster 4-BA and three additional genetic clusters were thus inferred, i.e. 4-BAA, 4-BAB and 4-BAC.

Table 2. *General analysis to assess the effect of landscape distance (LANDSCAPE: hydrological topographic distances in predictable environment, to account for both dendritic river network and topographic variation; topographic distances only in unpredictable environments) and metapopulation status (STATUS: unpredictable vs predictable environments) on pairwise genetic distance based on ANOVA F-test type III in four metapopulation of Bombina variegata.*

Fixed effects	DDL Res.	F	P
STATUS	2	0.03	0.87
LANDSCAPE	109	3818.27	<0.0001
STATUS × LANDSCAPE	109	766.68	<0.0001

Using the correlative approach, we found a clear evidence for the effect of the dendritic organization of the stream network on the genetic individual distance as revealed by the AIC associated to the two alternative models (respectively for the model including the stream network in the landscape distance and the alternative one: 100502.2 versus 103286.7). Partial analyses (i.e discarding metapopulations not located in a stream network) also indicate a clear support for the dendritic organization of streams network on the individual genetic distances within metapopulation systems (model's AIC: 74459.6 versus 77522.4). According to the best-supported model, the relationship between the individual genetic distance and the landscape distance significantly varies according to the metapopulation status (Table 2). Separate analyses for each metapopulation status reveal that the topological distance significantly and positively influence genetic distance in metapopulations experiencing environmental unpredictability, but that this effect is much higher in metapopulations not experiencing environmental unpredictability even after accounting for the stream network organization (Table 3).

Table 3. Partial analysis to assess the effect of landscape distances on pairwise genetic distance in four metapopulations of Bombina variegata. The outputs of fixed effect of the linear mixed model are provided for each type of environment. In the metapopulations occurring in predictable environments, the landscape distances (LANDSCAPE) consist in hydrological topographic distances to account for both dendritic river network (i.e. linear systems) and topographic variation. In the metapopulations facing unpredictable environments, the landscape distances topographic distances only (i.e. two-dimensional systems).

Fixed effects	Estimates	Std error	DDL	*t*	P
Predictable environments (linear systems)					
INTERCEPT	-0.26	4.60	1	-0.06	0.96
LANDSCAPE	0.41	0.003	2	122.46	<0.0001
Unpredictable environments (two-dimensional systems)					
INTERCEPT	-0.38	4.55	1	-0.08	0.95
LANDSCAPE	0.37	0.003	2	105.01	<0.0001

DISCUSSION

Our results provided clear evidences that metapopulation systems experiencing contrasting degrees of environmental unpredictability differ both on behavioral traits related to dispersal, demographic dispersal and genetic differentiation.

Does habitat unpredictability level entail a dispersal behavioral syndrome?

Our results showed that toadlets from predictable and unpredictable environments differ in terms of behavioral phenotype. Individuals from the metapopulations exposed to unpredictable environments were bolder and displayed a higher propensity for exploration than individuals from predictable environments. These behavioral traits seems weakly affected by individual morphological variation since we did not detected any significant effect of the juvenile body size whatever the behavioral traits considered (i.e. boldness and exploration propensity). These may be somewhat surprising concerning the exploratory propensity, since this behavior has been often reported to depend on body size in amphibians (Brodin et al. 2013, Maes et al. 2013). It could be simply that the latency to exit the arena is more related to the boldness of toadlet than to their exploratory propensity. Our results are congruent with other studies showing that boldness and exploration are positively correlated with dispersal propensity and ability in various vertebrates (Cote et al. 2010, Ronce & Clobert 2012). They also support the theoretical prediction that spatio-temporal environmental variation is an important driver of dispersal polymorphism (McPeek & Holt 1992, Paradis 1998). Our rearing experiments in common garden have allowed us to remove the effects of environmental variation during larval growth that usually strongly affects individual phenotype and performance at metamorphosis (Smith-Gill & Berven 1979, Werner 1986). After eliminating environmental effects, divergences in behavioral phenotypes may thus depend on either genotype or maternal effects, or the interaction of both. Concerning maternal effects, differences in the female resource allocation in egg yolk supply could for instance entail divergences in offspring ontogenetic pathways that may affect their behavioral phenotype. In *B. variegata*, a recent study has provided evidence that differences in the habitat predictability have a strong impact on the female's lifetime schedules of resource allocation to reproduction by shaping the trade-off between mean and variance of annual breeding investment and subsequent fitness gains (Cayuela et al. in press). Regarding genetic determinism hypothesis, the differences of behavioral phenotype we found could be associated with polymorphism in serotonin, dopamine and monoamine oxidase genes that are known to affect fear-, anxiety- and novelty-related behaviors (Momozawa et al. 2005, Flisikowski et al. 2009, Hejjas et al. 2009, Wan et al. 2013). In addition to molecular polymorphism, these behavioral divergences may also result from differential expression of these genes (Rey et al. 2013, Wong et al. 2015). Moreover, balancing selection acting on genetic polymorphism, such as overdominance and antagonistic pleiotropy, may also increase this behavioral variation (van Oers & Mueller 2010).

How habitat unpredictability affects dispersal rates in free-ranging metapopulations?

Our results showed that dispersal rates between pond archipelagoes were drastically higher in the metapopulations experiencing unpredictable environments than in those occupying predictable ones. These results confirm the prediction made by theoretical studies stating that spatio-temporal environmental variation should favor dispersal in highly stochastic environments Travis & Dytham 1999, Reigada et al. 2015). Moreover, our analyses revealed that apparent survival rates were lower in the metapopulations exposed to unpredictable environments. Due to a reduced sampling effort over time (only three year of survey), the survival estimates were likely biased by capture availability issues (for this problem in capture-recapture framework, see Kendall et al. 1997) due to skipping behavior in this species (Cayuela et al. 2014). Nevertheless, this pattern is congruent with the known life history characteristics of *B. variegata* in both environments, including a two times shorter life span and a two times higher fecundity in unpredictable environments (Cayuela et al. in press). All these results taken together, our study is one of the few to highlight an empirical link between dispersal behavioral syndrome and metapopulation functioning. Nevertheless, this link has to be considered with caution because our analyses have only focused on adult dispersal while natal dispersal is often thought to have a significant contribution to metapopulation dynamics (Sinsch 1997, Grant et al. 2010, Griffiths et al. 2010). Furthermore, the metapopulation used to infer divergences in the behavioral phenotypes were not necessarily the same than those in which dispersal rates were estimated using capture-recapture. Our analyses therefore only provide an indirect link between the dispersal behavioral syndrome and metapopulation dynamics.

How habitat unpredictability affects genetic structuring in free-ranging metapopulations?

Our results indicate substantial deviation from Hardy-Weinberg equilibrium as well as lower unbiased expected heterozygosity and higher *Fis* at almost all the loci in the metapopulations occurring in predictable environment than those facing unpredictable environments. This pattern suggests a significant decline of genetic diversity in predictable environments. Despite this lower genetic diversity, using a Bayesian clustering method, we highlighted complex hierarchical genetic structuring in the metapopulations occupying predictable environments while we did not detected any genetic divergence in unpredictable environments. This pattern was also confirmed using a correlative approach; genetic differentiation among pond archipelagoes was higher in the metapopulations occurring in predictable environments than those experiencing unpredictable ones. In the partial analysis focusing on the metapopulations occupying predictable environments, we found that genetic divergence among pond archipelagoes strongly depends on the dendritic river networks, suggesting that *B. variegata* preferentially moves between pond archipelagoes along the river stream. Classically, for species that preferentially disperse along the network branches, patterns of genetic differentiation

may reflect the constraints imposed by the network architecture (Rissler et al. 200, Lowe et al. 2006, Campbell Grant et al. 2007). When organisms are constrained to move within the dendritic network, as *B. variegata* in the predictable environments, strong demographic and genetic isolation may occur among subpopulations that are nearby in Euclidean space, but distant along network branches (Fagan 2002, Rissler et al. 2004). However, while accounting for dendritic river network in the model, our general analysis revealed that genetic differentiation occurs at a shorter landscape distance in predictable environments than in unpredictable. These results confirm the findings of two previous studies suggesting that population genetic differentiation is lower in amphibian species reproducing in highly temporary water bodies (Chan & Zamudio 2009, Mims et al. 2015). Yet, although it is tempting to state the divergence in the level of genetic differentiation within the metapopulations result from a reduction or an increase of gene flow among pond archipelagoes, one has to be cautious in interpreting these results (Anderson et al. 2010, Lowe & Allendorf 2010). Indeed, pairwise genetic differentiation metrics are directly impacted by the balance between gene flow and genetic drift, which interact as opposing evolutionary forces, the former decreasing and the latter increasing genetic divergence among populations as their respective influences increase (Slatkin 1977, Hutchison & Templeton 1999). Consistent differences in the effective population size within pond archipelagoes between predictable and unpredictable environments could therefore be a potential confounding factor. Nevertheless, demographic population size seems usually comparable between both environments (Beshkov & Jameson 1980, Massemin 2001, Pichenot 2008, Astruc et al. 2014), suggesting that this alternative hypothesis is unlikely.

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SUPPLEMENTAL MATERIAL

Appendix 1 (Cf. Annexe 2)

Appendix 2 (Cf. Annexe 2)

Appendix 3 (Cf. Annexe 2)

CHAPITRE II. Canalisation des traits d'histoire de vie et fluctuations environnementales : impact des variations climatiques sur la dynamique des populations

ARTICLE 1. Cayuela Hugo, Arsovski Dragan, Thirion Jean-Marc, Bonnaire Eric, Pichenot Julian, Boitaud Sylvain, Miaud Claude, Joly Pierre, Besnard Aurélien. Demographic responses to weather fluctuation are context dependent in a long-lived amphibian. Global Change Biology, 22:2076-2087. DOI: 10.1111/gcb.13290

ARTICLE 2. Cayuela Hugo, Besnard Aurélien, Bonnaire Eric, Perret Haize, Rivoalen Justine, Miaud Claude, Joly Pierre (2014). To breed or not to breed: past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian. Oecologia. 176:107–116. DOI 10.1007/s00442-014-3003-x

ARTICLE 3. Cayuela Hugo, Arsovski Dragan, Boitaud Sylvain, Bonnaire Eric, Boualit Laurent, Miaud Claude, Joly Pierre, Besnard Aurélien (2015) Slow life history and rapid extreme flood: demographic mechanisms and their consequences on population viability in a threatened amphibian. Freshwater Biology 60:2349-2361. DOI: 10.1111/fwb.12661

ARTICLE 4. Cayuela Hugo, Arsovski Dragan, Bonnaire Eric, Duguet Rémi, Joly Pierre, Besnard Aurélien. The impact of severe drought on survival, fecundity and population persistence in an endangered amphibian. Ecosphere 7:e01246. DOI:10.1002/ecs2.1246

Global Change Biology

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Demographic responses to weather fluctuations are context dependent in a long-lived amphibian

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Abstract

Weather fluctuations have been demonstrated to affect demographic traits in many species. In long-lived organisms, their impact on adult survival might be buffered by the evolution of traits that reduce variation in interannual adult survival. For example, skipping breeding is an effective behavioral mechanism that may limit yearly variation in adult survival when harsh weather conditions occur; however, this in turn would likely lead to strong variation in recruitment. Yet, only a few studies to date have examined the impact of weather variation on survival, recruitment and breeding probability simultaneously in different populations of the same species. To fill this gap, we studied the impact of spring temperatures and spring rainfall on survival, on reproductive skipping behavior and on recruitment in five populations of a long-lived amphibian, the yellow-bellied toad (*Bombina variegata*). Based on capture–recapture data, our findings demonstrate that survival depends on interactions between age, population and weather variation. Varying weather conditions in the spring result in strong variation in the survival of immature toads, whereas they have little effect on adult toads. Breeding probability depends on both the individual's previous reproductive status and on the weather conditions during the current breeding season, leading to high interannual variation in recruitment. Crucially, we found that the impact of weather variation on demographic traits is largely context dependent and may thus differ sharply between populations. Our results suggest that studies predicting the impact of climate change on population dynamics should be taken with caution when the relationship between climate and demographic traits is established using only one population or few populations. We therefore highly recommend further research that includes surveys replicated in a substantial number of populations to account for context-dependent variation in demographic processes.

Keywords: amphibian, *Bombina variegata*, climate, demographic responses, recruitment, skipping behavior, survival, weather fluctuation

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Introduction

The global climate is changing. Long-term records indicate that the global surface temperature has increased ≈0.2 °C per decade over the past 30 years (Hansen *et al.*, 2006). Global precipitation has also increased over the same period, particularly in Europe (Easterling *et al.* 2000). In parallel, climatologists have provided growing evidence that the degree of climatic variation has changed over recent decades as a consequence of human activities (Alexander *et al.*, 2006; Coumou & Rahmstorf, 2012), leading, for instance, to greater or lesser contrasts between wet and dry or hot and cold years. While global warming has been shown to have adverse effects on several species, changes in interannual variation of weather components (e.g., temperature and precipitation) can also increase interannual variation of demographic parameters, potentially leading to population decline or even to extinction in some vertebrates (Selwood *et al.*, 2014; Lawson *et al.*, 2015).

Weather variation can negatively affect survival when thermal and hygrometric conditions exceed the physiological tolerance limits of an organism (Addo-Bediako *et al.*, 2000), especially during energetically demanding phases of the life cycle (e.g., the reproductive period). Yet, the effects of weather variation on survival may vary between individuals; for example, it

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may be state or age dependent (Selwood *et al.*, 2014). Some studies have shown that weather can influence juvenile survival, while adult survival remains unaffected (Gaillard & Yoccoz, 2003; Lowe, 2012). Why such differences occur might be explained by life-history theory. This theory predicts that the degree to which demographic traits vary with weather fluctuations differs among species according to their position along the 'slow–fast continuum' (Stearns, 1992). For example, long-lived organisms, on the slow end of the continuum, are expected to display life-history tactics that allow them to mitigate the impact of weather on adult survival (Boyce *et al.*, 2006; Koons *et al.*, 2009). Such 'environmental buffering' (or 'canalization', *sensu* Gaillard & Yoccoz, 2003) results from selective pressures that select for phenotypic traits (behavioral or physiological) that reduce the interannual variability of adult survival as this demographic parameter has the highest impact on fitness in long-lived species (Boyce *et al.*, 2006).

One effective behavioral mechanism involved in environmental buffering is to skip breeding. This can reduce yearly variation in adult survival by decreasing the cost of reproduction on survival when harsh environmental conditions occur (Cubaynes *et al.*, 2011; Rideout & Tomkiewicz, 2011; Shaw & Levin, 2011). In iteroparous organisms, the repetition of reproductive episodes during an individual's lifetime induces a trade-off between fitness gains during the current reproduction and fitness losses in terms of survival and therefore the number of future breeding opportunities and potential fitness returns (Williams, 1966). The ability of an iteroparous organism to survive and reproduce depends on a combination of internal and external factors (McNamara & Houston, 1996), including weather conditions. Because weather variation influences yearly fluctuations in the level of resources and in turn the energetic costs for physiological regulation, it can affect a female's ability to recover the physiological state required to initiate oocyte development (Skjæraasen *et al.*, 2012) or to ensure lactation (Bårdsen *et al.*, 2010). Furthermore, even if a female is able to reproduce, she may 'choose' to skip breeding opportunities in order to safeguard her own survival (Brown & Sibly, 2006; De Roos *et al.*, 2009), for instance, when harsh weather conditions occur during the breeding season.

Although many researchers have studied the impact of weather variation on demographic parameters such as survival, recruitment and breeding probability (recently reviewed in Selwood *et al.*, 2014), only a few have examined the impact of weather conditions on all these demographic traits simultaneously (e.g., Pilastro *et al.*, 2003). Little is known about how weather variation may influence not only survival at the different ontogenetic stages, but also reproductive skipping behavior and the consequences of both on recruitment in long-lived organisms. Amphibians are useful biological models for investigating this issue as their population dynamics are particularly sensitive to weather variations (Daszak *et al.*, 2005; Cayuela *et al.*, 2012). In particular, rainwater deficit or excess or abnormally high or low temperatures can have various effects on breeding propensity, recruitment and survival before and after sexual maturity (e.g., Reading, 2007; Griffiths *et al.*, 2010; Lowe, 2012; Green & Bailey, 2014; Benard, 2015). Yet, because amphibians usually have a long period of immaturity, spending from months to years on land before returning to breeding ponds (Pittman *et al.*, 2014), little is known about the mean and variance of their vital rates during the immature stages of their life cycle in natural conditions. In relatively long-lived amphibians, survival generally increases with size and age (Schmidt *et al.*, 2012), as in other long-lived species (Gaillard & Yoccoz, 2003). These survival differences between age classes suggest that immature amphibians may differ from those of older age classes in their responsiveness to weather variation. Studies have shown that adult long-lived amphibians can buffer the impact of weather variation on survival (e.g., *Ambystoma tigrinum* in the meta-analysis of Morris *et al.*, 2008), for instance, by not breeding during several years (Church *et al.*, 2007; in *Ambystoma tigrinum*). Mature amphibians can thus skip breeding opportunities to reduce the cost of reproduction on survival, remaining on land during a year or more without breeding (Muths *et al.*, 2006, 2010), especially when harsh weather conditions occur (Church *et al.*, 2007; Cayuela *et al.*, 2014).

In this study, using capture–recapture data collected between 2000 and 2014 on five populations of the yellow-bellied toad (*Bombina variegata*), we simultaneously examined the impact of weather variation (i.e., spring temperature and cumulative rainfall from March–May) on survival, breeding decision and recruitment. As juveniles have an immature immune system, a lack of experience and an energy allocation pattern that prioritizes growth over maintenance, we expected them to be sensitive to weather variation (Gaillard & Yoccoz, 2003). In contrast, we predicted that weather fluctuations would have a marginal effect on adult survival because of environmental canalization, as in other long-lived organisms (Boyce *et al.*, 2006; Koons *et al.*, 2009). We also predicted that reproductive skipping, a behavioral mechanism that limits yearly variation in adult survival when severe environmental conditions occur (Rideout & Tomkiewicz, 2011), would strongly depend on weather conditions, leading to large interannual

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variation in recruitment. Lastly, we predicted that the impact of weather variation would be context depend and thus vary between populations, particularly since the five populations studied experience different degrees of habitat stochasticity, affecting their position along the slow–fast continuum (Cayuela *et al.*, 2016a).

Materials and methods

Biological model

Bombina variegata is a relatively long-lived anuran; the mean life expectancy ranges from 5 to 12.5 years in free-ranging populations, with some individuals reaching an age of more than 20 years in natural conditions and almost 30 years in captivity (Smirina, 1994). It breeds in small water bodies characterized by stochastic water-level variation (Cayuela *et al.*, 2011, 2013). Its long life span and iteroparity are assumed to be a response to breeding habitat stochasticity (Cayuela *et al.*, 2014). Females additionally display risk-spreading tactics through egg-clutch fractionation over space and time (Buschmann, 2002). The flexibility of the ovarian system of bombinatorids allows the continuous production or resorption of oocytes over the course of the breeding season (Guarino *et al.*, 1998).

Data collection and field work

The study was conducted on five populations in France using the capture–recapture method (Fig. 1). Two populations (POP1 and POP2) are located in northeastern France in woodlands with continental climatic conditions. Another population (POP3) is located in western France in a landscape matrix containing woodland and meadows and experiencing oceanic climatic conditions. The last two populations (POP4 and POP5) are located in southeastern France along a river channel in woodlands subject to a Mediterranean climatic influence. The details of the capture–recapture surveys are summarized in Table 1, and additional information (the number of capture sessions per year, the number of captured toads, etc.) is provided in Table S1.

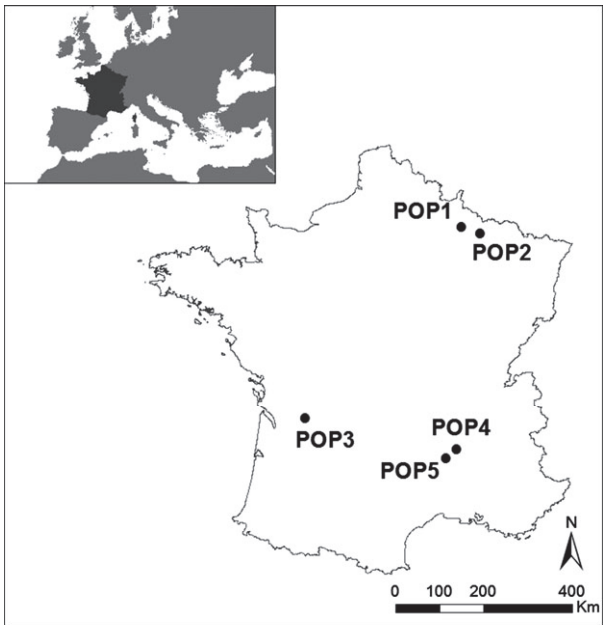

Fig. 1 Locations of the five populations of *B. variegata* studied between 2000 and 2014 in France.

In each population, toads were surveyed over periods ranging from 5 to 10 years between 2000 and 2014. Toads breed occupy for their reproduction 28 pond archipelagos in POP1, 64 pond archipelagos in POP2, three pond archipelagos in POP3, 14 pond archipelagos in POP4 and 18 pond archipelagos in POP5. The toads were caught by hand or with a dip net during the sunlight hours of the day (09:00–19:00 hours). Depending on the population, between 2 (POP4 in 2013) and 13 (POP3 in 2011) capture sessions were carried out during the breeding season from late May to July (Table S1). In each population, each pond archipelago was sampled at each session. Captures were carried out in the water bodies several times, and ceased when no new individual was detected. The time required to sample an entire network in a single session varied markedly between populations, taking from 1 day (POP3) to 13 days (POP2). During sampling sessions, the toads were caught and stored for measurement. We considered three age classes: juveniles captured after their first overwintering, subadults (two overwinterings) and sexually mature adults (at least three overwinterings). The size (snout–vent length) ranged from 17 to 29 mm in juveniles and from 30 to 35 mm in subadults. We assumed that individuals become sexually mature at the age of 3 (Plytycz & Bigaj, 1993), with a mean body length of 36 mm in males and 37 mm in females. Additional details concerning the method of individual assignment to the three ontogenetic stages and its robustness are provided in Table S2 and Figure S1. We identified

Table 1 Survey design characteristics for the five populations of *B. variegata* considered in the study: study period, survey duration, number of capture sessions performed during the survey period, total number of captures and the number of individuals identified during the survey

	Study period	Survey duration	Capture sessions	Number of captures	Number of individuals
POP1	2000–2008	9 years	45	953	581
POP2	2008–2014	7 years	23	12300	9418
POP3	2005–2014	10 years	111	1053	456
POP4	2010–2014	5 years	40	3053	1154
POP5	2010–2014	5 years	37	2086	758

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gender on the basis of strong forearms and the presence of nuptial pads in males. We identified each individual by the specific pattern of black and yellow mottles on its belly and recorded these in photographs. To minimize misidentification errors, multiple comparisons of individual patterns were performed by a single observer using the pattern-matching software Extract Compare (Hiby & Lovell, 1990).

Weather variables

We considered two climatic variables for each population: spring (March to May) cumulative precipitation (RRES) and mean spring temperatures (TXES) collected from weather stations (Source: Météo France) located in the vicinity of each study area (described in Table 2). In this species, several studies have suggested that spring precipitation and temperature could have a strong effect on demographic traits, including breeding probability (Cayuela *et al.*, 2014), recruitment (Barandun & Reyer, 1997; Barandun *et al.*, 1997) and survival (Cayuela *et al.*, 2014, 2015).

Modeling demographic parameters

The CR datasets were modeled using a reparameterized version of the robust design proposed by Cayuela *et al.* (2014). The model follows the typical structure of 'standard' robust design (Kendall *et al.*, 1997), that is, made up of two nested levels of capture occasions. 'Secondary sessions' encompass several field sessions performed over the same year. Sampling sessions were also conducted over successive years: 'primary periods' correspond to yearly sessions. Between secondary sessions, we assumed that the state of an individual was fixed; transitions between states were thus allowed between primary periods only.

The model was conditional on the first occasion, and an 'unborn individual' state was included, which allowed us to model the probability of being recruited as a juvenile between two primary periods. After being recruited, individuals could successively transit between three ontogenetic stages, that is juvenile, subadult and adult, given they survived. As is typical in a capture–recapture framework, survival estimates include both death and permanent emigration, that is apparent survival (see Schmidt *et al.* (2007) for a discussion on this point in amphibians). We assumed that sexually mature *Bombina variegata* individuals could breed or skip breeding each year (see Cayuela *et al.*, 2014). As individuals were captured in aquatic breeding sites only, nonbreeding toads were considered as not available for capture (Church *et al.*, 2007; Muths *et al.*, 2010). Skipping breeding in a given year was thus equivalent to becoming a temporary emigrant and shifting to an unobservable state (Kendall & Nichols, 2002). In the model, transitions between breeding–nonbreeding states were assumed to obey a Markov chain process.

Because gender is not identifiable in juveniles or subadults, we used a multi-event CR approach (Pradel, 2005) to model uncertainty in gender assignment; gender was thus coded as a state instead of as a group as is usual in CR data modeling. From an initial departure state (IS), individuals could be categorized with one of eleven distinct states: (UM) unborn male, (UF) unborn female, (JM) juvenile male, (JF) juvenile female, (SM) subadult male, (SF) subadult female, (BM) breeding male, (BF) breeding female, (NBM) nonbreeding adult male, (NBF) nonbreeding adult female and (†) dead individual. Ten state transitions (detailed in Table 3) were possible for the recruitment and age transition probabilities between two primary periods (matrix A; Fig. 2). Given that we examined recruitment without accounting for gender dependency, α^{IM}/α^{IF} were constrained to be equal (the parameter is hereafter quoted α). Moreover, age transition probabilities $\beta^{IM}/\beta^{IF}/\beta^{SM}/\beta^{SF}$ were fixed at 1 between secondary sessions and at 0 between primary periods. For the survival probability between two primary periods, ten state transitions (detailed in Table 3) were possible (matrix ϕ; Fig. 2). Given that the parameters ϕ^{BNM} and ϕ^{BNF} were not identifiable, ϕ^{BM}/ϕ^{BNM} and $\phi^{BF}/\phi N^{BF}$ were constrained to be equal in the model. Survival transition probabilities were fixed at 1 between secondary sessions. For breeder–nonbreeder transitions (detailed in Table 3) between two primary periods, four state transitions were possible (matrix Y; Fig. 2). The transition probabilities γ^{BM}/γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$ were fixed at 1 between secondary sessions. Concerning field observation, that is events *sensu* multi-event modeling formulation, six observation probabilities (detailed in Table 3) were considered (matrix P; Fig. 2). Note that as nonbreeding individuals were not available for recapture, their recapture probability was fixed at 0.

Table 2 Description of the three climatic factors recorded for the five populations of *B. variegata* considered in the study: identification number of the meteorological station, its distance from the barycenter of the population, REES, spring precipitation (March, April and May), TXES, spring temperature (March, April and May). Each variable is described by its mean, minimum–maximum and coefficient variation (CVs)

	Meteorological station ID number	Distance from the population	RRES mean	RRES min–max	RRES CV	TXES mean	TXES min–max	TXES CV
POP1	8490001	6.5 km	72.3	0.5–149	0.5	16.1	9.6–22.3	0.2
POP2	55484001	17.5 km	62.7	12.4–159.2	0.7	14.4	5.6–20.9	0.3
POP3	16283002	8.5 km	73.1	8.5–210.5	0.7	18.5	12.7–26.1	0.2
POP4	7096001	1.5 km	104.0	6.2–256.4	0.7	13.9	7.9–21.1	0.3
POP5	7161001	4.5 km	120.6	13.5–262	0.7	16.7	10.8–23.4	0.2

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Table 3 Definition of parameters estimated in the capture–recapture multi-event model

Parameter	Definition
α	Probability that a newly metamorphosed individual is recruited (Fig. 2, matrix A)
β	Probability that an individual does not reach the next ontogenetic stage (Fig. 2, matrix A)
ϕ	Probability that an individual survives (Fig. 2, matrix ϕ)
γ^{B}	probability that a sexually mature individual bred at time t, given it has bred at $t-1$ (Fig. 2, matrix Y)
γ^{NB}	Probability that a sexually mature individual skipped a breeding opportunity at time t, given it skipped breeding at $t-1$ (Fig. 2, matrix Y)
ρ	Probability that an individual was recaptured during a secondary session (Fig. 2, matrix P)

The analyses were carried out using the E-SURGE program (Choquet *et al.*, 2009), which provides robust tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters. For each population, competitive models were ranked through a model selection procedure using Akaike information criteria adjusted for a small sample size (AICc) (Burnham & Anderson, 2002). In all the models, initial state probability was held to be different between ontogenetic stages (AGE) and gender. Furthermore, recruitment probability was held to be different among years (YEAR). From a model in which survival and breeding probabilities were held constant between age, gender and year, we first tested whether recapture probability differed between ontogenic stages (AGE), gender (SEX) or year (YEAR). Then, we simultaneously tested whether breeding propensity depended on gender (SEX), spring precipitation (RRES) or spring temperature (TXES) and whether survival varied between ontogenetic stages (AGE), different levels of spring precipitation (RRES) and different spring temperatures (TXES). We tested all the possible linear combinations. However, the correlation between demographic parameters and weather covariates are similar to usual linear regressions. In multiple regressions, 10–30 observations are usually required for each covariate. As our populations were sampled over limited survey periods (5–10 years), weather variables were thus included separately in the models.

Results

Survival depends on age, weather variation and population

The five best-supported models for each population are provided in Table 4 (the complete model selection procedure is given in Table S3). In all populations, survival probability increased with age (Fig. 3). We also detected climatic effects on survival probability in four of the five populations (Fig. 4). Weather fluctuations from year to year during the toads' period of activity

matrix A (recruitment and age transition)

$$\begin{array}{c} \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ \mathrm{NBM} \\ NBF \\ \dagger \end{array} \begin{array}{c} \begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\ \begin{pmatrix} 1-\alpha^{JM} & 0 & \alpha^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-\alpha^{JF} & 0 & \alpha^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \beta^{JM} & 0 & 1-\beta^{JM} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta^{JF} & 0 & 1-\beta^{JF} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \beta^{SM} & 0 & 1-\beta^{SM} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \beta^{SF} & 0 & 1-\beta^{SF} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array}$$

matrix Φ (survival transition)

$$\begin{array}{c} \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger \end{array} \begin{array}{c} \begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\ \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{JM} \\ 0 & 0 & 0 & \phi^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi^{JF} \\ 0 & 0 & 0 & 0 & \phi^{SM} & 0 & 0 & 0 & 0 & 0 & 1-\phi^{SM} \\ 0 & 0 & 0 & 0 & 0 & \phi^{SF} & 0 & 0 & 0 & 0 & 1-\phi^{SF} \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi^{BM} & 0 & 0 & 0 & 1-\phi^{BM} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{BF} & 0 & 0 & 1-\phi^{BF} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBM} & 0 & 1-\phi^{NBM} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi^{NBF} & 1-\phi^{NBF} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array}$$

matrix Y (breeder/non-breeder transition)

$$\begin{array}{c} \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger \end{array} \begin{array}{c} \begin{array}{ccccccccccc} UM & UF & JM & JF & SM & SF & BM & BF & NBM & NBF & \dagger \end{array} \\ \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BM} & 0 & 1-\gamma^{BM} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{BF} & 0 & 1-\gamma^{BF} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBM} & 0 & \gamma^{NBM} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\gamma^{NBF} & 0 & \gamma^{NBF} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array}$$

matrix P (recapture)

$$\begin{array}{c} \\ UM \\ UF \\ JM \\ JF \\ SM \\ SF \\ BM \\ BF \\ NBM \\ NBF \\ \dagger \end{array} \begin{array}{c} \begin{array}{ccccc} NS & J & S & M & F \end{array} \\ \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1-p^{JM} & p^{JM} & 0 & 0 & 0 \\ 1-p^{JF} & p^{JF} & 0 & 0 & 0 \\ 1-p^{SM} & 0 & p^{SM} & 0 & 0 \\ 1-p^{SF} & 0 & p^{SF} & 0 & 0 \\ 1-p^{BM} & 0 & 0 & p^{BM} & 0 \\ 1-p^{BF} & 0 & 0 & 0 & p^{BF} \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \end{pmatrix} \end{array}$$

Fig. 2 Elementary matrices for state–state transitions and events: UM, unborn male, UF, unborn female, JM, juvenile male, JF, juvenile female, SM, subadult male, SF, subadult female, BM, breeding male, BF, breeding female, NBM, nonbreeding male, NBF, nonbreeding female, †, dead individual.

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influenced survival varyingly at the three ontogenetic stages. In POP4 and POP5, spring rainfall negatively influenced the survival probability of juveniles, while it had a slight positive impact on adult survival probability. When spring rainfall increased from 43 to 173 mm in POP4, juvenile survival probability fell by 19%, and when it increased from 65 to 194 mm in POP5, juvenile survival probability fell by 34%. In the intermediate 'subadult' ontogenetic stage, survival probability also fell by 13% in POP4 when rainfall increased from 43 to 173 mm and by 62% in POP2 when rainfall increased from 49 to 96 mm. Conversely, in POP5 for the same range of change in weather covariates (an increase in rainfall from 65 to 194 mm), subadult survival probability increased by 10%. For adults, survival probability increased with increased rainfall: by 6% in POP4, 15% in POP5 and 27% in POP2. In terms of the influence of an increase in spring temperatures, in POP1, juvenile survival probability increased by 37% with a temperature increase from 13 to 17 °C. Conversely, subadult and adult survival probability fell by 24% and by 18%, respectively, over the same range of temperatures.

Breeding probability depends on past breeding status, weather variation and population

We detected weather variation effects on breeding probability in four of the five populations (Fig. 5). In POP1, when the mean spring temperature increased from

Table 4 Model selection procedure for the five populations of *B. variegata* considered in the study (only the five best-supported models are included here; the complete model selection procedure is provided in Appendix S2): *r* model rank.

	Model definition						
r	Survival	Breeding	Recruitment	Recapture	*k*	Dev.	AICc
POP1							
1	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	36	12 023.63	12 097.10
2	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	36	12 096.35	12 099.83
3	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	33	12 046.74	12 113.98
4	AGE	CST	YEAR	AGE × SEX + YEAR	31	12 064.59	12 127.69
5	AGE	SEX	YEAR	AGE × SEX + YEAR	33	12 063.77	12 131.01
POP2							
1	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	32	127 945.92	128 010.03
2	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	32	128 097.73	128 161.84
3	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	30	128 150.22	128 210.32
4	CST × TXES	SEX	YEAR	AGE × SEX + YEAR	28	128 254.72	128 310.81
5	CST × RRES	SEX	YEAR	AGE × SEX + YEAR	28	128 310.43	128 336.52
POP3							
1	AGE	CST	YEAR	AGE × SEX + YEAR	33	19 703.59	19 770.20
2	AGE	SEX	YEAR	AGE × SEX + YEAR	35	19 699.57	19 770.26
3	AGE	RRES	YEAR	AGE × SEX + YEAR	35	19 699.64	19 770.33
4	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	38	20 064.71	20 141.52
5	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	38	20 095.56	20 172.37
POP4							
1	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	28	42 179.06	42 235.20
2	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	28	42 182.74	42 238.88
3	AGE	RRES	YEAR	AGE × SEX + YEAR	25	42 190.37	42 240.47
4	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	29	42 186.29	42 244.43
5	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	26	42 202.66	42 254.78
POP5							
1	AGE × RRES	SEX × RRES	YEAR	AGE × SEX + YEAR	32	27 024.37	27 088.64
2	AGE × TXES	SEX × TXES	YEAR	AGE × SEX + YEAR	32	27 027.58	27 091.85
3	AGE × TXES	SEX	YEAR	AGE × SEX + YEAR	28	27 037.20	27 093.40
4	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	29	27 050.11	27 108.33
5	AGE	CST × RRES	YEAR	AGE × SEX + YEAR	25	27 065.11	27 115.27

k, number of model parameters, Dev., deviance, AICc, Akaike information criterion adjusted for a small sample size, AGE, age-specific variation (three ontogenetic stages considered: juvenile, subadult, adult), CST, constant, SEX, gender-specific variation, YEAR, year-specific variation, TXES, spring temperature, RRES, spring precipitation.

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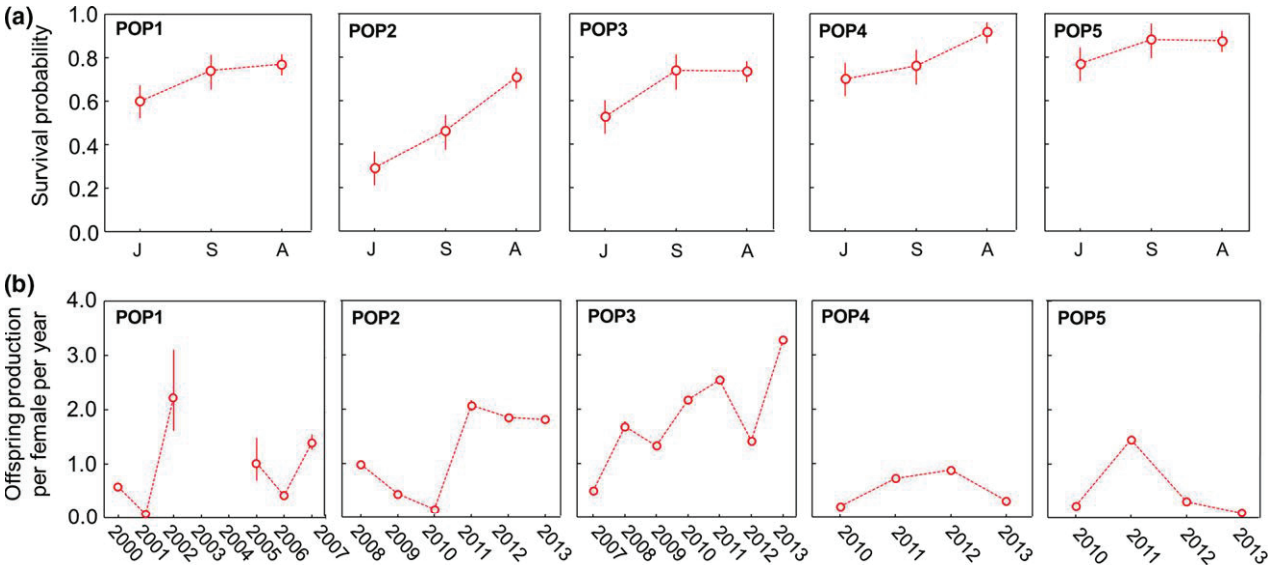

Fig. 3 Demographic parameters recorded in the five surveyed populations (POP1, POP2, POP3, POP4 and POP5) of *B. variegata* in France: (a) survival probability and 95% confidence intervals at three ontogenic stages: J, juvenile, S, subadult, A, adult; (b) offspring production (number of females recruited annually per female per year) and 95% confidence intervals.

12 °C to 17 °C, the probability of breeding two consecutive years increased by 27%, while the probability of skipping reproduction two consecutive years fell from 1 to 0. In POP2, when mean spring rainfall increased from 49 to 88 mm, the probability of breeding two consecutive years increased by 35%, while the probability of skipping breeding two consecutive years decreased by 88%. In POP4, when spring rainfall increased from 43 to 173 mm, the probability of breeding decreased by 20%, while the probability of skipping breeding two consecutive years decreased by 25%. In POP5, the probability of breeding or skipping breeding differed between genders and varied according to spring rainfall. When spring rainfall increased from 65 to 190 mm, the probability of breeding two consecutive years increased by 20% in females and 9% in males; the probability was slightly lower in females than males. In contrast, with the same increase in rainfall, the probability of skipping breeding two consecutive years did not vary in males (−2%) while it decreased by 63% in females. In all populations, variable year-to-year breeding propensity led to highly temporally variable recruitment (Fig. 3).

Discussion

Our findings show that intraspecific variation in survival is the result of complex interactions between age, population and weather variation. They also suggest that breeding probability depends on the individual's breeding status at the previous breeding opportunity, on population and on current weather conditions, leading to strong variation in offspring production.

Survival probability depends on age, population and weather variation

Our results indicate that survival probability increased with age (and therefore size), which is in line with previous studies in amphibians (Altwegg & Reyer, 2003; Schmidt *et al.*, 2012). They also demonstrate that survival differed between ontogenetic stages and was influenced by weather conditions in four of the five study populations (all populations except POP3). Weather variables systematically have a stronger effect on the survival of immature individuals (juveniles and subadults) than on that of adults.

Yet the strength, and also the direction of the impact of weather, varies between populations, particularly before sexual maturity. In POP4 and POP5, the survival of juveniles (and subadults in POP2) was negatively affected by spring rainfall, while in POP1, it was positively influenced by increased mean spring temperatures. In POP3, we did not find any effect of weather variation on juvenile survival. In populations that breed and hibernate in the close vicinity of a river channel (in our study, POP4 and POP5), a recent study has shown that juvenile survival in *B. variegata* is negatively impacted by severe flooding after heavy precipitation, while adult survival is unaffected (Cayuela *et al.*, 2015). Equally, another study has shown that in stream-dwelling salamanders, a higher volume and frequency of spring and fall floods did not result in a decrease in adult survival and fecundity; however, it did generate a drop in recruitment due to increased mortality of metamorphosing individuals (Lowe, 2012). In POP1, our

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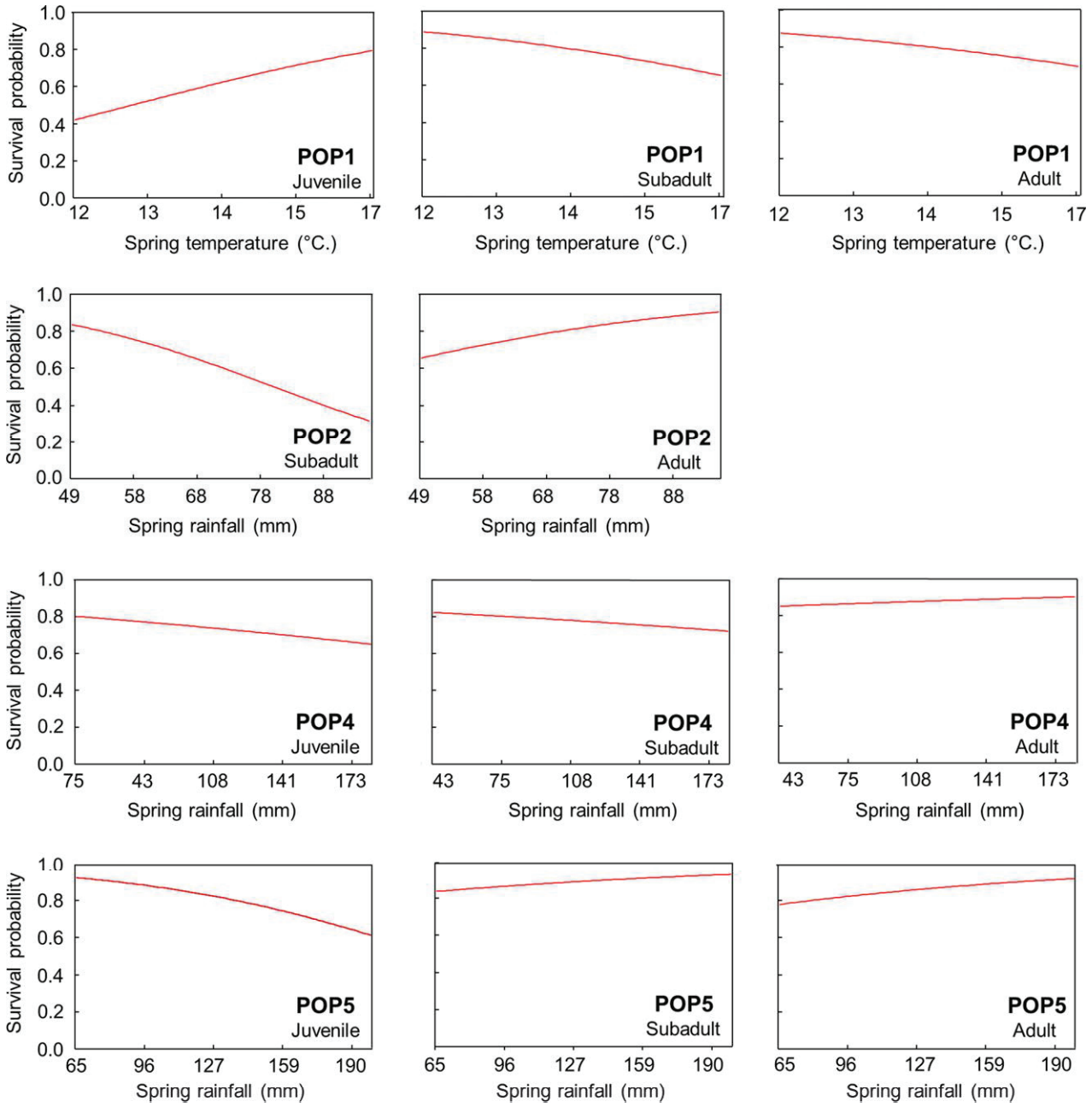

Fig. 4 Effects of climate variation, that is spring temperature and spring rainfall (March, April and May), on survival probability at three ontogenetic stages (juvenile, subadult, adult) in four populations (POP1, POP2, POP4 and POP5; no significant effect has been detected in POP3) of *B. variegata* in France.

results indicate that juvenile survival depends on spring temperatures rather than precipitation. In juveniles, low temperatures in the spring might slow the rate of development, resulting in a smaller body size before overwintering (see the 'temperature–size rule' in ectotherms, *sensus* Atkinson, 1994). This is usually correlated to low survival in amphibians (Altwegg & Reyer, 2003; Schmidt *et al.*, 2012).

In terms of adult survival, we detected an effect due to weather in only two of the five populations (POP1 and POP2). In these two populations, high spring temperatures and low levels of spring rainfall had a slightly negative impact on the survival of adults (and subadults in POP1). In the other populations, adult survival marginally covaried (a slight slope in POP4 and POP5) or did not covary at all (POP3) with weather

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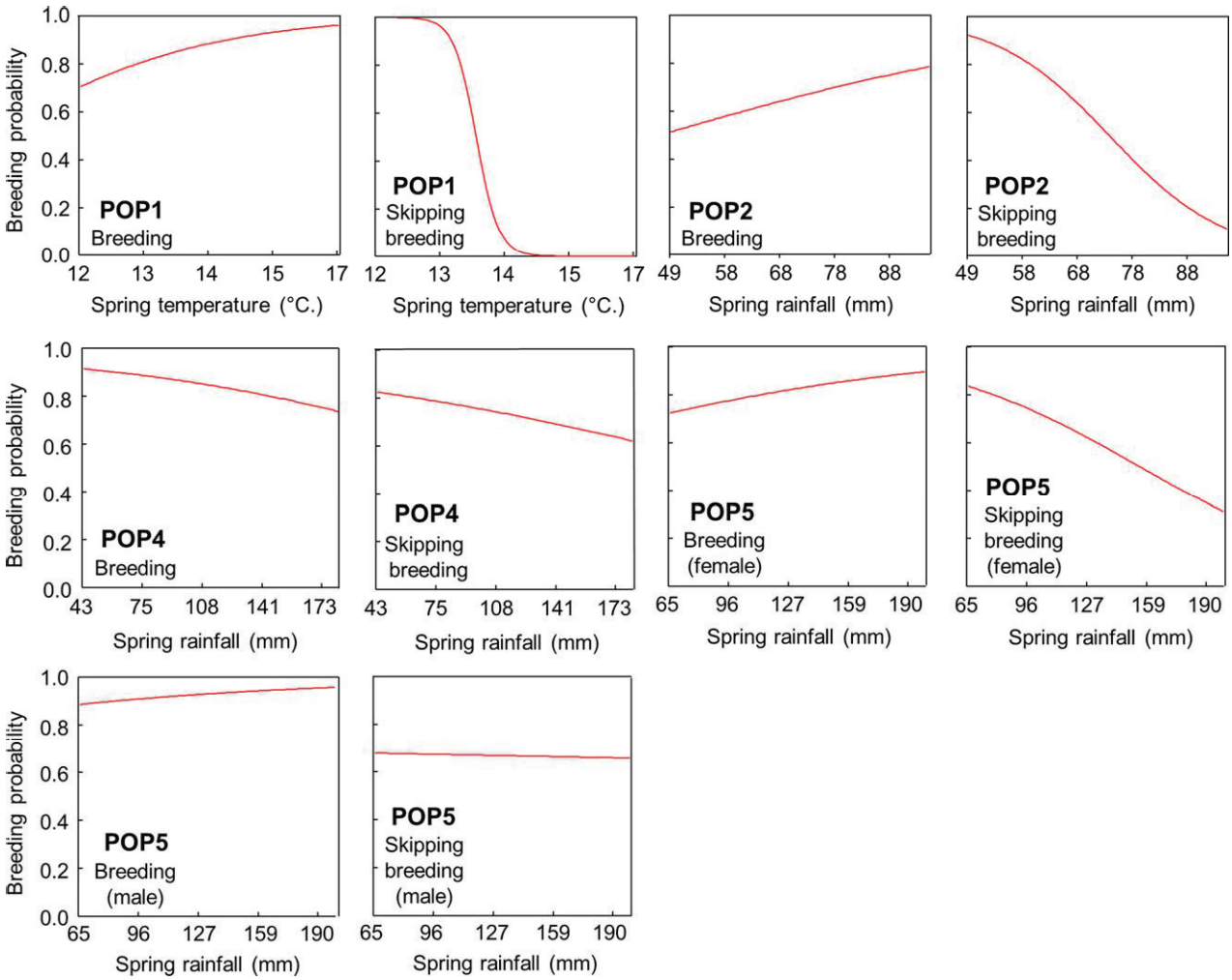

Fig. 5 Effects of climatic variation, that is spring temperature and spring rainfall (March, April and May) on breeding probability in four populations of *B. variegata* in France (POP1, POP2, POP4, POP5; no significant effect has been detected in POP3). Breeding probability is conditional on the reproductive status of individuals in the previous year. The probability of breeding or skipping breeding two consecutive years is modeled as a function of spring temperature and rainfall during the current breeding opportunity.

fluctuations. Concerning the pattern found in POP1 and POP2, this result is in line with two recent studies that show that extreme droughts (in 2011 in northern and southern France) may decrease adult survival in *B. variegata* (Cayuela *et al.*, 2014, 2016b). A similar pattern has also been found in other frog and salamander species (Berven, 1990; Church *et al.*, 2007; Rittenhouse *et al.*, 2009). Desiccation risk during prenuptial or postnuptial migration can enhance the cost of reproduction on survival during a drought year (Church *et al.*, 2007), especially as severe dehydration can have deleterious effects on amphibian physiological systems, organs and tissues (Hillman, 2009). In anurans, pulmonary compliance and lung volume can facilitate lymph mobilization, which appears to be a key adaptation in avoiding dehydration as it stabilizes plasma volumes (Hillman *et al.*, 2010). However, in bombinatorids, small lung and lymph volumes resulting from a small body mass may reduce their ability to cope with dehydration resulting from severe drought (Withers *et al.*, 2014). Despite these slight weather effects found in POP1 and POP2, the general pattern shown in our results indicates that weather variation has only a marginal effect on adult survival, presumably resulting from the canalization process that limits variation in adult survival in long-lived organisms (Gaillard & Yoccoz, 2003; Boyce *et al.*, 2006; Morris *et al.*, 2008).

In POP3, we did not find any evidence that weather variation affects survival at any ontogenetic stage (as well as breeding decisions), which is surprising because the survey duration in this population is the longest (10 years) in our study. We can explain this result in

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two ways: first, we cannot rule out the possibility that potential effects on demographic traits are not detected in the models due to a lack of statistical power; the population size is indeed one of the smallest (from 39 to 95 adults) in our study. Second, POP3 is the only population experiencing an oceanic climate, which is characterized by mild and wet spring and by relatively buffered monthly variation of temperature and rainfall. Low variation of the climate components could result in buffered variation of the demographic traits in yellow-bellied toad populations in western France.

Breeding probability depends on past breeding status, weather variation and population

We detected the effect of weather variation on breeding decisions in three of the five populations (POP1, POP2 and POP5). Our results indicate that when weather has an impact on this variable, its effect also differs between populations. In POP1, the probability of breeding two consecutive years was lower during a cold spring, and the probability of skipping breeding two consecutive years was higher when low spring temperatures occurred. In amphibians, high temperatures positively affect ovarian follicular growth in toads and frogs (Rastogi *et al.*, 1983; Panchratna & Saidapur, 1990; Saidapur & Hoque, 1995), which increased female fecundity and breeding probability. In males, mating behavior, especially calling (Oseen & Wassersug, 2002) and auditory performance (Mohneke & Schneider, 1979) are positively influenced by high temperatures. Temperature is also assumed to be the main external factor that regulates spermatogenesis in amphibians (for a review, see Paniagua *et al.*, 1990). In particular, increased temperatures stimulate spermatogonial proliferation and spermatogenesis, which usually influences male breeding investment and performance. Particularly in bombinatorids, there seems to be a relationship between an increase in testis weight and increased spring temperatures (Guarino *et al.*, 1998).

In POP4, the breeding probability slightly decreased according to spring rainfall. In this population, breeding sites are located along a river channel and strong rainfalls often increase the river's water level, which locally makes aquatic sites unsuitable for breeding. As a result, yellow-bellied toads could likely skip reproduction due to the temporary submersion of riverbanks and the reduction of available breeding sites where rainfall levels were high. Conversely, in POP2 and POP5, increased spring rainfall positively influenced the probability of breeding two consecutive years, while it negatively influenced the probability of skipping breeding two consecutive years. In POP5, this relationship was stronger in females, while the effect of rainfall appears more tenuous in males' breeding decisions, likely because of the higher cost of reproduction in *B. variegata* females (Cayuela *et al.*, 2014) and amphibians in general (Wells, 2010). These results might be explained in two ways. First, a water deficit at the beginning of the breeding season may be an environmental indicator that allows animals to predict to some extent the water conditions that will prevail during larval growth (i.e., predictive plasticity, *sensu* Cooper & Kaplan, 1982). Because low spring rainfall enhances the risk of tadpole mortality due to pond desiccation (Barandun & Reyer, 1997; Barandun *et al.*, 1997), adults may skip breeding to cope with uncertainty of the breeding success (Cayuela *et al.*, 2014). Second, animals may decide to skip a reproductive opportunity when the breeder's own survival is threatened by the risk of desiccation during migration. Such behavior has been observed in other amphibians in which adults may skip breeding to limit the cost of reproduction on survival during a drought year (Church *et al.*, 2007).

Environmental canalization and the context dependence of demographic processes

Our findings indicate that intraspecific variation in survival patterns results from complex interactions between age, population and weather variation. The general pattern we detected in our populations was that weather variation has a strong impact on juvenile and subadult survival, but a low or even nonexistent impact on adult survival. The analyses provided in Cayuela *et al.* (2016a) show that mean survival increased with age in all five populations, while temporal variation of survival decreased with age in three populations. These results support the hypothesis of environmental canalization, a demographic process resulting from the selection for alleles that reduce variation in the demographic parameters that have the greatest impact on population growth rate (Gaillard & Yoccoz, 2003; Morris *et al.*, 2008). Environmental canalization is likely to be an adaptive strategy that allows *B. variegata* to cope with the uncertainty of reproductive success due to stochastic environmental variation (e.g., weather variation or pond desiccation). In this species, the phenotypic traits that minimize variation in adult survival may be multiple, including antipredator and antimicrobial strategies (Conlon, 2011; König & Bininda-Emonds, 2011) as well as reproductive skipping behavior that may allow adults to reduce the cost of reproduction on survival when harsh environmental conditions occur (Cayuela *et al.*, 2014; present study).

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Our findings also demonstrate that, apart from the general pattern of adult survival canalization, the impact of weather variation on demographic processes seems largely context dependent. A recent study on the same populations (Cayuela *et al.*, 2016a) shows that contrasting degrees of breeding habitat stochasticity resulted in variation in the speed of the life-history cycle in *B. variegata*. In particular, populations experiencing highly stochastic habitats (POP1, POP2 and POP3) exhibited faster life-history strategies involving lower survival of juveniles, subadults and adults, but had a fecundity that was twice as high as in populations experiencing relatively stable, predictable habitats (POP4 and POP5). Such life-history differences may explain the intraspecific variation in demographic responses to weather variation found in this study, as we would predict stronger canalization of survival in 'slower' populations than in 'faster' populations, for example.

We show that weather variation may shape the population dynamics of amphibians, the most threatened group of vertebrates in the world. Evolutionary mechanisms such as environmental canalization may to some extent buffer demographic traits against climatic fluctuations in certain animal species. Nonetheless, our study emphasizes that local environmental variation may make demographic processes context dependent. This precludes any general assessment regarding the effect of climatic change on the viability of populations when studies focus only on data collected on a single population or few populations. This is not to suggest that the numerous studies based on reduced datasets that predict either negative or positive effects of climate change on population dynamics are wrong – simply that their results should be considered with caution. We strongly recommend further research based on surveys replicated in a substantial number of populations to account for context-dependent variation in demographic processes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Survey design and additional information regarding capture-recapture data in the five studied populations of *Bombina variegata*.
Table S2. Morphometric data supporting the consideration of three ontogenetic stages.
Table S3. Complete model selection procedure for the five studied populations of *Bombina variegata*.
Figure S1. Additional analyses supporting the consideration of three ontogenetic stages.

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POPULATION ECOLOGY - ORIGINAL RESEARCH

To breed or not to breed: past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian

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Abstract Iteroparity is an adaptive response to uncertainty in reproductive success. However, spreading reproductive success over multiple reproduction events during a lifetime is constrained by adult mortality and the stochasticity associated with interactions between external factors and physiological states. The acquisition of information about environmental conditions during the growth of progeny and sufficient resources during the non-reproductive period are key factors for breeding success. Consequently, we hypothesized that long-lived animals may skip a breeding opportunity when information about unfavourable environmental conditions is available. In addition, nutritional constraints could prevent an animal from replenishing its reserves sufficiently to invest in the current breeding period. We investigated these questions using capture–recapture data from a 5-year study on a large population of yellow-bellied toads in a forest in north-eastern France. We took advantage of various advances in multi-state capture–recapture models (e.g. unobservable states and mixture models) to test our hypotheses. Our results show that the combined effects of rainfall deficit and the breeding/non-breeding state of individuals during the past breeding season affect breeding probability during the following breeding opportunity. We also found that females breed less frequently than males, suggesting that the overall energy cost of reproduction differs between genders. Finally, the results indicate that toad survival appears to be negatively influenced by rainfall deficits. We discuss the yellow-bellied toad's reproductive behaviour in term of bet-hedging strategy and life history trait evolution.

Keywords Iteroparity · Survival · Skipped breeding · Amphibian · Multi-event models

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Introduction

Life history theory predicts that the lifetime schedule of resource allocation to maintenance, dispersal and reproduction is the result of interactions between three main selective forces: age-dependent mortality (Stearns 1992), uncertainty of reproductive success (Schaffer 1974; Bulmer 1985; Roff 1992) and resource availability (Pianka 1976). By increasing the contribution of the youngest individuals to the reproductive output of a population, adult mortality selects for semelparity (earlier maturation, smaller body size and high reproductive effort, driving the population toward a semelparous lifestyle). In contrast, uncertainty of reproductive success due to temporal environmental stochasticity (e.g. climate variation) selects for iteroparity (Roff 1992) and diversified bet-hedging (Wilbur and Rudolf 2006). In addition, resource availability during

the growth period [i.e. density dependence (Reznick et al. 1992)], density-dependent fertility (Wilbur and Rudolf 2006) or the cost of reproduction on adult survival (Orzack and Tuljapulkar 1989) can also influence the evolution of life history strategy. Repeating reproductive events over a lifespan involves trade-offs between current reproduction and survival (and therefore future reproduction) that are greatly influenced by current resource availability and mortality risk. Accordingly, a state-based approach to life history postulates that an organism's ability to survive and reproduce strongly depends on a combination of external factors and the animal's physiological state (McNamara and Houston 1996). The physiological state includes the level of protein and fat reserves, foraging skill, parasite load and the responsiveness of the immune system. Given these constraints, at each breeding opportunity, an iteroparous organism has to make a decision whether or not to breed (Bull and Shine 1979).

The ability to acquire information about the quality of the environment that will determine offspring growth and survival could contribute to the decision to skip breeding when breeding success is at risk. This process comes under the definition of 'predictive plasticity' (sensu Cooper and Kaplan 1982). Pianka (1976) stated that reproductive effort should vary inversely with residual reproductive values (expectation of future reproductive success). Such skipping behaviour has been highlighted in various animal groups [fish (Jørgensen et al. 2006; Rideout et al. 2005); amphibians (Whiteman 1997; Muths et al. 2010); birds (Jenouvrier et al. 2005); reptiles (Shine 2008)]. For example, female cod skip spawning when energy reserves are insufficient to initiate oocyte development (Skjaeraasena et al. 2012). Another pertinent example is the fat dormouse: adults skip breeding when the probability of progeny surviving their first winter is reduced by low food availability (e.g. low density of beech seeds) (Pilastro et al. 2003). The investment required for current reproduction could thus be economised by the organism and invested in future survival and breeding success. Additionally, acquiring information about external factors allows animals to safely decide to skip a reproduction opportunity when the breeder's own survival is threatened by stressful environmental conditions (e.g. extreme climatic variations). Some studies have highlighted a trade-off between a parent's future survival (subsequent reproductive opportunities) and investment in current reproduction (Williams 1966; Stearns 1992; Shaw and Levin 2011). Accordingly, breeders could safeguard their own survival probability by temporarily ceasing to breed at any stage (Warner 1998; Rideout et al. 2005). For example, adult fat dormice modulate their yearly breeding investment to increase longevity (Ruf et al. 2006).

Acquiring sufficient resources during the non-reproductive period to improve breeding success [capital breeding tactic, sensu Jönsson (1997)] could allow the organism to capitalize on available fat reserves for further reproduction. Conversely, food scarcity and low foraging efficiency could prevent the organism from storing sufficient reserves for breeding at the next opportunity, thus delaying breeding at the cost of being exposed to mortality risks for 1 more year (Lambert and Dutil 2000; Jenouvrier et al. 2003). A good example is the grey-headed albatross: poor diet and significant weight loss prevent incubating birds from breeding the following year (Prince et al. 1981). When the reproductive effort is particularly high, the physiological state over the following year may be below the critical threshold that determines the decision to breed (Sæther 1997; Coulson et al. 2001). Similarly, in Northeast Arctic cod, insufficient energy to initiate oocyte development seems to be the proximate cause for skipping spawning, suggesting that this behaviour may be partly a density-dependent response (Skjæraasena et al. 2012).

In this study, we examined how the combined effects of an external factor (specifically, rainwater levels at the end of winter, 4 months before breeding activity) and the individual's breeding/non-breeding state during the previous breeding season affect current breeding probability in amphibians. We carried out the study on the yellow-bellied toad (*Bombina variegata*), whose high longevity (Plytycz and Bigal 1993) makes it possible to space out reproductive effort over several years. It usually breeds in small and highly unstable water bodies (e.g. ruts, ditches or rocky pools) filled mainly with rainwater (Barandun and Reyer 1997; Cayuela et al. 2011, 2013). Water duration in these small water bodies is usually considered the most important determinant of reproductive success. Like many other amphibians, survival after metamorphosis is expected to be affected by transepidermal water loss, which becomes intense in dry conditions (Tracy 1976; Wardziak et al. 2013).

We used the data from a 5-year capture–mark–recapture (CMR) study of a large population of yellow-bellied toads and various advances in multi-state mark–recapture models (Kendall and Nichols 2002; Lebreton et al. 2009; Péron et al. 2010) to test the following hypotheses:

1. Breeding is facultative in a given year.
2. Toads more frequently skip breeding in the event of a rainwater deficit [defined by a lower amount of rainfall during the 4-month period preceding breeding activity; see Electronic supplementary material (ESM) 1].
3. Females are less prone to breed than males because of higher investment in reproduction (cost of oocyte production and the absence of male parental care).
4. Rainwater deficits negatively affect yellow-bellied toad survival.

Materials and methods

Study area, field sampling and identification of individuals

The study was conducted in a national forest in northeast France consisting of approximately 9,600 ha of deciduous and coniferous trees. Located near Verdun, this forest sits on the site of the largest and most devastated battlefield of the First World War, an area that was bombed heavily in 1916–1917 (2 million tons of ammunition were dropped during 10 months of fighting). Subsequently, spontaneous colonization and active planting reforested this battlefield. The average elevation is 320 m (range 190–389 m). The climate is continental with slight oceanic influences, characterized by cold winters and hot summers. During the 5-year study (2008–2012), monthly precipitation varied from less than 15 mm to 175 mm, with 2011 as the driest year (annual cumulative rainfall 750 mm) and 2008 as the wettest (1,015 mm). The precipitation data were collected in a weather station located within the study area (see ESM1). Rainfall during the pre-breeding period (January–April) was 155 mm in 2011 (minimum) versus 455 mm in 2008 (maximum).

In the study area, yellow-bellied toads breed in distinct networks of small water bodies that consist of a set of ruts, ditches and puddles (a given network can contain between two and 20 water bodies). We studied 64 of these breeding-site networks. The maximum distance between the water bodies within a network was less than 50 m, and adjacent networks were separated by more than 50 m.

The toads were surveyed using the capture–recapture method over a 5-year period (2008–2012). We caught the toads by hand or with a dip net during the sunny hours of the day (0900–1900 hours). Three capture sessions were carried out during the breeding season (males at calling places; females at egg-laying sites) in 2008, 2011 and 2012 (May, June and July), while four were carried out in 2009 and 2010 (May, June, July and August) because breeding was prolonged during these summers. We sampled each water body of the 64 networks at each session. The toads of a set of closed water bodies were caught and stored for measurements. Catching effort was performed in the water bodies several times, and stopped when no new individual was detected. The time required to achieve sampling the whole networks in a single session varied from 6 to 15 days, as toad abundance varies between months. We assumed that toads became sexually mature at 3 years old (Plytycz and Bigal 1993; Morand 1997), with a mean body length (snout–vent length) of 35 mm in males and 36 mm in females; smaller individuals were excluded from the analysis. We identified gender on the basis of strong forearms and the presence of nuptial pads in males (Kyriakopoulo-Sklavouno et al. 2012). We identified each individual by the specific pattern of black and yellow mottles on its belly, recorded by photographs. Multiple comparisons of patterns were performed using a robust computing tool to minimize misidentification errors (Hiby and Lovell 1990).

Multi-event capture–recapture models

We parameterized the robust design proposed by Kendall (1999) using a multi-event capture–recapture model (MECR). Robust design data types are normally made up of two nested levels of capture occasions. Several field sessions carried out over the same year are referred to as 'secondary sessions', and at this level the population is considered closed. Sampling sessions are also conducted over several successive years; the yearly sessions are referred to as 'primary periods', in which the population is considered open. Transitions between breeding/non-breeding states were assumed to obey a Markov chain process. During a primary period, we assumed that the state of an individual was fixed. Transitions between states were thus allowed between primary periods only.

Breeding toads were captured in aquatic sites that were exhaustively sampled three to four times per year. Non-breeding toads were not available for capture since, by definition, they were in terrestrial environments. Skipping breeding in a given year was thus equivalent to becoming a temporary emigrant and shifting to an unobservable state (Kendall and Nichols 2002; Fujiwara and Caswell 2002).

Heterogeneity of recapture, breeder/non-breeder transitions and survival probability were assessed using mixture models [i.e. heterogeneity-level states (Péron et al. 2010)]. We specified our states as conditional on first capture. From an initial departure state of *IS*, animals could be categorized with one of five distinct states: (1) toad was alive with an above-average probability of surviving and breeding (line 1 in state-transition matrices), (2) toad was alive with a below-average probability of surviving and breeding (line 2), (3) toad was alive with an above-average probability of surviving and skipped the current breeding opportunity with an above-average probability of skipping breeding (line 3), (4) toad was alive with a below-average probability of surviving and skipped the current breeding opportunity with a below-average probability of skipping breeding (line 4), and (5) toad was dead (line 5).

Four state transitions were possible for the survival probability between two primary periods (matrix labelled Φ; Table 1): ϕ^{b+} the probability that a toad with an above-average survival would survive, given it had bred (line 1); ϕ^{b-} the probability that a toad with a below-average survival would survive, given it had bred (line 2); ϕ^{nb+} the probability that a toad with an above-average survival would survive, given it had skipped breeding (line 4); ϕ^{nb-} the probability that a toad with a below-average survival

Table 1 Elementary matrices

Elementary matrix labelled Φ

$$\begin{bmatrix} \phi^{b+} & 0 & 0 & 0 & 1-\phi^{b+} \\ 0 & \phi^{b-} & 0 & 0 & 1-\phi^{b-} \\ 0 & 0 & \phi^{nb+} & 0 & 1-\phi^{nb+} \\ 0 & 0 & 0 & \phi^{nb-} & 1-\phi^{nb-} \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Elementary matrix labelled Y

$$\begin{bmatrix} 1-\gamma^{nb+} & 0 & \gamma^{nb+} & 0 & 0 \\ 0 & 1-\gamma^{nb-} & 0 & \gamma^{nb-} & 0 \\ \gamma^{b+} & 0 & 1-\gamma^{b+} & 0 & 0 \\ 0 & \gamma^{b-} & 0 & 1-\gamma^{b-} & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Elementary matrix labelled P

$$\begin{bmatrix} 1-\mathrm{p}^{b+} & \mathrm{p}^{b+} \\ 1-\mathrm{p}^{b-} & \mathrm{p}^{b-} \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \end{bmatrix}$$

State-state transitions regarding apparent survival are specified in the matrix labelled Φ. State-state transitions regarding breeder/non-breeder transitions are specified in the matrix labelled Y. Field observations are specified in the matrix labelled P. Symbols are defined in the "Multi-event capture–recapture models" section

would survive, given it had skipped breeding (line 4). Given that the parameters ϕ^{nb-} and ϕ^{nb+} were not identifiable, ϕ^{b-}/ϕ^{nb-} and ϕ^{b+}/ϕ^{nb+} were constrained to be equal in the model. Note that in a capture–recapture framework, survival estimates include both death and permanent emigration, i.e. apparent survival [see Schmidt et al. (2007) for an interesting discussion on this point in amphibians].

Four state transitions were possible (matrix labelled Y; Table 1) for breeder/non-breeder transitions between two primary periods: γ^{b+} the probability that a toad with an above-average probability of breeding bred at time t, given it skipped a breeding opportunity at $t-1$ (line 3); γ^{b-} the probability that a toad with a below-average probability of breeding bred at time t, given it skipped a breeding opportunity at $t-1$ (line 4); γ^{nb+} the probability that a toad with an above-average probability of skipping breeding skipped a breeding opportunity at time t, given it bred at $t-1$ (line 1); γ^{nb-} the probability that a toad with a below-average probability of skipping breeding skipped a breeding opportunity at time t, given it bred at $t-1$ (line 2).

To take into consideration the potential heterogeneity of recapture probability, two observation probabilities were possible (matrix labelled P; Table 1): p^{b+} the probability of being recaptured during a secondary session, given that the animal was highly likely to be recaptured (line 1); p^{b-} the probability of being recaptured during a secondary session given the animal was highly unlikely to be recaptured (line 2). Note that as non-breeding individuals were not available for recapture (see above), their recapture probability was fixed at 0.

Building biological scenarios with the E-SURGE program

We entered this parameterization into the E-SURGE program (Choquet et al. 2009), which has the advantage of using tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters. Competitive MECR models were ranked through a model-selection procedure using Akaike information criteria adjusted for a small sample size and their derivate quantities (QAICc) and QAICc relative weights (Burnham and Anderson 2002) (Table 2). We tested our hypotheses concerning recapture, initial state, and state–state transition probabilities from the general model [$\phi^{in}(D \times S)$, $\gamma^{b}(D \times S)$, $\gamma^{nb}(D \times S)$, $p(T \times H)$], including four covariates: rainwater levels (D), a group effect including two modalities (rainwater deficit for 2011 only since it was by far the driest year, normal rainwater level for the other years included in the 5-year study period); a group effect for gender-specific variation (S), inter-individual heterogeneity effect (H), time variation between capture sessions applied only to recapture probability (T). Complex interactions (i.e. $D \times S$, $T \times H$, $D \times H$, $T \times S$) between these factors were incorporated in this model.

From this general model, we first modelled field observation processes and tested whether recapture probability varied: (1) between capture sessions (T), (2) between genders (S), (3) depending on rainwater levels (D), and (4) according to inter-individual heterogeneity (H). For this last test, we specified that p^{b+} and p^{b-} differed. Then we tested whether initial state probability differed: (1) between genders (S), or (2) depending on rainwater levels (D). We then tested whether breeder/non-breeder transitions varied: (1) between genders (S), (2) and depending on rainwater levels (D), (3) according to inter-individual heterogeneity (H) or not. The parameters of each pair of transition probabilities, γ^{b+} and γ^{b-}, γ^{nb+} and γ^{nb-} were held to be different to test for the presence of inter-individual heterogeneity. Conversely, these transitions were constrained to be equal under the non-heterogeneity hypothesis. Note that the presence of heterogeneity was not simultaneously tested in breeder/non-breeder transitions and survival, since we aimed to examine the inter-individual heterogeneity of each independently. Finally, we tested (4) whether breeder/non-breeder transitions at the current breeding opportunity depended on the breeding state at the previous opportunity. This effect was incorporated in the model by specifying that state transitions follow a first-order Markovian process and that the parameters of each pair of transition probabilities, γ^{b+} and γ^{nb+}, $\gamma^{b-}$and γ^{nb-} were different. Conversely, transitions between states were

Table 2 Model-selection procedure

r	Model	Transition process	ΔQAICc	*w*	*np*
1	$IS\,(.), \phi^{b}\,(D), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p(H \times T)$	Markovian	0.00	0.78	43
2	$IS\,(.), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−4.58	0.08	46
4	$IS\,(D), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−5.78	0.04	47
5	$IS\,(S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−5.92	0.04	47
6	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−6.01	0.04	49
7	$IS\,(.), \phi^{b}\,(D \times S), \gamma^{b}\,(D), \gamma^{nb}\,(D), p\,(H \times T)$	Markovian	−8.56	0.04	45
8	$IS\,(.), \phi^{b}\,(S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−11.52	0.01	43
10	$IS\,(.), \phi^{b}\,(H \times D \times S), \gamma^{b}\,(H \times D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Markovian	−12.51	0.00	53
11	$IS\,(.), \phi^{b}\,(H \times D \times \mathrm{S}), \gamma^{b}\,(H \times D \times \mathrm{S}), \gamma^{nb}\,(H \times D \times \mathrm{S}), p\,(H \times T)$	Markovian	−13.60	0.00	49
12	$IS\,(.), \phi^{b}\,(D \times \mathrm{S}), \gamma^{b}\,(D \times \mathrm{S}), \gamma^{nb}\,(D \times \mathrm{S}), p(H \times T)$	Random	−22.92	0.00	45
13	$IS\,(.), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Random	−67.64	0.00	41
14	$IS\,(.), \phi^{b}(D \times S), \gamma^{b}\,(D), \gamma^{nb}\,(D), p\,(H \times T)$	Random	−67.78	0.00	39
16	$IS\,(.), \phi^{b}\,(S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Random	−71.11	0.00	39
17	$IS\,(.), \phi^{b}\,(D), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p(H \times T)$	Random	−80.94	0.00	39
18	$IS\,(.), \phi^{b}\,(H \times D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H \times T)$	Random	−92.94	0.00	46
19	$IS\,(.), \phi^{b}\,(D \times S), \gamma^{b}\,(S), \gamma^{nb}\,(S), p\,(H \times T)$	Markovian	−147.84	0.00	41
20	$IS\,(.), \phi^{b}(D \times S), \gamma^{b}\,(S), \gamma^{nb}\,(S), p\,(H \times T)$	Random	−160.74	0.00	40
21	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p(T \times S)$	Markovian	−200.55	0.00	45
22	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(T)$	Markovian	−211.13	0.00	29
23	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(H)$	Markovian	−307.75	0.00	19
24	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times \mathrm{S}), \gamma^{nb}\,(D \times \mathrm{S}), p\,(H \times \mathrm{S})$	Markovian	−311.08	0.00	21
25	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(.)$	Markovian	−444.41	0.00	15
26	$IS\,(D \times \mathrm{S}), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(S)$	Markovian	−446.01	0.00	14
27	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(D \times S)$	Markovian	−873.77	0.00	17
28	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(D)$	Markovian	−875.00	0.00	15
29	$IS\,(D \times S), \phi^{b}\,(D \times S), \gamma^{b}\,(D \times S), \gamma^{nb}\,(D \times S), p\,(D \times H)$	Markovian	−881.75	0.00	21

r Model rank, *QAICc* Akaike information criterion adapted to small samples and its derivate quantities, *w QAICc* weight, *np* number of model parameters. Model parameters vary between capture sessions (*T*), two classes of heterogeneity (*H*), gender (*S*), water levels (*D*) or are constant (.). For explanations of the other symbols, see the "Multi-event capture–recapture models" section

specified at random and were constrained to be equal. Finally, we tested whether survival probability varied: (1) between genders (*S*), (2) depending on water conditions (*D*), and (3) according to inter-individual heterogeneity (*H*). As breeding probabilities, the transitions ϕ^{b+} and ϕ^{b-} were held to be different when testing the presence of heterogeneity. In contrast, these transitions were held equal under the non-heterogeneity hypothesis.

Results

We captured 7,280 toads (3,878 females and 3,402 males) and identified 3,585 different individuals (1,988 females and 1,597 males). The number of captured individuals varied annually, ranging from 155 females in 2011 (following a rainwater deficit) to 628 in 2010, and from 175 males in 2011 to 626 in 2009. The number of captured individuals per secondary session ranged from 55 to 369 females and from 32 to 396 males. CMR data are summarized in the sex-specific M-array matrices (see ESM2).

Model selection and predictions

The best model retained after the selection procedure was [$IS(\mathrm{D} \times \mathrm{S})$, $\phi^{\mathrm{in}}(\mathrm{D})$, $\gamma^{\mathrm{in}}(\mathrm{D} \times \mathrm{S})$, $\gamma^{\mathrm{out}}(\mathrm{D} \times \mathrm{S})$, $p(\mathrm{H} \times \mathrm{T})$]. This included variation in recapture probability between capture sessions and between two classes of heterogeneity (p^{b+} and p^{b-}) (Fig. 1). Initial state probability was constant over time and between genders: 0.51 ± 0.05 [95 % confidence interval (CI) 0.41–0.60]. Apparent survival rate depended on rainwater levels, without any gender differences (Fig. 2). Indeed, apparent survival rates collapsed from 0.74 ± 0.02 (95 % CI 0.67–0.76) in conditions of normal rainwater levels to 0.52 ± 0.03 (95 % CI 0.45–0.59) in conditions of rainwater deficit. No inter-individual heterogeneity of apparent survival was detected. Transitions between breeding/non-breeding states, γ^{b} and γ^{nb}, were

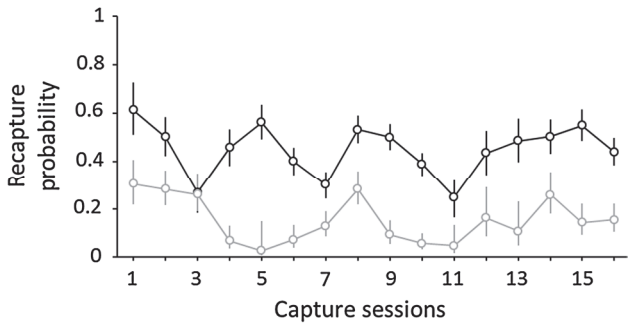

Fig. 1 Recapture probability of *Bombina variegata* fluctuates according to capture session and has two classes of heterogeneity ($n = 3{,}585$): high capture probability (*black lines*, *black circles*) and low capture probability (*grey lines*, *grey circles*); 95 % confidence intervals are shown as *error bars* around mean parameter estimates

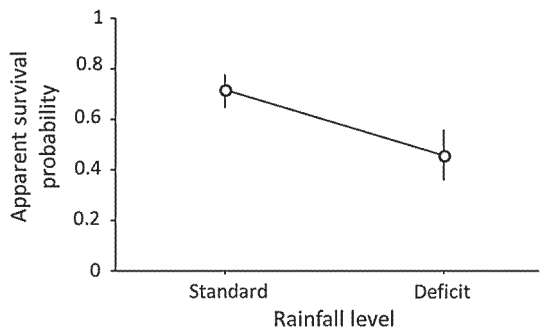

Fig. 2 Apparent survival probability ($n = 3{,}585$) fluctuates according to rainwater levels; 95 % confidence intervals are shown as *error bars* around mean parameter estimates

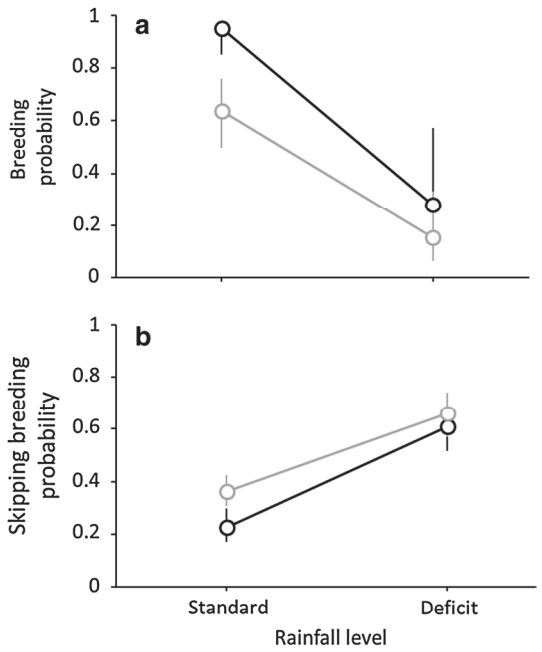

Fig. 3 Conditional breeding probability fluctuates according to gender and rainwater levels. Male ($n = 1{,}597$) breeding probability is shown as *black lines* and *black circles*, female ($n = 1{,}988$) breeding probability as *grey lines* and *grey circles*; 95 % confidence intervals are shown as *error bars* around mean parameter estimates. **a** Probability of breeding during the current breeding opportunity if the animal has skipped breeding at the previous opportunity. **b** Probability of skipping the current breeding opportunity if the animal bred at the previous opportunity

best modelled by a first-order Markovian transition, indicating that breeding probability for a given year depended on the breeding status of the previous year. After skipping a breeding opportunity, toads were more likely to breed at the next opportunity. Conversely, having bred at the previous breeding opportunity, toads were more likely to skip the following one. Transitions between breeding and non-breeding states were also affected by the interaction between gender and rainwater levels. Rainwater deficit negatively influenced breeding probability (Fig. 3). The probability of breeding after skipping the previous breeding opportunity was lower in conditions of poor water levels for both genders (Fig. 3a). In females γ^{b} declined significantly from 0.64 ± 0.07 (95 % CI 0.49–0.76) in conditions of normal rainwater levels, to 0.15 ± 0.07 (95 % CI 0.09–0.18) in conditions of rainwater deficit. In males γ^{b} also decreased from 0.95 ± 0.02 (95 % CI 0.85–0.97) to 0.28 ± 0.12 (95 % CI 0.10–0.57). Likewise, the probability of skipping the current breeding opportunity after having bred during the previous opportunity was higher in both genders when a rainwater deficit was recorded (Fig. 3b). In females γ^{nb} increased from 0.36 ± 0.03 (95 % CI 0.31–0.42) to 0.66 ± 0.04 (95 % CI 0.57–0.74), and in males γ^{nb} increased from 0.23 ± 0.03 (95 % CI 0.17–0.29) to 0.61 ± 0.05 (95 % CI 0.52–0.69).

Breeder/non-breeder transition probability also differed between genders. The probability of breeding after skipping a previous breeding opportunity was lower in females (0.64 ± 0.07, 95 % CI 0.49–0.76) than in males (0.95 ± 0.02, 95 % CI 0.85–0.97) in conditions of normal rainwater levels (Fig. 3a). However, we were not able to detect a gender-specific variation in breeding probability when there was a rainwater deficit, suggesting that both genders responded equally to the stresses of dry conditions. Likewise, we did not find any evidence of gender-specific differences in the probability of skipping breeding (Fig. 3b). Finally, we did not detect any significant inter-individual heterogeneity in breeder/non-breeder transition probability.

Discussion

Our findings suggest that reproduction in the yellow-bellied toad can be facultative and that the probability of transition

between breeding and non-breeding states varies between genders and is Markovian in pattern. Furthermore, the data support the idea that such variation is influenced by rainwater levels. Our findings also emphasize that apparent survival probability is negatively influenced by a rainwater deficit. The results did not indicate inter-individual heterogeneity in breeder/non-breeder transition probability or survival probability.

Recapture probability: time-specific variation and inter-individual heterogeneity

Recapture probability varied over sessions in the field and between two classes of inter-individual heterogeneity (animals highly likely to be recaptured and animals highly unlikely to be recaptured). For a long time, inter-individual heterogeneity of capture probability received considerable attention in the framework of mark–recapture studies since it biases the estimation of population size and survival, for example (Otis et al. 1978; Chao et al. 1992; Agresti 1994). Only recently it has been acknowledged that capture heterogeneity may provide relevant biological information, revealing hidden biological features (e.g. social structure) of wild populations (Crespin et al. 2008). In our study, heterogeneity in recapture probability may be due to differing habitat characteristics among ponds, influencing either capture effectiveness or the amount of time an individual spends in a pond in a given year (i.e. their availability for capture).

Rainwater deficit impacts apparent survival

The results of our study show that toad survival is impacted by rainwater deficit (Fig. 2), but without distinguishing the respective contributions of mortality and permanent emigration. Although this result could reflect the detrimental effect of stressful water conditions on toad survival, we were unable to draw a clear conclusion regarding this relationship. In both genders, survival could be negatively affected by a water deficit because dry conditions promote permanent emigration from the study area. This would be in line with previous studies on amphibians: for instance, one study suggests that pond desiccation during a dry year leads to a significant rise in newt movements (Kopecky et al. 2010). However, survival could also be affected by mortality induced by excessive water loss by evaporation through the skin (Tracy 1976; Wardziak et al. 2013). Severe dehydration has deleterious effects on many amphibian physiological systems, organs and tissues, affecting, for instance, an amphibian's capacity for muscle contraction, locomotion and aerobically supported activities (Hillman 1980, 1987). The same negative link between rain deficit and yellow-bellied toad survival has also been detected in two other populations in southern France (H. Cayuela, unpublished data). Finally, we did not detect any evidence of consistent inter-individual heterogeneity in apparent survival probability. To our knowledge, although inter-individual heterogeneity in survival probability has been explored in birds (Burnham and Rexstad 1993; Pledger and Schwarz 2002; Péron et al. 2010), our study is the first to address this issue in an amphibian species. It is therefore not possible to compare these data with those of other species or populations and to generalize this finding.

Rainwater deficit leads to facultative breeding

Our results suggest that the yellow-bellied toad avoids breeding when water conditions are not suitable for tadpole development, which is in line with the facultative breeding hypothesis. In amphibians, facultative breeding has been acknowledged (Bull and Shine 1979), although few studies have rigorously quantified yearly breeding frequency in individuals (Church et al. 2007; Grayson et al. 2011; Muths et al. 2006, 2010, 2013). Among these, some suggest that a water deficit at the beginning of the breeding season is an environmental indicator that allows amphibians to predict to some extent the water conditions that will prevail during larval growth. We assume that breeders 'make a choice' about when or whether to breed or not, which further affects tadpole development and survival probability, and ultimately their own fitness and that of their offspring. In the species studied here, this 'decision-making' flexibility is facilitated by certain characteristics of the reproductive cycle, particularly prolonged spermiation and the presence of post-vitellogenic follicles throughout the breeding activity period. These permit reproductive plasticity (Guarino et al. 1998), which enables the synchronization of oviposition with rainfall patterns (Barandun et al. 1997).

Gender and past breeding state influence current breeding decisions

Our results also indicate that breeding probability varies according to both the animal's state (breeder or non-breeder) during the previous year and to its gender (Fig. 3a, b). In conditions of suitable rainfall levels, females are more likely than males to skip a breeding opportunity after having bred at the previous opportunity. In addition, even after skipping a breeding opportunity, females are less likely to breed than males. This gender-specific pattern appears to be less marked during stressful water conditions, suggesting that water deficit affects both genders equally. These findings are in line with the state-based approach to life histories (McNamara and Houston 1996) which postulates that the decision of an organism to reproduce may depend on a combination of external factors and the

physiological state of the animal. This theory also suggests that males and females differ in their ability to recover from the breeding state, probably because the overall energy cost of sexual reproduction and the main elements of energy expenditure differ between genders. In females, this cost is related to internal sexual mechanisms (especially oogenesis), escaping unwanted sexual attention and possible injuries inflicted by males during attempts at amplexus. Such costs likely restrict female breeding frequency, a hypothesis supported by Beshkov and Jameson's findings (1980) showing that many yellow-bellied toad females bred only once (and more rarely twice) during their 3-year study. Finally, we did not find any evidence of consistent inter-individual heterogeneity of breeder/non-breeder transitions for either gender, suggesting relative inter-individual homogeneity in breeding and skipped breeding behaviour on an intra-population scale in this species. To our knowledge, this question has been only rarely addressed for vertebrates in general (e.g. Cam et al. 2002) or for amphibians. Future studies on amphibians are needed to clarify the role of inter-individual heterogeneity in demographic processes.

Coexistence of various forms of plasticity as a response to environmental stochasticity

As well as revealing that toads (particularly females) are unlikely to breed in consecutive years, our findings show that they also make strategic decisions over their lifetime about when to reproduce or not, especially when environmental conditions enhance the risks of reproductive failure. Such predictive plasticity is based on a consistent relationship between organism fitness and environmental cues. However, when unpredictable variations in the environment repeatedly affect the consistency of this link, natural selection may favour risk-spreading strategies (Crean and Marshall 2009). In the yellow-bellied toad, some data suggest that females exhibit egg-clutch fractionation during a breeding season, which specifically consists of dividing their egg capital into several clutches (up to seven) spread across different water bodies. This reproductive behaviour is considered as diversified bet-hedging, an adaptive response to the unpredictability of a water body's duration (Barandun et al. 1997; Buschmann 2002). These elements indicate that facultative breeding presumably coexists with spatial bet-hedging to balance the risk of larval mortality, enhanced by water level stochasticity. The surprisingly long lifespan of this small-sized toad [life expectancy, 11–14 years, longevity, 20 years; see Morand (1997) for a review] might be the common correlate of these two forms of plasticity. However, the co-evolutionary relationships between these fitness-related traits require further investigation to better understand life history evolution in species experiencing highly stochastic environments.

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Slow life history and rapid extreme flood: demographic mechanisms and their consequences on population viability in a threatened amphibian

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SUMMARY

1. In the Northern Hemisphere, an increase in both the frequency and magnitude of violent flooding events has been reported due to climate change. According to life history theory, one might postulate that in 'slow' species: (i) environmental canalisation may act as a selective force that minimises to some extent adult survival variations caused by catastrophic flood and (ii) extreme flooding events would cause important variations in recruitment and young survival. Hence, it may be hypothesised that (iii) the population growth rate of 'slow' species might be relatively insensitive to changes in the frequency of extreme climatic events if adult survival remains largely unaffected.

2. In this study, we investigated how extreme rainfall events resulting in severe flood impact population dynamics of a long-lived endangered amphibian, the yellow-bellied toad (*Bombina variegata*: Bombinatoridae). To address this issue, we used capture–recapture (CR) data collected on two populations (768 and 1154 individuals identified) in southern France and developed multi-event CR models.

3. Our results indicated that extreme flooding did not cause any variation in sub-adult or adult survival, whereas recruitment and juvenile survival were negatively impacted. Furthermore, our simulations indicated that the population growth rate was only marginally sensitive to potential changes in the frequency of extreme flooding in the future.

4. Hence, we suggest that extreme flooding does not appear to be a proximal factor of extinction risk for this endangered amphibian species.

Keywords: amphibian, *Bombina variegata*, flood, life history, multi-event capture–recapture model

Introduction

The global climate is changing. Long-term records indicate that global surface temperature has increased *c.* 0.2 °C per decade in the past 30 years (Hansen *et al.*, 2006). In addition, there has been an increase in minimum daily temperatures that is more significant than the increase in the maximum temperatures (Fyfe & Gillett, 2014). Global precipitation has also increased over the same period, as well as the frequency and magnitude of extreme climatic events (Alexander *et al.*, 2006). More specifically, an increased frequency of extreme rainfall events has been reported in the Northern Hemisphere, especially in Europe, where the number of days with heavy precipitation increased by 4% per decade in the period from 1936 to 1994 (Easterling *et al.*, 2000). In combination with landscape artificialisation (e.g. soil sealing, stream and rainwater channelisation), this has led to an increase in both the frequency and magnitude of violent flooding events (Wilby, Beven & Reynard, 2008), and climatic models suggest that the phenomenon could be intensified in the future (Dankers & Feyen,

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2008). Researchers have generally focussed their attention on the impact of mean changes in climatic factors on wild populations; only a few studies have examined the role of catastrophic climatic events such as extreme floods (Wilson & Peach, 2006; Tryjanowski, Sparks & Profus, 2009; Wuczyński & Jakubiec, 2013). The scarcity of sound demographic data recorded on animal populations in floodplains combined with the low frequency of extreme flooding makes studies of this type rare and difficult. However, investigating this issue is critical since it is likely that mean changes in climatic factors and variation in the frequency of extreme climate events have a different influence on population dynamics. Understanding the role of such events is a crucial challenge to optimise local and global wildlife conservation policies in the context of a changing climate (Heller & Zavaleta, 2009; Mawdsley, O'Malley & Ojima, 2009).

Extreme climate events may impact different demographic parameters of different wild populations (Wilson & Peach, 2006; Welbergen *et al.*, 2008; Moses, Frey & Roemer, 2012), suggesting that population susceptibility to these events may vary according to life history characteristics. In particular, one might expect that the sensitivity of the population growth rate to changes caused by catastrophic climate events on different demographic parameters differs among species according to their position along the 'fast–slow continuum' (*sensu* Sæther, 1987). This concept states that life history traits of species show covariation patterns that allow classifying them on a continuum from 'fast' to 'slow'. A slow life history is characterised by late reproduction, long generation time, long lifespan, large adult body size, large offspring size and low fecundity; a fast life history has the opposite characteristics. In age- or stage-structured life histories, similar changes in fitness component values on a proportional scale at different ages or ontogenetic stages generally have different effects on the population growth rate (Gaillard & Yoccoz, 2003). Accordingly, it has been demonstrated that while the rate of population growth of fast species is particularly sensitive to changes in recruitment, the rate of slow species is more susceptible to changes in adult survival (Gaillard, Festa-Bianchet & Yoccoz, 1998; Sæther & Bakke, 2000). According to environmental canalisation (or buffering) hypothesis (Gaillard & Yoccoz, 2003), life histories should evolve to minimise the effects of environmental variation on fitness by favouring traits that buffer important vital rates from temporal environmental variation, that is adult survival in slow species. This demographic mechanism has been acknowledged in reptiles (Miller *et al.*, 2011), birds (Jenouvrier, Barbraud & Weimerskirch, 2005; Rolland, Weimerskirch & Barbraud, 2010) and mammals (Owen-Smith & Mason, 2005; Rotella *et al.*, 2012). As a result, one might postulate that in long-lived species: (i) environmental canalisation may act as a selective force that minimises to some extent adult survival variations caused by catastrophic climatic events. In contrast, one might expect that; (ii) extreme climate events would cause important variations in recruitment and young survival. Therefore, it may be hypothesised that the population growth rate of slow species might be relatively insensitive to changes in the frequency of extreme climatic events if adult survival remains largely unaffected.

In this study, we investigated how extreme rainfall events resulting in severe flood impact population dynamics of long-lived endangered amphibian, the yellow-bellied toad (*Bombina variegata*). The recent extinction of this 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 (Lescure, Pichenot & Cochard, 2011), although the proximate causes (i.e. habitat loss and fragmentation or disease) often remain poorly documented (Canessa *et al.*, 2013; Cayuela *et al.*, 2015; Scheele *et al.*, 2015). Using capture–recapture (CR) data collected in two independent river catchments, we tested the hypotheses that: (i) survival probability would increase in line with each ontogenetic stage as is typical in slow species (Gaillard *et al.*, 1998); (ii) adult survival would be high, displaying only slight variations as postulated by Gaillard & Yoccoz (2003); (iii) since the breeding decisions of *B. variegata* adults usually result from a combination of internal factors and environmental cues (Cayuela *et al.*, 2014), breeding would be facultative and breeding propensity would depend on individual's past breeding status and (iv) recruitment would be low and widely variable since phenotypic traits related to recruitment are not expected to experience a canalisation process in slow species (Gaillard & Yoccoz, 2003). Next, we examined the influence of extreme flooding on both survival and recruitment and more specifically hypothesised that (v) adult survival would not be affected by extreme flooding, due to the selective forces resulting from the environmental canalisation process. In contrast, we hypothesised that (vi) recruitment and juvenile survival would be negatively influenced by extreme flooding. Finally, we used the demographic parameters estimated by our CR models to build stochastic matrix population models (Caswell, 2001) to assess the sensitivity of the population growth rate to changes in the frequency of extreme flood events. We postulated that the

population growth rate should be only marginally susceptible to variation in the frequency of extreme floods.

Methods

Biological model

B. variegata is a species with long-lived adults: some individuals reach more than 20 years in age in natural conditions (Dino, Milesi & Di Cerbo, 2010) and can live up to 30 years in captivity (Smirina, 1994). Compared to other pond-breeding anurans, they also have low reproductive outputs, that is around 120 eggs per female per year (Morand, 1997) in contrast to 250–25 000 eggs for bufonids and ranids. This slow life history allows *B. variegata* to breed in highly stochastic environments (Morand, 1997; Cayuela *et al.*, 2015) consisting of small temporary waterbodies (e.g. ruts, ditches or rocky pools). In the southern part of its range in France, populations breed and hibernate in the vicinity of torrential river channels (Cayuela, Cheylan & Joly, 2011; Cayuela, Besnard & Joly, 2013). In these rivers, seasonal variations in discharge result from the typically Mediterranean rainfall regime, which includes short bursts of violent rainfall and long dry periods. Heavy precipitation sometimes leads to extreme flooding (so-called *Cévénol* events; see Ducrocq *et al.*, 2008), and climatic models suggest that the frequency and magnitude of these events could be drastically intensified in the future (Sánchez *et al.*, 2004).

Study area and field sampling

The study was carried out on two yellow-bellied toad (*B. variegata*) populations in the Ardèche department of southern France. Both populations were located along rivers with seasonally torrential regimes. The first population was located in 'La Bourge' (POP1), and the second in 'La Gluèyre' (POP2) (Fig. 1). This species breeds and hibernates in the vicinity of archipelagoes of ponds (Fig. 2). The rivers are located in two independent river catchments (the Ardèche River and the Eyrieux River, respectively, both of which are tributaries of the Rhône River) separated by a distance of 25 km. These rivers experience marked variations in discharge; for instance, the Gluèyre River exhibits a discharge pattern with flow maxima in November–January (3.68 m^3 s^{-1}) and flow minima in July–August (0.37 m^3 s^{-1}). In standard years from 2010 to 2012, the water level during the November–January period ranged from 0.30 m (November 2010) to 2.20 m (November 2011) (Fig. 2). In December 2013, cumulative rainfall has been one and a half times higher than normal levels reported over the reference period 1981–2010 – cumulative rainfall locally exceeded 750 mm.

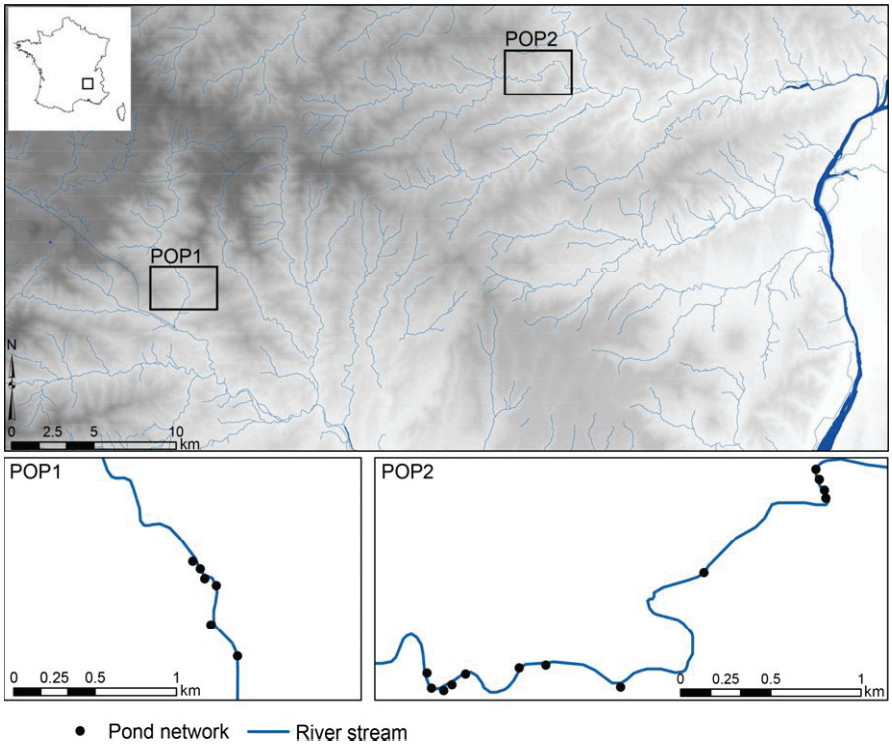

Fig. 1 Location of the two studied populations of *Bombina variegata* sampled from 2010 to 2014 in the Ardèche department in France in two independent river catchments to the west of the Rhône River. The two populations breed and hibernate in the close vicinity of pond networks along the river channel.

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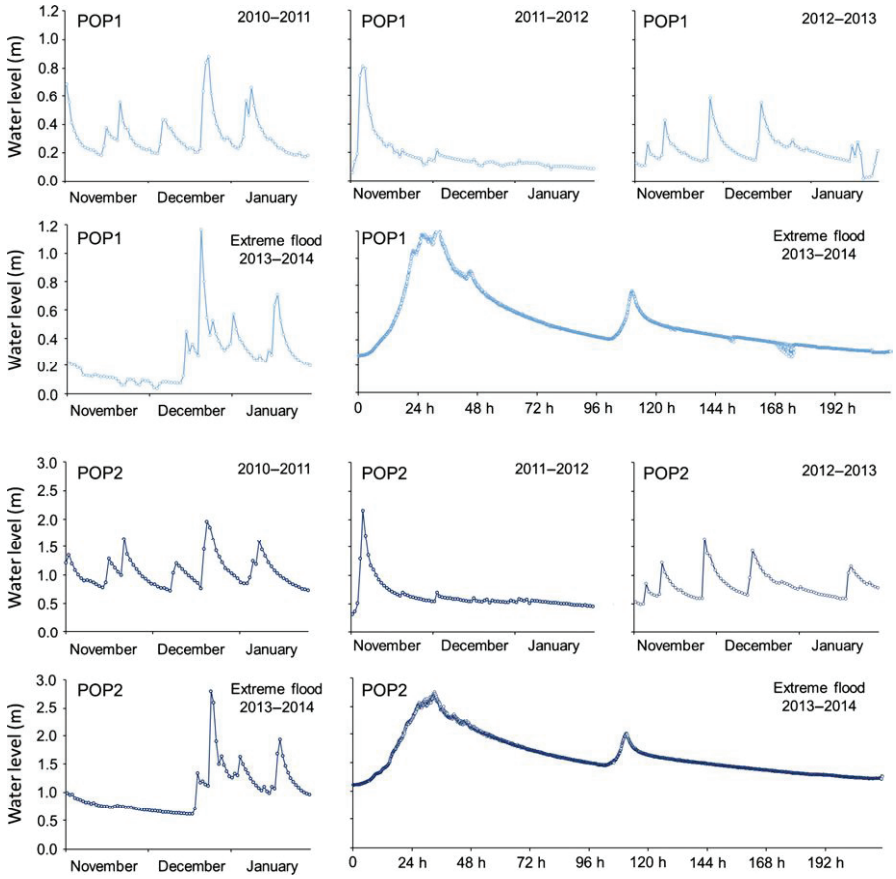

Fig. 2 Stream water levels recorded in the Bourge River (POP1) and the Gluyère River (POP2) during *Bombina variegata* hibernation (November–January) from 2010 to 2014: daily records of 'standard' water levels (2010–2011, 2011–2012, 2012–2013) and during extreme flooding (2013–2014); 5-minute records of stream water levels during the extreme flood event (December 24–31, 2013).

Both rivers experienced a 50-year flood, with water levels increasing from 0.30 to 1.20 m in POP1 and from 1.10 to 2.80 m in POP2 within 2 days (Fig. 2). The extreme flood lasted 5 days, from 24 December to 29 December, reaching a maximum on 25 December (Fig. 2).

The toads were intensively surveyed using the CR method over a 5-year period (from spring 2010 to spring 2014). The toads were caught by hand or with a dip net during the sunlight hours (09:00–19:00) of the species' breeding season. Each year, between six and nine capture sessions were carried out in late April, May and June. At each capture session, we sampled each network of waterbodies located along the surveyed river segment (Fig. 1), catching any toads and storing them for measurement. The time required to sample the whole river segment in a single session varied from 3 to 4 days.

We considered three ontogenetic stages: juveniles (captured after their first overwintering), sub-adults (captured after their second overwintering) and sexually mature adults (captured after at least three overwinterings). The size (snout–vent length) of juveniles ranged from 22 to 29 mm, and of sub-adults from 30 to 34 mm. We assumed that individuals became sexually mature at the age of three (Plytycz & Bigaj, 1993; Morand, 1997), with a mean body length of 35 mm in males and 36 mm in females. In sexually mature individuals, we identified gender on the basis of larger forearm size and the presence of nuptial pads in males (Kyriakopoulou-Sklavounou, Papaevangelou & Kladisios, 2012). We identified each individual by the specific black and yellow mottled pattern on its belly, which was recorded in photographs. To minimise misidentification errors, multiple comparisons of individual patterns were performed using the pattern-matching software Extract Compare (Hiby & Lovell, 1990).

Designing the multi-event model

The CR data were modelled using a reparameterised version of the robust design proposed by Cayuela *et al.* (2014). The model followed the typical structure of the 'classic' robust design (Nichols *et al.*, 1994; Kendall, Nichols & Hines, 1997), which is made up of two nested levels of capture occasions. 'Secondary sessions' encompass several field sessions performed over the same year. Sampling sessions were also conducted over successive years. 'Primary periods' correspond to yearly sessions. During a primary period (i.e. between sec-

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ondary sessions), we assumed that the state of an individual was fixed and transitions between states were thus allowed between primary periods only.

The model was conditional on the first capture occasion and an 'unborn individual' state was included, which allowed modelling the probability that an individual that had been observed in the population recruited as a juvenile between two primary occasions. After being recruited, individuals could successively move between three ontogenetic stages, that is juvenile, sub-adult and sexually mature adult, given that they survived. As usual in a CR framework, survival estimates include both death and permanent emigration, that is apparent survival (for an interesting discussion on this point in amphibians, see Schmidt, Schaub & Steinfartz, 2007). When an individual was sexually mature, we assumed that it could breed or skip breeding each year (Cayuela *et al.*, 2014). Since individuals were captured only in aquatic breeding sites, non-breeder toads were considered as not available for capture. Skipping breeding in a given year was thus equivalent to becoming a temporary emigrant and shifting to an unobservable state (Kendall & Nichols, 2002). In the model, transitions between breeding and non-breeding states were assumed to obey a Markov chain process.

Because sex identification was not possible for juveniles and sub-adults, we used a multi-event CR (Pradel, 2005) approach to model the uncertainty in sex assignment, and sex was thus coded as a state instead of as a group as is usual in CR data modelling. From an initial departure state of IS (initial state), individuals could be categorised as one of eleven distinct states: unborn male (UM), unborn female (UF), live juvenile male (JM), live juvenile female (JF), live sub-adult male (SM), live sub-adult female (SF), live sexually mature breeding male (BM), live sexually mature breeding female (BF), live sexually mature non-breeding male (NBM), live sexually mature non-breeding female (NBF) and dead individual (†).

Ten state transitions were possible for recruitment and age transition probability between two primary periods (matrix A; Table 1): α^{JM} is the probability that a newly metamorphosed male would be recruited (line 1); and α^{JF} is the probability that a newly metamorphosed female would be recruited (line 2). Given that we examined recruitment without accounting for gender dependency, α^{JM}/α^{JF} were constrained to be equal (the parameter is hereafter referred to as α). Age transition probabilities $\beta^{JM}/\beta^{JF}/\beta^{SM}/\beta^{SF}$ were fixed at 0 between secondary sessions and were fixed at 1 between primary periods.

Ten state transitions were possible for the survival probability between two primary periods (matrix Φ; Table 1): ϕ^{JM} is the probability that a juvenile male would survive (line 3); ϕ^{JF} the probability that a juvenile female would survive (line 4); ϕ^{SM} the probability that a sub-adult male would survive (line 5); ϕ^{SF} the probability that a sub-adult female would survive (line 6); ϕ^{BM} the probability that a sexually mature male would survive, given it has bred (line 7); ϕ^{BF} the probability that a sexually mature female would survive, given it has bred (line 8); ϕ^{BNM} the probability that a sexually mature male would survive, given it has skipped breeding (line 9); and ϕ^{BNF} the probability that a sexually mature female would survive, given it has skipped breeding (line 10). Given that the parameters ϕ^{BNM} and ϕ^{BNF} were not identifiable, ϕ^{BM}/ϕ^{BNM} and ϕ^{BF}/ϕ^{BNF} were constrained to be equal in the model. Survival transition probabilities were fixed at 1 between secondary sessions.

Four state transitions were possible for breeder–non-breeder transitions between two primary periods (matrix Y; Table 1): γ^{BM} is the probability that a sexually mature male bred at time t, given it had bred at $t-1$ (line 7); γ^{BF} the probability that a sexually mature female bred at time t, given it had bred at $t-1$ (line 8); γ^{NBM} the probability that a sexually mature male skipped a breeding opportunity at time t, given it had skipped breeding at $t-1$ (line 9); and γ^{NBF} the probability that a sexually mature female skipped a breeding opportunity at time t, given it had skipped breeding at $t-1$ (line 10). The transition probabilities γ^{BM}/γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$ were fixed at 1 between secondary sessions.

Concerning field observation, that is events *sensu* multi-event modelling formulation, six observation probabilities were considered (matrix P; Table 2): p^{JM} referred to the probability that a juvenile male was recaptured during a secondary session and was observed as a juvenile (sex unidentified in the field); p^{JF} the probability that a juvenile female was recaptured during a secondary session and was observed as a juvenile (sex unidentified in the field); p^{SM} the probability that a sub-adult male was recaptured during a secondary session and observed as a sub-adult (sex unidentified in the field); p^{SF} the probability that a sub-adult female was recaptured during a secondary session and observed as a sub-adult (sex unidentified in the field); p^{BM} the probability that a sexually mature male (sex identified in the field) was recaptured during a secondary session; and p^{BF} the probability that a sexually mature female (sex identified in the field) was recaptured during a secondary session.

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Table 1 Elementary matrices for state–state transitions

Elementary matrix A: recruitment–ontogenetic stage transitions

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

Elementary matrix Φ: survival transitions

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

Elementary matrix γ: breeder–non-breeder transitions

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

Note that as non-breeding individuals were not available for recapture (only breeding sites were sampled), their recapture probability was fixed at 0.

Building biological scenarios in E-SURGE

The parameterisation described was implemented in the E-SURGE program (Choquet *et al.*, 2009), which provides robust tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters. Competitive models were ranked through a model-selection procedure using Akaike information criteria adjusted for a small sample size and their derivate quantities (QAICc) and QAICc relative weights (Burnham & Anderson, 2002).

We tested our hypotheses concerning recapture and state transition probabilities using the general model [α (POP × YEAR), ϕ(POP × FLOOD × AGE), γ(POP × SEX), *p*(YEAR + AGE + SEX)]. The influence of an extreme flooding event (FLOOD) on survival probability was tested by incorporating a time effect in the model; that is, the state transitions between the primary periods 2013–2014 were specified as different from the others. The variation in survival between ontogenetic stages (AGE) was tested by specifying state transition differences between the three stages coded as states in the model. In addition, gender-dependent variation (SEX) in breeding probability was tested by considering state transition differences between genders coded as states in the model. Population-dependent variation in recruitment, survival and breeding probability was tested by adding a group effect (POP). Initial-state probability (IS) was held to be different between ontogenetic stages and gender as well as distinct between populations. Furthermore, recruit-

Table 2 Elementary matrix P: field observations (NS = not captured; JC = captured juvenile; SC = captured sub-adult; MC = captured sexually mature male; MF = captured sexually mature female)

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

ment probability α was held to differ among years (YEAR) and between populations (POP).

From this general model, we successively modelled field observation probability, breeding probability and survival probability. We used a backward stepwise procedure by removing the effects one by one and retained the best linear combination at each step. First, we tested whether recapture probability p varied: (i) among years (YEAR) and (ii) between ontogenetic stages (AGE) and genders in sexually mature adults (SEX). For the last hypothesis, p^{JM}/p^{JF}, p^{SM}/p^{SF} and p^{BM}/p^{BF} were held to be different. Next, we tested whether breeder–non-breeder transitions γ varied: (i) between populations (POP) and (ii) between genders (SEX). For this last hypothesis, the pair of transitions were held to be different γ^{BM} / γ^{BF} and $\gamma^{NBM}/\gamma^{NBF}$. We then tested whether survival probability ϕ differed: (i) between populations (POP); (ii) depending on an extreme flood event (FLOOD) and (iii) between ontogenetic stages (AGE). For the third hypothesis, ϕ^{JM}/ϕ^{JF}, ϕ^{SM}/ϕ^{SF} and ϕ^{BM}/ϕ^{BF} were constrained to be equal.

From the best-supported model, we derived the number of recruited juvenile females at t per breeding female at $t-1$ per year 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.

Simulating stochastic growth rate

We built a three-age-class, female-dominant and pre-breeding Leslie matrix (juveniles, sub-adults, adults; see Table 3) (Caswell, 2001) using the survival probability from the previous CR data analysis. Fecundity was possible only for adult individuals and consisted of the recruitment estimations (number of recruited juvenile females at t per breeding female at $t-1$) multiplied by the female breeding proportion. Female breeding proportion was obtained using the stable stage distribution of a two-stage matrix (breeding and non-breeding females) with transitions between states estimated in the CR data modelling step.

Table 3 Female-dominant pre-breeding Leslie matrix for *Bombina variegata* with three age classes (juvenile, sub-adult and adult): S_1 is the survival of juveniles, S_2 the survival of sub-adults and S_3 the survival of adults; F is the number of recruited females per breeding female (BF); and BP is the proportion of BFs

$$\begin{pmatrix} 0 & 0 & F*\mathrm{BP} \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{pmatrix}$$

As we were interested in the impact of flood frequency on the population dynamic, we built stochastic projections based on two matrices: one based on the demographic parameter estimates of 'standard' years and one based on the demographic parameters of 'flooding' years. The frequency of flood events was then increased from 1/200 years to 1/10 years. We simulated 1000 population trajectories over 10 000 years (k) using the stochastic process and calculated for each simulation 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.

Results

In POP1, we captured 7827 toads (3630 males, 1659 females, 1184 sub-adults and 1354 juveniles) and identified 768 individuals (328 males, 237 females, 73 sub-adults and 130 juveniles; state at last capture). In POP2, we captured 12 262 toads (5021 males, 3552 females, 1499 sub-adults and 2190 juveniles) and identified 1154 individuals (440 males, 377 females, 145 sub-adults and 192 juveniles; state at last capture). Details of the number of captures carried out each year are provided in Table 4.

Model selection and predictions

The model-selection procedure is provided in Table 5. The best-supported model [α (POP × FLOOD), ϕ (POP × FLOOD × AGE), γ(SEX), p(TIME + AGE + SEX)] (deviance = 55124.30, QAICc = 55196.45, QAICc

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Table 4 The number of identified animals and the recapture probabilities during secondary sessions (with standard errors) per ontogenetic stage and per gender during the study period (2010–2014) in two populations of *Bombina variegata* (POP1 and POP2) in France

	Number of identified animals					Recapture probability				
	2010	2011	2012	2013	2014	2010	2011	2012	2013	2014
POP1										
Juvenile	145	36	60	82	31	0.69 ± 0.01	0.63 ± 0.01	0.69 ± 0.01	0.63 ± 0.01	0.61 ± 0.01
Sub-adult	8	132	35	55	52	0.57 ± 0.01	0.50 ± 0.01	0.57 ± 0.01	0.51 ± 0.01	0.48 ± 0.01
Female	109	94	109	110	139	0.66 ± 0.01	0.60 ± 0.01	0.66 ± 0.01	0.60 ± 0.01	0.58 ± 0.01
Male	155	150	177	186	221	0.54 ± 0.01	0.50 ± 0.01	0.57 ± 0.01	0.51 ± 0.01	0.48 ± 0.01
POP2										
Juvenile	154	52	235	56	14	0.69 ± 0.01	0.63 ± 0.01	0.69 ± 0.01	0.63 ± 0.01	0.61 ± 0.01
Sub-adult	62	124	53	177	42	0.57 ± 0.01	0.50 ± 0.01	0.57 ± 0.01	0.51 ± 0.01	0.48 ± 0.01
Female	200	174	197	170	190	0.66 ± 0.01	0.60 ± 0.01	0.66 ± 0.01	0.60 ± 0.01	0.58 ± 0.01
Male	236	214	241	214	248	0.54 ± 0.01	0.50 ± 0.01	0.57 ± 0.01	0.51 ± 0.01	0.48 ± 0.01

relative weight = 0.91) indicated that recapture probability p varied among years and between gender and ontogenetic stages (Table 4). Survival probability differed between ontogenetic stages and was slightly lower in POP2 (time-constant estimates): in POP1, 0.67 (95% CI 0.62–0.73) for juveniles, 0.84 (95% CI 0.79–0.89) for sub-adults and 0.86 (95% CI 0.82–0.89) for adults; and in POP2, 0.64 (95% CI 0.59–0.68) for juveniles, 0.75 (95% CI 0.70–0.79) for sub-adults and 0.80 (95% CI 0.77–0.83) for adults. Extreme flooding negatively influenced juvenile survival in both populations (Fig. 3a & d). In contrast, the survival of sub-adults and adults remained unchanged (Fig. 3a & d). The model also indicated that breeding probability slightly depended on past breeding status and varied between genders but not between populations. The probability of breeding during two consecutive years was 0.92 for males (95% CI 0.90–0.94) and 0.87 for females (95% CI 0.82–0.90). The probability of skipping breeding during two consecutive years was 0.31 (95% CI 0.16–0.51) for males and 0.58 for females (95% CI 0.40–0.71). Derived from the parameters provided by the best-supported model, the number of recruited females per female and per year widely varied between year: in POP1, from 0.31 (95% CI 0.31–0.32) in 2013 to 0.88 (95% CI 0.86–0.90) in 2012; and in POP2, from 0.10 (95% CI 0.10–0.10) in 2013 to 1.45 (95% CI 1.45–1.46) in 2011. The number of recruited individuals decreased when both populations experienced an extreme flood event (Fig. 3b & e).

Population growth simulations

Stochastic matrix models indicated that population growth rate λ exceeded 1 in POP1 although it was slightly lower than 1 in POP2. Population growth rate displayed very marginal sensitivity to variations in extreme flood frequency (Fig. 3c & f). In POP1, the rate of population growth did not significantly differ (λ = 1.03, 95% CI 1.03–1.03) between the most pessimistic scenario (one extreme flood per decade) and the most optimistic (one extreme flood every two centuries) (1.03, 95% CI 1.03–1.04). In POP2, the rate of population growth marginally increased from 0.96 (95% CI 0.96–0.97) in the most pessimistic scenario to 0.98 (95% CI 0.98–0.98) in the most optimistic.

Table 5 Models to test our assumption concerning *Bombina variegata* vital rate variation in two populations in France

	Model definition						
r	Survival	Breeding	Recruitment	Recapture	*k*	Dev.	QAICc
1	AGE × POP × FLOOD	SEX	YEAR × POP	YEAR + AGE + SEX	36	55124.30	55196.45
2	AGE × POP × FLOOD	SEX × POP	YEAR × POP	YEAR + AGE + SEX	40	55122.62	55202.79
3	AGE × POP × FLOOD	POP	YEAR × POP	YEAR + AGE + SEX	36	55131.28	55203.42
4	AGE × FLOOD	SEX × POP	YEAR × POP	YEAR + AGE + SEX	34	55157.33	55225.46
5	AGE × POP	SEX × POP	YEAR × POP	YEAR + AGE + SEX	34	55174.62	55242.75
6	AGE × POP × FLOOD	SEX × POP	YEAR × POP	AGE + SEX	37	55188.99	55263.14
7	AGE × POP × FLOOD	SEX × POP	YEAR × POP	YEAR	37	55367.41	55441.56
8	POP × FLOOD	SEX × POP	YEAR × POP	YEAR + AGE + SEX	32	55254.64	55318.75

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, sub-adult, adult); POP = variation between populations; FLOOD = flood effect; YEAR = variation between years.

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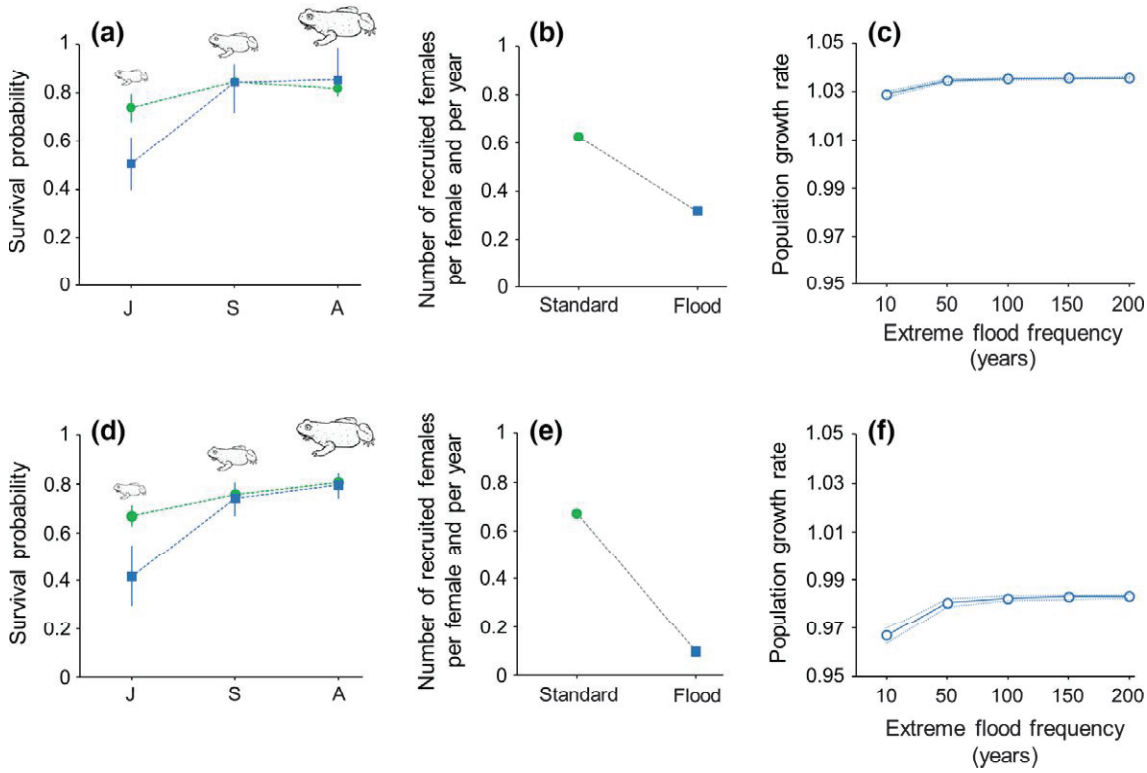

Fig. 3 Predictions provided by the best-supported multi-event capture–recapture model (see Table 3) concerning flood impact on survival (mean estimates and 95% CI) in two populations (POP1 and POP2) of *Bombina variegata* surveyed between 2010 and 2014 in France: (a) Survival at three ontogenetic stages (J = juvenile; S = sub-adult; and A = adult) in standard conditions (circle) and extreme flood conditions (square) in POP1; (b) Estimates derived from the bootstrapping method of the number of recruited females per female and per year in POP1 [the 95% CIs are not shown due to their narrowness: in standard conditions (0.62–0.63) and extreme flood conditions (0.31–0.32)]; (c) Sensitivity of the population growth rate as a function of the frequency of extreme flooding in POP1: mean prediction (full line) and 95% CI (dotted line); (d) Survival at three ontogenetic stages (J = juvenile; S = sub-adult; and A = adult) in standard conditions (circle) and extreme flood conditions (square) in POP2; (e) Estimates derived from the bootstrapping method of the number of recruited females per female and per year in POP2 [the 95% CIs are not shown due to their narrowness: in standard conditions (0.67–0.67) and in extreme flood conditions (0.10–0.10)]; and (f) Sensitivity of the population growth rate as a function of the frequency of extreme flooding in POP2: mean prediction (full line) and 95% CI (dotted line).

Discussion

Our findings validated our hypotheses concerning the influence of extreme flooding on the population dynamics of a slow amphibian species. As predicted by the environmental canalisation paradigm, extreme flooding did not cause variation in sub-adult or adult survival. In contrast, recruitment and juvenile survival were negatively influenced by extreme flooding. Our simulations indicated that the population growth rate was only marginally sensitive to potential changes in extreme flood frequency.

High survival, facultative breeding and low recruitment

Our results indicate that survival differs between ontogenetic stages and that the survival rate increases with age. This is in accordance with previous studies suggesting that post-metamorphosis survival is positively correlated with age and size in vertebrates (Stearns, 1992), and especially in amphibians (Altwegg & Reyer, 2003; Schmidt, Hödl & Schaub, 2012). In the latter, larger and older individuals outperform smaller and younger ones in osmoregulation and hydroregulation performance (Wells, 2010), which decreases mortality risks and the cost of biological functions such as dispersal. The survival estimates for adults in our study (POP1, $\phi = 0.86$; POP2, $\phi = 0.80$) are congruent with those found in previous studies ($\phi = 0.80$ in Plytycz & Bigaj, 1993; $\phi = 0.74$ in Cayuela *et al.*, 2014). Compared to most anurans, the survival rates and longevity (Smirina, 1994) recorded for *B. variegata* are high when corrected for size (see the HAGR website: http://genomics.senescence.info). This likely results, at least to some extent,

from antipredator and antimicrobial strategies; specific and unique families of antimicrobial peptides in the skin secretions of bombinatorids protect them against the invasion of pathogenic microorganisms and also play a role in protecting the toad from ingestion by predators (Conlon, 2011; König & Bininda-Emonds, 2011).

In sexually mature individuals of both populations, breeding is facultative and breeding propensity slightly varies between genders and depends on the past reproductive status of the individual, confirming the results of a recent study on another population of this species (Cayuela *et al.*, 2014) and observations made for other amphibians (Church *et al.*, 2007; Muths, Scherer & Lambert, 2010) and vertebrates (Stearns, 1992). Males and females differ in their capacity to recover from a reproductive physiological state (including fat and lipid reserves), probably because the energy cost related to internal sexual mechanisms (especially oogenesis) differs between genders, a hypothesis that is supported by the findings of Cayuela *et al.* (2014) in *B. variegata*. Recruitment widely fluctuated among years (from 0.10 to 1.50 recruited females per female and per year), suggesting high variation in reproductive success. In addition to the impact of flooding, this likely results from high mortality rates during larval growth due to the unpredictability of the hydroperiod in oviposition sites; only up to 10% of larvae successfully reach metamorphosis (Morand, 1997).

Extreme flood events cause crashes in recruitment and juvenile survival

Although extreme flooding did not cause variation in either adult or sub-adult survival, it negatively influenced both juvenile survival and recruitment. These results are in line with the prediction of the environmental canalisation paradigm stating that phenotypic traits related to adult survival experience canalisation for fitness components whose variation has the highest demographic impact on fitness in slow species. In amphibians, increased body size (and therefore age) promotes acute locomotor performance (Wilson, Franklin & James, 2000). As newly metamorphosed and young individuals usually display low post-natal dispersal abilities (Pittman, Osbourn & Semlitsch, 2014), their ability to reach and detect high-quality terrestrial refugia is reduced, which may have a detrimental influence on both recruitment and juvenile survival when extreme flooding occurs during overwintering. In a study on stream-dwelling salamanders, a higher volume and frequency of spring and autumn floods were not found to cause variation in adult survival and fecundity but did show a drop in recruitment due to increased mortality in metamorphosing individuals (Lowe, 2012). Our results, as well as Lowe's findings, suggest that newly metamorphosed and young individuals may be unable to develop the flood-avoidance strategies used by older individuals. Studies have shown that prolonged environmental stressors (e.g. habitat fragmentation) could promote the rapid evolution of dispersal syndrome (behavioural and morphologic adaptations reinforcing the performance of the dispersing phenotype; see Clobert *et al.*, 2012) enhancing the post-natal dispersal abilities of toadlets (Janin, Léna & Joly, 2012). However, the selective mechanisms reinforcing phenotypic traits (e.g. boldness, exploration behaviour, hind leg length) that optimise the ability of juveniles to reach and detect good terrestrial refugia could be constrained by the current low frequency of extreme flood events and the cost of developing such abilities.

Population growth rate sensitivity to changes in frequency of extreme flood events

In both the toad populations in our study, our simulations suggest that the population growth rate is only marginally sensitive to changes in extreme flood frequency. These findings fit our expectation that the population viability of slow species is unaffected by extreme flood events when adult survival remains unchanged. In the most pessimistic scenario, even if the population experienced one extreme flood per decade, recruitment and juvenile survival should be too marginally affected to have a significant influence on the population growth rate because of their low demographic impact on fitness. Our findings, as well as those published by Tryjanowski *et al.* (2009) in birds and by Wuczyński & Jakubiec (2013) in mammals, suggest that extreme flooding should not appear to be a proximal factor in extinction risk for slow species. However, multiple stressors (e.g. extreme drought, habitat alteration or disease) could potentially interact with more frequent catastrophic flooding events to have combined critical effects on population viability. Projections provided by climate envelop modelling approaches also suggest that a combination of land use changes and variations in several climatic components may lead to local extinctions and subsequent shifts in species distribution boundaries (e.g. Jetz, Wilcove & Dobson, 2007).

Most studies of the influence of climate change on population viability focus on the impact of mean and progressive modifications in climate. The consequences

of changes in climate fluctuation patterns on variations in life history traits remain poorly documented. Despite their apparent severity, extreme climate events may have a varying impact on the vital rates of wild populations according to the species' life history characteristics. Due to the scarcity of studies investigating this issue, we strongly encourage future research of the interacting effects of the changing frequency of catastrophic climate events alongside additional stressors on vital rate variation and population persistence.

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The impact of severe drought on survival, fecundity, and population persistence in an endangered amphibian

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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

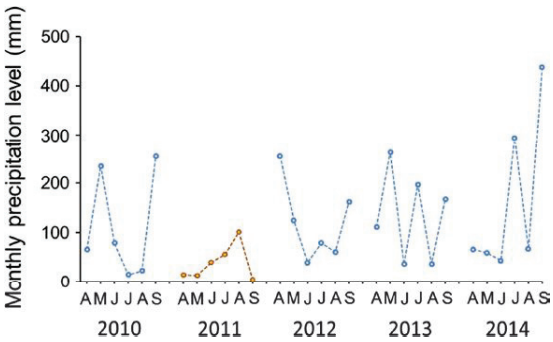

Fig. 1. Variation in precipitation levels during the active period (April to September) of *Bombina variegata* in a population in southern France between 2010 and 2014: in blue, "standard" years; in orange, drought.

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)

$$\begin{pmatrix} 1-\alpha^{JM} & 0 & \alpha^{JM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-\alpha^{JF} & 0 & \alpha^{JF} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \beta^{JM} & 0 & 1-\beta^{JM} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta^{JF} & 0 & 1-\beta^{JF} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \beta^{SM} & 0 & 1-\beta^{SM} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \beta^{SF} & 0 & 1-\beta^{SF} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad (1)$$

Given that we examined recruitment without accounting for gender-dependency, α^{JM}/α^{JF} were constrained to be equal (hereafter the parameter is shown as α). Moreover, age transition probabilities $\beta^{JM}/\beta^{JF}/\beta^{SM}/\beta^{SF}$ 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)

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

Given that the parameters ϕ^{BNM} and ϕ^{BNF} were not identifiable, ϕ^{BM}/ϕ^{BNM} and ϕ^{BF}/ϕ^{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:

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 [α(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

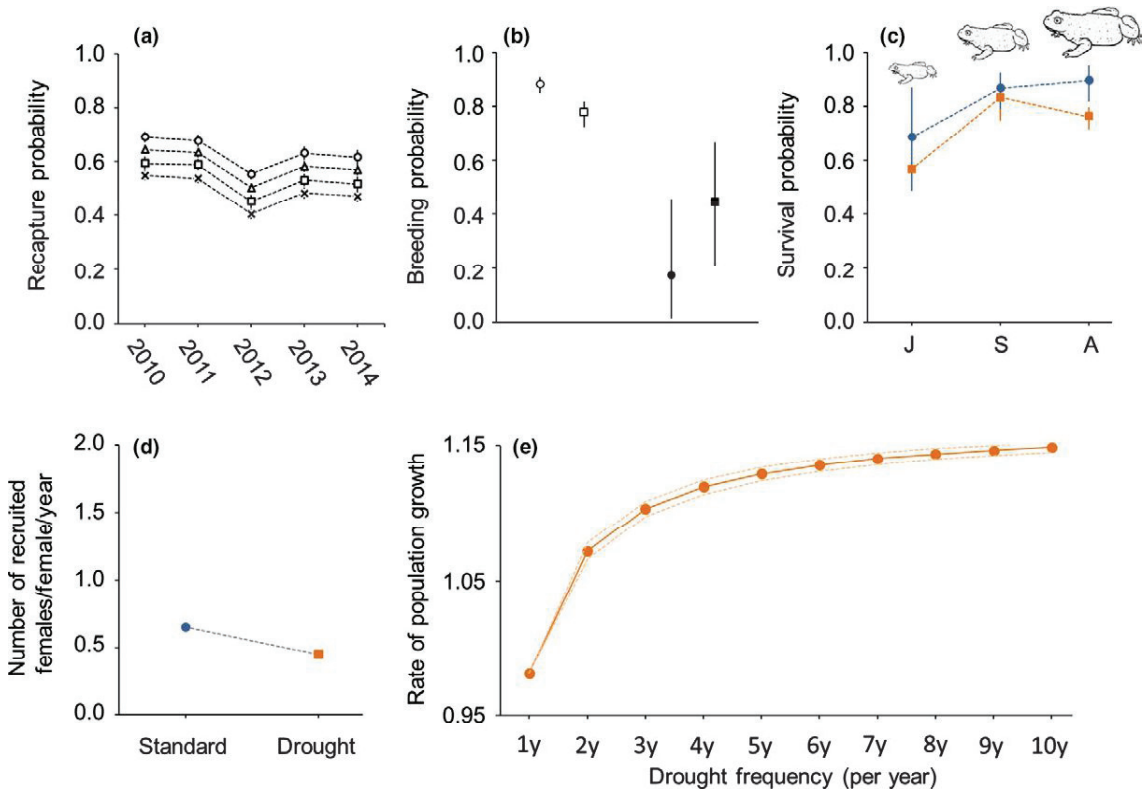

Fig. 2. Demographic parameters (mean and 95% CI) in a population of *Bombina variegata* in southern France: (a) recapture probability: circle = juvenile, triangle = subadult, cross = adult female, square = adult male, (b) breeding probability: empty circle = probability of a male breeding two consecutive 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*.

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CHAPITRE III. Sélection sexuelle et fluctuations environnementales: bons gènes, gènes compatibles et qualité de l'habitat

ARTICLE 1. Cayuela Hugo, Lengagne Thierry, Kauffman Bernard, Joly Pierre, Léna Jean-Paul. Larval competition risk shapes male–male competition and female mate choice in an anuran. *Behavioral* Ecology, arw100. DOI: 10.1093/beheco/arw100

ARTICLE 2. Cayuela Hugo, Lengagne Thierry, Joly Pierre, Léna Jean-Paul. How females trade-off the uncertainty of breeding resource with male quality during mate choice in an anuran?. Animal Behaviour, 123:179-185. DOI: 10.1016/j.anbehav.2016.11.002

ARTICLE 3. Cayuela Hugo ,Léna Jean-Paul, Lengagne Thierry, Kaufman Bernard, Mondy Nathalie, Konecny Lara, Dumet Adeline,Vienney Anthonin, Poncet Charles, Joly Pierre. Testosterone levels and relatedness predict male mating success in a pond-breeding amphibian. *In prep.*

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Original Article

Larval competition risk shapes male–male competition and mating behavior in an anuran

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Mate preference was long assumed to be static and open-ended. However, a growing body of evidence actually suggests that the predominant factor in mate choice fluctuates due to the context dependence of the factors involved in sexual selection. In particular, fluctuation in the local environment, the density of individuals, and the presence of heterospecifics can all alter the strength, form, or direction of sexual selection by shaping the fitness costs and benefits of the traits that mediate male–female interactions. Amphibians constitute useful biological models to examine context dependence in sexual selection as the availability of suitable breeding resources may significantly impact the cost–benefit trade-off between mating strategies. Using an experimental approach, we examined how the risk of larval competition in breeding ponds affects pond occupancy, male–male spacing behavior, and spawning decisions in an anuran, the yellow-bellied toad (*Bombina variegata*). Then, we examined how female mate choice is affected by male body condition and how the risk of larval competition might influence females when choosing a mate. Our results indicate that male pond preference is strongly affected by the presence of conspecific tadpoles. Males preferentially selected ponds free of tadpoles, and spawning mainly occurred in these same ponds. This preference influenced male spacing behavior by enhancing the proximity of competing males when the availability of good-quality sites was experimentally manipulated, which had further significant consequences on females' choice of mate. The article also discusses the evolutionary causes and consequences of such context-dependent mate choice in amphibians and beyond.

Key words: **amphibian, *Bombina variegata*, larval competition, male–male competition, mate choice, sexual selection.**

INTRODUCTION

The theory of sexual selection (Darwin 1871; Bateson 1983; Andersson 1994) has long considered that the gains obtained by the selective gender (typically females) are quantified relative to conditions that are considered as constant and general pressures from the environment such as disease risks, territory quality, or food availability (Kokko et al. 2003; Wong and Candolin 2005). The signals and indices used in mate selection are often reliable indicators of the efficiency of the selected gender (typically males) to deal with variation of these conditions. However, a growing body of evidence actually suggests that mating patterns fluctuate due to the context dependence of the factors involved in sexual selection (Qvarnström 2001; Fricke et al. 2009). In particular, biotic and abiotic characteristics in the local environment (Edward and Gilburn 2007; Robinson et al. 2012; Grazer et al. 2014), operational sex ratio (Jann et al. 2000; Punzalan et al. 2010), and the presence of heterospecifics (e.g., closely related species, see Rundle et al. 2008) can all result in changes in the strength, form, or direction of sexual selection by shaping the fitness costs and benefits of the traits that mediate male–female interactions (Rowe and Day 2006; Fricke et al. 2009). Variation in male density, resulting from demographic or environmental factors for instance, could also have a substantial influence on mating patterns (Jann et al. 2000; Kokko and Rankin 2006; Punzalan et al. 2010; Rittschof 2010). On the one hand, sexual selection should be relaxed when male density decreases, resulting in a reduction or a loss of ornaments, armament, or the strength of sexual conflicts (Gavrilets 2000; Martin and Hosken 2003; Levitan 2004). On the other hand, when male density and interference competition strongly increase, selection strength is first expected trivially to increase (Kokko and Rankin 2006). However, this trend could be balanced by deleterious effects of interference behaviors on population dynamics, the deleterious effects of intense competition at high density possibly leading to population decline. This evolutionary process could regulate the expression of the genetic factors driving competition among males, making their

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expression sensitive to density (Kokko and Rankin 2006). Several empirical studies have therefore showed that competitively superior males may be unable to monopolize females or resources valued by females (McLain 1992; Reichard, Jurajda, et al. 2004; Reichard, Smith, et al. 2004). However, aside from the studies cited above, relatively few have actually investigated empirically how environmental factors influencing male density could shape mating patterns.

Several features make pond-breeding anurans relevant to investigate how environmental factors may affect breeding habitat selection and how this choice may consequently affect male density. First, because of their aquatic larval stage, breeding resources for offspring early growth do not overlap with resources for other behaviors (i.e., nonsexual behaviors such as foraging) so the selective agents acting on mating success can be more easily segregated from the others (Arnold and Wade 1984). Second, both the availability and the suitability of ponds may vary greatly within and across reproductive seasons, especially for species that breed in temporary small ponds (Werner et al. 2007; Cayuela et al. 2012). In particular, varying environmental conditions such as the risk of intraspecific and/or heterospecific larval competition, cannibalism, predation, and pond drying have been reported to dramatically alter amphibians' reproductive outcome as indicated by metamorphosis achievement or size at metamorphosis (Travis 1984; Skelly and Werner 1990; Griffiths et al. 1991; Denver et al. 1998; Relyea and Hoverman 2003; Gomez-Mestre et al. 2010). The rules of mating behavior can also depend on expected water duration as evidenced in between heterospecific and conspecific males in spadefoot toads (Pfennig 2007). Therefore, the choice of egg-laying site should play a critical role in reproductive outcome (Resetarits 1996). This hypothesis is largely supported by empirical studies (Rieger et al. 2004; Binckley and Resetarits 2008) that show that the availability of suitable breeding resources could significantly impact the cost–benefit trade-off between mating strategies. More specifically, because males usually arrive first at the pond and produce advertisement calls to attract females and/or deter competitors, one may expect the availability of suitable ponds to modify male density and spacing behavior, and subsequently the strength of competition and the local context of mating behavior. When density increases, the increase in the costs of interference behaviors (advertising, threatening, fighting) can make them costly to be maintained because of the costs due to increasing signal strength against increasing background noise.

In this study, we investigate the influence of male density resulting in the reduction of breeding site availability in the yellow-bellied toad (*Bombina variegata*), an anuran reproducing in small and ephemeral water bodies (e.g., ruts, ditches, residual puddles, rocky pools). We conducted 2 set of experiments in seminatural enclosures containing 2 artificial small ponds. In experiment 1, we examined how the risk of larval intraspecific competition affects breeding site selection. If breeding toads avoid ponds already occupied by tadpoles, density should increase in tadpole-free pools. This question has not been frequently examined in anurans, despite the pioneer work by Resetarits and Wilbur (1989) in *Hyla chrysoscelis*, showing in this species a preference for tadpole-free pools by egg-laying females. First, we hypothesized that preference for tadpole-free ponds is also expressed by males because they usually arrive first on the breeding sites. After establishing these prerequisites, a second experiment (i.e., experiment 2) was carried out to test the hypothesis that this preference for tadpole-free sites results in increasing density of competing males in tadpole-free ponds. Then, we examined how the availability of tadpole-free breeding sites might influence mating patterns. Because body condition usually correlates with call performance (Castellano et al. 2009; Humfeld 2013) as well as with health status and survival in amphibians (Brodeur et al. 2011; Janin et al. 2011; Hegde and Krishnamurthy 2014), we expected that the mating success of larger males would be higher when density was reduced when all the ponds are free of tadpoles. Conversely, we expected that the increasing male density resulting from reduced availability of tadpole-free sites would modify mating pattern with regard to the relative body condition of competing males. As shown previously, theory is unable to predict the outcome of increasing male density on mating behavior. A first hypothesis based on the model developed by Kokko and Rankin (2006) predicts an intensification of sexual selection due to an increase in male density, leading to a reinforcement of the mating success of larger males; a second alternative hypothesis based on the model by Kokko and Rankin (2006) predicts that high proximity between males prevents the larger ones to monopolizing the female, thus leading to a reduction of the strength of sexual selection. Here, we examined the impact of an increase of male density on the mating success of large and small males in the yellow-bellied toad.

MATERIALS AND METHODS

Biological model

The yellow-bellied toad is a prolonged-breeder anuran reproducing in small temporary water bodies. Both stochastic variations in water level (Cayuela et al. 2011, 2013) and competition experienced by larvae (Jasieński 1988) have been reported to strongly affect the success of metamorphosis and the survival of juveniles in this species. As a result, this species is best described as an income breeder (Cayuela et al. 2014): Females continuously invest in vitellogenesis throughout the breeding season (Guarino et al. 1998) and use a risk-spreading strategy that consists of dividing their reproductive investment among different ponds (Buschmann 2002). Newly excavated ponds are rapidly colonized by males (Hugo Cayuela, unpublished data), which use advertisement calls to attract females and/or deter competitors (Schneider and Eichelberg 1974; Sanderson et al. 1992). When clustered together within the same pond, fighting among calling males can occur (Schneider et al. 1986). In this species, body condition is considered a good indicator of male quality because this can be altered by harsh environmental conditions and environmental changes over the breeding season (Băncilă et al. 2010; Scheele et al. 2014; Cayuela et al. 2015).

Studied animals and general experimental conditions

The yellow-bellied toads used in this study were caught from 3 populations in the Rhône-Alpes region (southeastern France). In 2002, 40 males and 29 females were caught to investigate both male breeding pond preference and female spawning pond choice with regard to larval competition risk. Experiments on the availability of tadpole-free ponds on male spacing behavior and mating behavior were performed in 2003 using 165 males and 84 females. All experiments were performed with the agreement of the French Ministry of Environment (authorization for temporary capture with delayed release of toads, License N°2003.09162). All animals (adults and larvae) were released at their site of capture after the experiments.

The experiments were performed from mid-June to early August in 20 seminatural enclosures (4 m L × 1.5 m W) installed within the outdoor experimental facility of the University Lyon 1 campus. In each experimental enclosure, 2 artificial ponds (half-cylinder

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polyethylene tanks: 0.9–1 m L × 0.3 m W) were buried 2 m apart (0.3 m from a small side fence). Both lengths of each pond were equipped with a strip of large-meshed material to make it easier for toads to get in and out of the pond. Grass tufts were placed in the water along each of the widths as oviposition sites. Before each experiment, the ponds were drained and refilled with ground water and the material strips and the grass were replaced. All enclosures were sprayed with water 10 min each day at the end of the afternoon (6:00 PM) because rainfall has been observed to enhance sexual activity in this species.

Experiment 1: the influence of larval competition risk on the pond preference of males and the egg deposition of females

In order to test male preference for larva-free ponds, males were offered one of the 2 following situations: 1) both ponds free of tadpoles (control group, $n = 20$), 2) one of the 2 ponds containing 15 *B. variegata* tadpoles (at stage 30–35, Gosner 1960) (Bv group, $n = 20$). For the Bv experimental treatment, the tadpoles were randomly assigned to one of the 2 artificial ponds. Males were released in the center of the enclosure at 6:00 PM and their position (i.e., outside the pond or inside the pond) was recorded every 4 h between 6:00 AM and 10:00 PM during 2 successive days (i.e., 40 h, 8 successive records). In order to control the adequacy of our experimental settings (to avoid an enclosure bias effect), each enclosure was used in a random order to perform a control experiment and either 1 or the 2 other experimental treatments. Pond temperature was also recorded 3 times each day (at 6:00 AM, 2:00 PM, and 6:00 PM) to check for homogeneity in the thermal conditions within each pair of artificial ponds, because this abiotic factor is thought to influence oviposition site choice in *B. variegata* (Cayuela et al. 2011). Given the relatively small number of males caught in 2002, 10 were used twice; in this case, the male was always assigned to 2 different experimental treatments, which were performed in 2 different enclosures in order to avoid pseudoreplication.

After individual choice experiments, males were enrolled in mating experiments ($n = 29$) to investigate the influence of larval competition risk on females' pond choice for egg deposition. For each experiment, 2 males and 1 female were introduced at the center of the enclosure. For ethical and conservation purposes, all animals involved in a mating experiment always originated from the same population. The protocol differed from that previously described in terms of experiment duration (4 days, 100 h, 21 records) and also because mating and spawning were recorded at each visit. Eggs deposited in the 2 ponds were counted at the end of each experiment in order to infer pond preference for egg deposition. These mating experiments were also used as a pilot study of experiment 2 dealing with male spacing behavior and female mate preference. For this purpose, each male was equipped with a randomly assigned white or red linen belt in order to allow identification. As no spawning was observed during the first day, we extended the experiment duration to 6 days (148 h, 31 records) in 14 out of the 29 mating experiments in order to evaluate the adequacy of experimental duration.

Experiment 2: the effect of suitable pond availability on male spacing behavior and mating behavior

As the orientation of the enclosures was found to influence toad pond choice in the experiment 1, all enclosures were moved and repositioned before the experiment 2 to remove this bias. All other setting and experimental conditions were kept unchanged.

After collection in the field, the length and body weight of toads were measured. We used the residuals of the linear regression between weight and size (snout–vent length) to evaluate male body condition (see Supplementary Material S1). Males were then assigned to a dyad so as to maximize difference in body condition between the 2 males (mean absolute body condition difference: 0.0544, range: 0.001–0.16, $N = 84$ dyads). As for the pilot study, a colored belt (white or red) was assigned to each dyadic male allowing their identification. However, we systematically inverted the color assignment according to their relative body condition between the successive dyads we formed in order to avoid any confounding effect between the belt color assignment and the relative body condition of dyadic males. Each dyad was then enrolled in an 8-day experiment. Specifically, each dyad was introduced to one of the 2 following situations: both ponds free of tadpoles (control group, $n = 46$) or one of the ponds containing 15 *B. variegata* tadpoles (Bv group, $n = 38$). Both dyadic males were released in the center of the enclosure at 12:00 AM and their position was recorded every 2 h except between 6:00 AM and 2:00 PM because the experiment 1 showed low mating activity during this time slot. Fighting was also recorded although this behavior was infrequent. The female was released in the enclosure 34 h after the introduction of the males, and her position as well as mating attempts (i.e., amplexus without egg deposition) and spawning episodes were then recorded at each subsequent visit. When spawning was detected, supplemental sightings were performed (i.e., every hour) to verify that the amplexed male did not change during spawning. Because male switching never occurred, these supplemental visits were not considered in the statistical analyses. At the end of each spawning episode, the grass for oviposition sites was replaced and the eggs were counted at the laboratory to determine clutch size. In cases where no mating was observed during the experiment, males could be reused to form an alternative dyad. If so, they were never introduced to the same enclosure nor used for the same experimental treatment.

Statistical analysis

Generalized linear mixed models (GLMM) were used to investigate the effect of the risk of larval competition on male pond preference. For each experiment, the visits in which the animal was found outside of the pond were discarded, and the position of the ponds (i.e., right or left) occupied at the other visits was used to construct a repeated binary choice response. An exponential temporal covariance structure was used to take into account non-independence between the successive choices recorded during the experiment. The experimental treatment (control group or Bv group) associated with the position of larvae if present (i.e., right or left pond) was introduced as explanatory terms in the fixed part of the model. Because each enclosure was used to perform a control experiment in addition to the experimental treatments, enclosures were introduced as a random effect, thus allowing the estimation of the Bv treatment effect conditioned to the inherent and specific effect of enclosures. We then used the contrast method to test the effect of larvae presence on male pond choice. The significance of the effects was based on F-statistic tests using the Kenward–Roger method to approximate the degree of freedom (Littell et al. 2006).

In all mating trials conducted in experiment 1, eggs were always laid in only one pond even when multiple spawning episodes occurred. We therefore used a simple binomial test to estimate the influence of larval competition risk on female pond choice for egg deposition.

The effect of suitable pond availability on male spacing behavior was tested in experiment 2. Specifically, we tested whether the

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occupancy of the same pond by both males varied according to the experimental treatment and the presence of the female (i.e., before or after the introduction of the female). For this purpose, we retained only the visits in which both males were found in ponds, and we constructed a repeated binary variable corresponding to their respective pond choice for each visit. A GLMM using a logistic link was then constructed to analyze this response variable as follows: the experimental treatment (control group vs. Bv group), the presence of the female (before vs. after introduction), and their interactive effect were introduced as explanatory terms in the fixed part of the model. An exponential temporal covariance structure was also used to take into account non-independence between the successive (relative) choices recorded during the experiment. Because the presence of the female corresponds to time-varying sampling periods, temporal autocorrelation was allowed to vary between the 2 periods. We also performed a partial analysis to test whether dyadic males avoided the pond containing tadpoles within the Bv group. For this purpose, we retained all visits in which at least 1 male was found in a pond to construct (for each male within a dyad) a repeated binary variable corresponding to its successive pond choices. The presence of the female, the relative body condition of males, and their interactive effect were introduced as explanatory terms in the model. A similar exponential temporal covariance structure as described above was also introduced for each dyadic male. Because fighting was infrequent whatever the experimental treatment (see Results for details), a Fisher exact test was used to examine whether the probability of fighting varied according to the experimental treatment.

In contrast to experiment 1, a substantial proportion of females spawned in both ponds even when only one was free of tadpoles (i.e., 6 out of 16). We therefore used a log-linear model to test female preference for the tadpole-free pond within the Bv group. For this purpose, the number of eggs deposited in the tadpole-free pond was treated as the dependent variable and the overall clutch size was introduced as an offset variable. We used a quasi-likelihood approach (i.e., including a scale parameter in the variance function) to accommodate extra-Poisson variation. In order to test whether the availability of suitable ponds altered females' mate preference, we first computed the body condition difference between males to infer the expected female mate preference. For this purpose, individual body condition was estimated as the regression residuals of body weight against body length (see Supplementary Material S1 for detail). The relative performance of dyadic males was then assessed as the body condition difference between the 2 dyadic male using the white belt equipped male as pivot. We also used a GLMM to test whether the relationship between the relative mating attempt and relative male performance was altered depending on the experimental treatment (i.e., control group vs. Bv group). For this purpose, we retained only the visits in which a mating attempt was observed in order to construct a binary repeated measurement of the relative mating attempt. As for the relative male performance, the white belt equipped male was used as pivot to construct this binary variable (i.e., 1 if mating attempt performed by the white belt equipped male, 0 if performed by the other male). Both explanatory terms and the temporal correlation structure were specified as above. In order to infer the reproductive success of males, we used the number of clutches rather than the total number of eggs sired by each male because successive clutches were found to be sired by only 1 male in all but 4 cases. The analysis was performed in the same way as previously explained. All analyses were carried out using SAS 9.3 software (SAS Institute Inc.).

RESULTS

Experiment 1: the influence of the risk of larval competition on males' pond preference and females' egg deposition

Males significantly preferred the pond free of tadpoles (Table 1). Of the 29 mating experiments performed in experiment 1, 14 gave rise to spawning. All but one reproduction occurred in the tadpole-free pond, indicating a clear avoidance of the risk of larval competition at the time of egg deposition ($n = 14$, CI 95% probability of choosing the tadpole-free pond = 0.66–0.99, $P = 0.0018$).

Experiment 2: the effect of suitable pond availability on males' spacing behavior and mating behavior

The type of experimental treatment had a significant effect on male spacing behavior, but the magnitude of this effect varied depending on the introduction of the female in the enclosure (treatment effect: $F_{1,615.7} = 15.16$, $P < 0.0001$; female presence effect: $F_{1,159.4} = 0.14$, $P = 0.71$; treatment × female presence effect: $F_{1,159.4} = 3.8$, $P = 0.053$, see Figure 1). Before the introduction of a female, males were found sharing the same pond 2.48 times more frequently when only 1 pond was free of tadpoles in comparison with when both ponds were free of tadpoles (contrast: $F_{1,109.7} = 9.0$, $P = 0.0033$). However, this relative odds ratio falls to 1.29 after the introduction of the female (contrast: $F_{1,411.2} = 3.41$, $P = 0.065$). Our analyses also indicate that both males significantly avoided the pond containing tadpoles when present (i.e., male occupancy probability of the tadpole-free pond = 0.63, $F_{1,132.1} = 21.78$, $P < 0.0001$), and this avoidance was affected neither by their relative body condition nor by the introduction of the female (relative body condition effect: $F_{1,132.1} = 1.66$, $P = 0.20$; female presence effect: $F_{1,132.1} = 0.89$, $P = 0.34$; relative body condition × female presence effect: $F_{1,132.1} = 0.24$, $P = 0.62$). Fighting was rarely observed and did not significantly vary depending on the experimental treatment (i.e., fighting was observed in 10 out of the 46 control experiments and in 7 out of the 38 Bv experiments, $P = 0.79$).

Among the 84 experiments performed, 40 gave rise to mating attempts and at least 1 clutch deposition was observed in all except 7 of these 40. When tadpoles were present in one of the 2 ponds, the female's pond choice clearly confirmed her preference for the tadpole-free pond, which was also detected in experiment 1 (clutch size proportion deposited in the tadpole-free pond = 0.82, $F_{1,15} = 6.62$, $P = 0.0212$). As for male spacing behavior, the relationship between the relative success of each male within a dyad and their relative body condition varied according to the experimental treatment (see Table 2, Figure 2): The heavier male made significantly more mating attempts and also sired more clutches than the

Table 1

Testing the effects of *Bombina variegata* tadpole presence on male breeding site preference: tadpoles in the pond on the right ("Tadpole R"), tadpoles in the pond on the left ("Tadpole L"), and no tadpoles in either pond ("Control")

Contrasts between fixed effects	df res.	*F*	*P*
Tadpole L versus Control	54.45	5.70	0.02
Tadpole R versus Control	54.45	0.14	0.71
Tadpole L versus Tadpole R	55.25	5.51	0.02

Outputs of Anova *F*-test Type III: df res., degrees of freedom associated with residual variance; *F*, *F*-test values; *P*, probability values.

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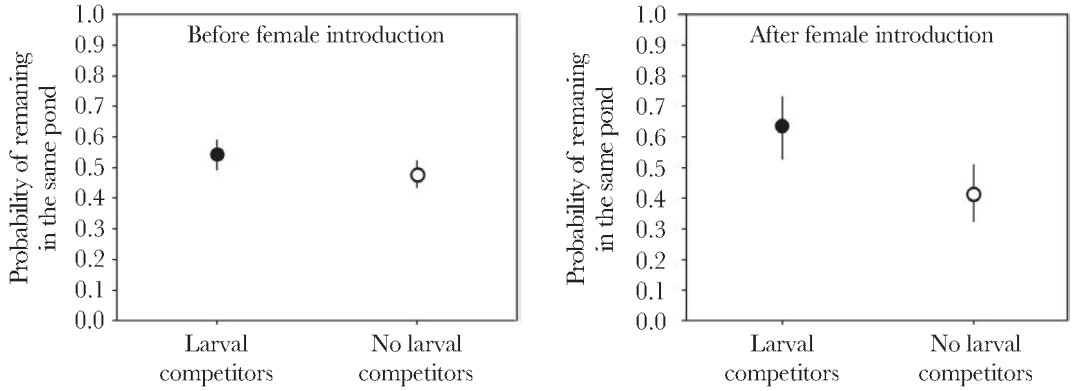

Figure 1
Testing the effect of the experimental treatment (one of the 2 ponds containing larval competitors vs. no larval competitors in either pond) and the introduction of a female on male spacing behavior. The probability of both males remaining in the same pond is provided with the associated 95% confidence interval.

Table 2
Testing the effects of experimental treatment (pond containing tadpole competitors vs. tadpole-free pond) and the relative body condition of males on mating attempt probability and the number of clutches sired

Fixed effects	df res.	*F*	*P*
Mating attempt			
Experimental treatment	43.70	0.06	0.81
Relative body condition	44.35	0.96	0.33
Treatment × relative body condition	43.70	5.43	0.02
Number of clutches sired			
Experimental treatment	29.60	0.09	0.77
Relative body condition	28.91	2.48	0.12
Treatment × relative body condition	28.91	4.32	0.046

Outputs of Anova *F*-test Type III: df res. = degrees of freedom associated with residual variance; *F*, *F*-test values; *P*, probability values.

slimmer male when both ponds were free of tadpoles (contrast for 1-unit deviation of the relative body condition, respectively, for the mating attempt and the number of clutches sired: $F_{1,42.36} = 4.32$, $P = 0.0437$; $F_{1,29.17} = 4.87$, $P = 0.0353$), whereas this difference vanished when only 1 pond was free of tadpoles (contrast for 1-unit deviation of the relative body condition, respectively, for the mating attempt and the number of clutches sired: $F_{1,43.83} = 1.63$, $P = 0.21$; $F_{1,28.26} = 0.15$, $P = 0.70$).

DISCUSSION

Our results indicate that male pond preference is strongly affected by the presence of conspecific tadpoles. Males preferentially selected ponds free of tadpoles, and spawning mainly occurred in these ponds. This preference influences male spacing behavior, by enhancing proximity of competing males when the availability of good-quality sites was experimentally manipulated, which has further significant consequences on the outcome of mating behavior.

Oviposition sites without larval competitors are preferred

Males preferred breeding sites where future offspring would not experience intraspecific larval competition. As well, females' egg deposition primarily occurs in aquatic sites without larval competitors. Such breeding habitat preference has previously been highlighted in other amphibians that breed in temporary environments (Resetarits and Wilbur 1989, 1991; Dillon and Fiaño 2000; Halloy and Fiaño 2000; Matsushima and Kawata 2005). Avoiding competition at larval stage usually results in a fitness benefit for offspring because high larval density negatively impacts growth rate and size at metamorphosis (Travis 1984; Alford and Harris 1988). An increased growth rate can reduce mortality risks linked to prolonged exposure to predators (for a review, see Relyea 2007), epidemic diseases (Touchon et al. 2006), and desiccation (Denver et al. 1998; Enriquez-Urzelai et al. 2013). Furthermore, a larger body mass at metamorphosis is positively correlated with overwinter survival (Altwegg 2003; Schmidt et al. 2012), postmetamorphic dispersal ability (Chelgren et al. 2006, 2008), and size at sexual maturity (Altwegg and Reyer 2003). In *B. variegata*, a previous study showed that kin aggregation (when tadpoles develop in groups composed of relatives) results in an increase in growth rate (Jasieński 1988). Preferring oviposition sites that may lead to an increase in the growth rate of offspring at larval stage therefore constitutes a behavioral mechanism likely to improve offspring fitness by limiting mortality risk due to pond desiccation before metamorphosis, which is the most critical factor for larval survival (Morand 1997).

Breeding site preference shapes male–male competition

Our results indicate that the availability of breeding sites without larval competitors regulates male–male competition. In the experimental situation where both oviposition sites were free of tadpoles, males avoided direct intrasexual competition, each occupying a different pond. In anurans that emit acoustic courtship signals, such intermale spacing behavior is widespread (reviewed in Wells and Schwartz 2007; Wells 2010). In *B. variegata*, intermale spacing is usually maintained by means of territorial behavior including advertisement calls, water-wave communication, and, in some cases, fighting (Schneider et al. 1986; Elepfandt 1992; Seidel et al. 2001). These spacing behaviors usually have the aim of keeping other calling males at a distance and preventing intrusions by sneaker males (Zamudio and Chan 2008).

In the experimental situation in which only one of the 2 available ponds was free of tadpoles, males no longer limited direct intrasexual competition, choosing the most suitable pond regardless of proximity with other males. Such proximity did not enhance aggressiveness in competing males—fighting remained infrequent whatever the experimental treatment. This low level of aggressiveness between competing males is likely linked to the high costs

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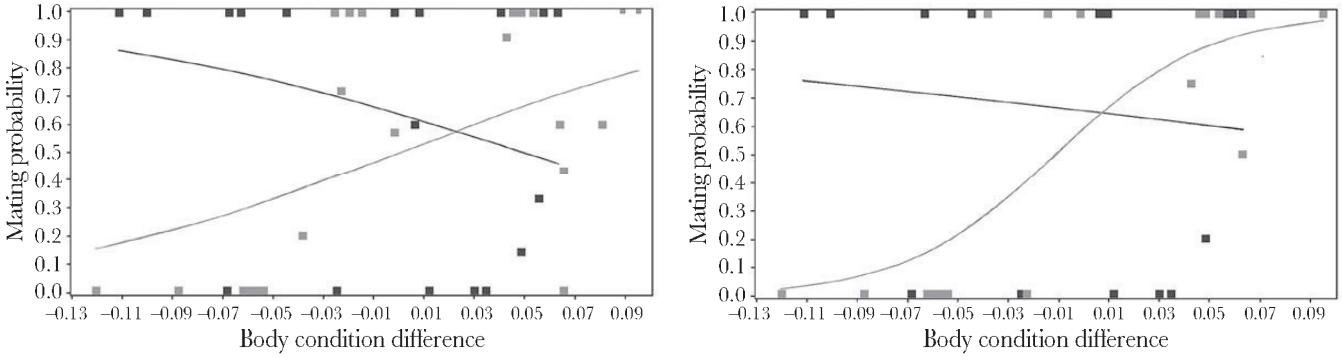

Figure 2
Male mating probability (achieving amplexus on the left and siring an egg clutch on the right) depends on body condition in the yellow-bellied toad. The predicted and the observed relative male mating probabilities according to the relative body condition of dyadic males are indicated, respectively, by the solid lines and squares. The gray color is for the experiments where both ponds were free of tadpoles; the black color is for the experiments where only 1 pond was free of tadpoles. The relationship between the relative mating probability and the relative body condition was found significant only in the former situation.

that would be incurred by defending suitable breeding resources as exclusive. Indeed, both high turnover and temporary scarcity of these sites make them hardly defensible (Wells 2010). Taken together, our results suggest that males display hierarchical decision making: First, based on environmental conditions that could affect offspring fitness during the larval stage, and second, on the presence of intrasexual competitors that could directly influence their own fitness. A male's final decision about which breeding site to settle on is likely based on an exploratory mechanism whereby he assesses the fitness costs and benefits of possible choices using chemical, visual, and acoustic cues.

Breeding site preference influences female mating behavior

In the experimental situation in which both ponds were free of tadpoles, each male in a dyad tended to occupy a different pond and the heavier toad made more mating attempts and also sired more eggs than the slimmer toad. These findings are in accordance with previous studies showing that the investment in breeding and the mating success of male anurans is related to body size and body condition (Castellano et al. 2009; Humfeld 2013), which are an indirect measure of the amount of energy potentially available for breeding. In particular, body condition is usually related to call performance and mating, 2 sexual behaviors known to be energetically costly in male anurans. Indeed, vocal production is one of the most energetically demanding behaviors in vertebrate ectotherms (Sullivan and Kwiatkowski 2007; Leary 2009), frequently elevating metabolic rates 20 times above basal rates (Wells 2010). Vocal production is linked to male size (Voituron et al. 2012). Furthermore, the energetic cost of amplexus itself may be high, affecting the success of further fertilizations (McLister 2003; Lengagne et al. 2007). In *B. variegata*, our results suggest that male fitness is directly linked to the energetic reserves that can be allocated to amplexus, as well as to call production and the defense of calling places.

In the experimental situation in which only one of the 2 available ponds was free of larvae, the heavier male no longer outcompeted the slimmer one, and females did not exhibit a preference with respect to male condition. These results are congruent with previous studies showing that density may affect female anurans' mating behavior (Zamudio and Chan 2008; Lengagne and Joly 2010; Richardson and Lengagne 2010). In cases where male behavior is not modified by enhanced intrasexual competition (i.e., absence of female harassment and forced copulation), an increase in male density may negatively influence females' capacity to discriminate good callers (Bee 2008; Richardson and Lengagne 2010), therefore affecting her ability to select the bearers of good genes. In other cases, an increase of intrasexual competition can influence male breeding tactics, which may affect females' ability to select mates. First, high proximity among males can promote caller–satellite associations; satellite behavior is usually considered the best tactic for males in poor condition to maximize reproductive success over the course of the breeding season (Leary et al. 2004; Humfeld 2013; Leary and Harris 2013, but also see Brepson et al. 2012). In this alternative mating tactic, poor-condition satellite males sit silently near good-condition vocalizing males; usually satellites are either attempting to intercept females attracted to callers or waiting to take over calling sites or territories vacated by the resident male (reviewed in Zamudio and Chan 2008). Second, an increase in male density may favor scramble competition (Wells 1977; Arak 1983), leading to an increase in female harassment. This may create sexual conflicts, in which competing males impose sexual coercion and thus restrict female opportunity for mate choice (Bergen et al. 1997; Lengagne et al. 2006; Lengagne and Joly 2010).

In the present work, we used the variable "amplexed male" to assess the outcome of competition between males. Other metrics would have been used such as paternity analysis that would have provided a more effective estimation of male success, considering the possibility of sneaking behavior (Candolin and Vlieger 2013). The demonstration of multiple paternity in *Rana dalmatina* despite both territoriality and amplexus behavior of the selected male (Lodé and Lesbarrères 2004) supports that questioning. We nevertheless considered our metrics to suitably cope with the addressed question.

CONCLUSION

Our results show that the availability of suitable breeding resources may strongly influence male proximity and ultimately the mating decisions of females. Females may display hierarchical mate-choice decisions based on male quality and the prevailing environmental conditions during offspring development, both of which affect offspring fitness. However, our knowledge concerning the rules that govern female decision making in situations in which good genes do not align with the quality of breeding sites is incomplete. We therefore strongly recommend future studies to

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investigate how females deal with the trade-offs between improving the genetic quality of offspring and selecting breeding sites in which the environmental conditions will improve the chances of offspring development.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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Females trade off the uncertainty of breeding resource suitability with male quality during mate choice in an anuran

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In many species, females may be particularly selective about the expected direct benefits of choosing a potential mate or the male's genetic contribution to their offspring. Growing evidence suggests that female choosiness can also be influenced, for instance, by local abiotic factors, the social environment or the presence of heterospecifics. In amphibians that breed in highly temporary ponds with limited trophic resources (such as the yellow-bellied toad, *Bombina variegata*), competition during larval development may have a strong impact on the fitness of offspring. Accordingly, one might expect females to apply hierarchical decision making, balancing intraspecific competition risks during larval growth against the relative indirect benefits associated with the quality of the male. To investigate this issue, we conducted experiments in seminatural enclosures to test whether the preference of yellow-bellied toad females for good call attractiveness (determined by fundamental frequency) is affected by the risk of larval competition within the pond occupied by the callers. Overall, our results showed that females have a preference for low-frequency calls when prior information does not enable them to assess the relative quality of ponds. However, when prior information enables females to unambiguously determine relative pond quality, females appear to apply hierarchical decision making in which the quality of a pond prevails over call cues related to the quality of the male.
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In many species, females may be particularly selective when they come to mate based on the expected benefits they might receive: either direct benefits resulting from male gifts or parental care, or indirect benefits related to a male's genetic contribution (Andersson, 1994). Males differ in heritable traits, and females would be expected to choose those bearing genes that will improve the offspring's genetic quality. This is affected by two main components: nonadditive genetic variance (the 'compatible genes' model) and additive genetic variance (the 'good genes' model) (Neff & Pitcher, 2005; Puurtinen, Ketola, & Kotiaho, 2009). In line with the latter, a clear female preference for costly male advertisements such as visual or acoustic signalling has frequently been documented (Iwasa & Pomiankowski, 1994). Yet evidence of enhanced offspring fitness resulting from female choosiness is more rare and, when reported, the benefit appears relatively weak (Head, Hunt, Jennions, & Brooks, 2005; Hine, Lachish, Higgie, & Blows, 2002; Neff & Pitcher, 2005; Petrie, 1994; Sheldon, Merilö, Qvarnström, Gustafsson, & Ellegren, 1997; Welch, Semlitsch, & Gerhardt, 1998). This low indirect benefit may result from environmental variance markedly blurring the effect of male sexual characteristics as well as offspring fitness (Kirkpatrick & Barton, 1997; Welch, 2003). There is now growing evidence suggesting that female choosiness is not trivial and can involve multimodal cues (Candolin, 2003; Gomez, Théry, Gauthier, & Lengagne, 2011) related to expectancy about different aspects of fitness (i.e. direct and indirect benefits) or unrelated (for instance, complementary or redundant information about male quality), and that these can be processed either as an amalgamated criterion or hierarchically (Candolin, 2003; Hebets et al., 2016). It is also now acknowledged that female choosiness is often context dependent (Bussiere, Hunt, Stölting, Jennions, & Brooks, 2008; Chaine & Lyon, 2008; Fricke, Perry, Chapman, & Rowe, 2009; Qvarnström, 2001). For example, it can vary greatly depending on the local environment (Edward & Gilburn, 2007; Grazer, Demont, Michalczyk, Gage, & Martin, 2014; Robinson, Sander van Doorn, Gustafsson, & Qvarnström, 2012), the social environment (Jann, Blanckenhorn, & Ward, 2000; Punzalan, Rodd, & Rowe, 2010; Richardson & Lengagne, 2010; Schwartz, Buchanan, & Gerhardt, 2001) and the presence of heterospecifics (Pfennig, 2000, 2007; Rundle, Chenoweth, & Blows, 2008;

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Svensson, Eroukhmanoff, Karlsson, Runemark, & Brodin, 2010). Such environmental constraints can increase the costs of searching for a mate, thus potentially leading to a reduction in the female's sampling and assessment accuracy, making them more permissive when it comes to less attractive males (Candolin, 2003). However, a clearer understanding of the outcome of a female's choices requires investigating the mechanisms underlying decision making, in particular how all this different information is processed and how uncertainty assessment is incorporated in the decision-making process (Castellano & Cermelli, 2011; Luttbeg, 1996, 2002).

Pond-breeding amphibians are a useful biological model for investigating context dependence in sexual selection. In these species, males usually produce advertisement calls, and females display choosiness in regard to particular call features, especially call frequency (dominant or fundamental; Bosch & Márquez, 2005; Burke & Murphy, 2007; Richardson, Joly, Léna, Plénet, & Lengagne, 2010), which is related to the caller's size (Wells, 2010). Female mate choice has also been linked to other call features, including pulse rate (Castellano & Rosso, 2006; Wagner & Sullivan, 1995), call rate (Smith & Roberts, 2003; Taylor, Buchanan, & Doherty, 2007) and call duration (Castellano, Rosso, Laoretti, Doglio, & Giacoma, 2000; Tarano & Herrera, 2003). While many studies have highlighted the fact that calling performance and male attractiveness are reliable predictors of offspring fitness components such as larval growth (Forsman & Hagman, 2006; Gerhardt & Huber, 2002; Jaquiéry, Broquet, Aguilar, Evanno, & Perrin, 2010; Reinhold, 2011; Welch et al., 1998), others have also suggested that such indirect benefits depend on the environmental context (Doty & Welch, 2001; Welch, 2003). The aquatic habitat required for larval development is the primary breeding resource in pond-breeding amphibians; this habitat varies across species from very small ephemeral water bodies to large permanent ponds (Cayuela, Besnard, Bechet, Devictor, & Olivier, 2012; Van Buskirk, 2005; Werner, Skelly, Relyea, & Yurewicz, 2007). For amphibians that breed in ephemeral water bodies, offspring fitness is strongly affected by competition between conspecifics for limited trophic resources (Morey & Reznick, 2004; Newman, 1998; Wells, 2010). Competition experienced during larval development can severely reduce offspring fitness as it can result in decreased body size at metamorphosis, a life-history trait that affects overwinter survival (Cabrera-Guzmán, Crossland, Brown, & Shine, 2013; Morey & Reznick, 2001; Schmidt, Hödl, & Schaub, 2012), dispersal ability (Chelgren, Pearl, Adams, & Bowerman, 2008; Chelgren, Rosenberg, Heppell, & Gitelman, 2006), juvenile growth (Altwegg, 2003) and size at sexual maturity (Altwegg & Reyer, 2003). In addition, high tadpole density decreases growth rate at the larval stage and consequently prolongs the exposure of tadpoles to predation (for a review, see Relyea, 2007), epidemic diseases (Touchon, Gomez-Mestre, & Warkentin, 2006) and desiccation (Denver, Mirhadi, & Phillips, 1998; Enriquez-Urzelai, San Sebastián, Garriga, & Llorente, 2013). Since the degree of larval competition may affect spawning decisions (Dillon & Fiaño, 2000; Halloy & Fiaño, 2000; Matsushima & Kawata, 2005; Resetarits & Wilbur, 1989, 1991), one might expect females to apply hierarchical decision making regarding both the environmental conditions prevailing in potential breeding ponds and the relative indirect benefits associated with male quality.

We investigated this issue in the yellow-bellied toad, *Bombina variegata*, an anuran that breeds in relatively small and highly temporary water bodies (Barandun & Reyer, 1998; Cayuela, Besnard, & Joly, 2013; Cayuela, Cheylan, & Joly, 2011). This species displays the four criteria distinguishing resource-based lek species: (1) the breeding resources (in this case, small temporary ponds) are occupied by males and act as an arena (or lek) to which females come to mate and in which most of the mating occurs (Schneider & Eichelberg, 1974; Schneider, Hussein, & Akef, 1986); (2) males do not provide direct benefits such as parental care or resources (except perhaps external fertilization) (Buschmann, 2002; Schneider & Eichelberg, 1974); (3) as in other anurans, males likely do provide indirect benefits through the effects of genetic contribution (Forsman & Hagman, 2006; Jaquiéry et al., 2010; Welch et al., 1998); (4) males actively defend call sites, but not spawning sites (Wells, 2010), and produce advertisement calls to attract females and/or deter competitors (Sanderson, Szymura, & Barton, 1992; Schneider et al., 1986; present study). In this species, the metamorphosis success and the local recruitment strongly depend on low desiccation risk and low competition experienced during larval development (Barandun & Reyer, 1997; Barandun, Reyer, & Anholt, 1997; Cayuela, Arsovski et al., 2016), so one would expect breeders to be particularly sensitive to these environmental factors when making mating decisions. Indeed, in a recent study we demonstrated that breeders strongly prefer occupying, mating and spawning in larvae-free ponds (Cayuela, Lengagne, Kaufmann, Joly, & Léna, 2016). This recent study also showed that females preferred the heavier male in a pair when each solely occupied a larvae-free pond, but this mating preference vanished when both males shared the same larvae-free pond. In all contexts, females usually mated successively with the same male and bred in ponds only when they did not contain larvae.

Following these results, one could hypothesize that pond quality overrides male quality in a female's decision-making process (Cayuela, Lengagne et al., 2016). The main objective of the present study was to investigate in detail the rules that govern female decision making in order to test this hypothesis. To do this, we envisioned two possibilities. First, females are unable to resolve uncertainty associated with the relative quality of a pond before a visit. This could occur if females do not use direct cues (notably waterborne odours) to determine pond quality, or if the available information does not allow an accurate assessment of the relative pond quality. In such cases, females might bet on the most attractive males if the preferred trait indicates either the intrinsic quality of the bearer or his ability to locate the most suitable ponds. However, if females were allowed to breed a second time, one would expect their subsequent decision to no longer depend on the male occupying each pond, but rather on the information gathered about the pond itself during the first visit. In the second, alternative, situation, direct cues would enable females to unambiguously determine the relative quality of a pond without visiting it. In this case, females would be able to select the most suitable pond whatever the relative quality of the male occupying it.

To investigate these two possible scenarios, we conducted pond choice experiments in seminatural enclosures that mimicked the situations described above. Pond quality was manipulated using larval competition as done in Cayuela, Lengagne et al. (2016) to be either of good quality (i.e. larvae-free) or of poor quality (i.e. presence of larvae). To manipulate the attractiveness of the male associated with each pond, we created soundtracks with contrasting call frequency as this call feature is usually related to female preference in anurans (females have been shown to prefer low-frequency calls; Bosch & Márquez, 2005; Burke & Murphy, 2007; Wells, 2010). Call frequency has also been found to be related to the size of the male in our model species, with larger males making lower-frequency calls (present study, see below). Three experiments were performed in which females had to choose between a pond associated with a low-frequency call and another associated with a high-frequency call. In the first two experiments, the ponds had an identical quality level, either at the upper quality limit (both ponds larvae-free, experiment A), or at the lower quality level (both ponds containing larvae, experiment B). In experiment C, pond quality was inversely contrasted with call attractiveness for

both ponds (i.e. the high-frequency call was associated with the larvae-free pond, and the low-frequency call was associated with the pond containing larvae). To examine whether females assess the relative quality of a pond before visiting it, we observed females' pond preference in experiment C, and then compared their call preferences with those observed when both ponds were of the same quality (i.e. experiments A and B). Just after this first choice, females were allowed to make a second choice in exactly the same conditions, except this time the location of call advertisements was inverted. This second trial ended up being restricted to experiments A and B; in experiment C, it was uninformative, as females consistently selected ponds by quality in the first trial (see Experimental Procedure and Statistical Analyses). We then compared the consistency of a female's two successive choices between trials to test whether the rules governing female decision making incorporate uncertainty about pond quality.

METHODS

Animal Captivity

The toads were captured from a population located in the Rhône-Alpes region in France at the beginning of the *B. variegata* breeding season. On arrival at the laboratory, the females were held outdoors in a common garden (4 × 8 × 0.5 m) in a cool, shaded place. The garden included a shallow water body (2 × 2 × 0.05 m) with a large amount of plant debris and six terrestrial shelters (half-buried curved tiles). As female ovulation is synchronized with rainfall (Barandun et al., 1997), we simulated artificial rainfall once a day (~1 h) using an irrigation system with water sprayers. To ensure sexual responsiveness, the females were then placed in an enclosure (1.2 × 1.2 × 0.5 m) that contained a buried plastic box mimicking a natural breeding site in which three males were located. When amplexus began, a female was collected and subjected to our choice experiments.

Soundtrack Broadcasting and Overall Experimental Device

We conducted a pilot study the year before the choice experiments to verify the correlation between the dominant frequency of a call and body size in *B. variegata*; during this pilot study we created the soundtrack for the choice experiment. For this purpose, 36 males from populations in the Rhône-Alpes region were kept in warm conditions (24.5 ± 1 °C) and recorded using a Sennheiser ME67-K6 microphone mounted on a pole and connected to a SONY TCD5M. Signals were then digitized (16-bit, sampling rate of 22.125 Hz) and analysed using Avisoft©. Three parameters were used to describe a call sequence: call rate (calls/s), call duration (in ms) and dominant frequency (i.e. the frequency with the highest amplitude level, in Hz). As expected, dominant frequency was correlated with the body size of a male ($R^2 = 0.33$, $N = 36$, $P < 0.001$). The average call characteristics of the population (call rate 1.6 ± 0.4 call/s; duration 191.9 ± 34.8 ms; frequency 1213.4 ± 49.5 Hz) allowed us to build a synthetic call sequence (see Fig. 1). The resulting soundtrack corresponded to the average call rate and call duration observed in the studied population. We then modified the frequency in order to obtain one low-frequency track (mean − 1 SD) and one high-frequency track (mean + 1 SD).

All experiments were carried out in an enclosure (2 × 1.2 m) that included two water bodies (each made from a buried plastic box of 0.8 × 0.5 × 0.3 m). The ground of the enclosure was covered with a low-pile carpet that was changed between each test. To create the poor quality pond, 35 *B. variegata* tadpoles (Gosner stage 30) were introduced, corresponding to a high larval density (ca. 2 × larval density used in Cayuela, Lengagne et al., 2016); the tadpoles were reared in the laboratory from two egg clutches collected from the same population as the captured females.

The acoustic stimuli were broadcast antiphonally from two Monacor SP155X speakers placed at either end of the enclosure just above the water bodies and amplified by a Monacor Stageline STA102 stereo amplifier connected to a MP3-WAV player. Prior to each test, using a Voltcraft MT-8820 Sound Level Meter (C-weighted, fast setting, tolerance 1.5 dB), we adjusted the peak sound pressure of calls from both loudspeakers to 75 dB at 1 m, which is equivalent to the values measured for natural calls at the same distance. Trials were performed in total darkness between 2200 and 0300 hours. Throughout the testing process, a dim red headlight was used during toad handling that was just powerful enough for us to monitor the animal's behaviour. We also set up 1.2 m high frames around the enclosure to shield observers from detection by the females.

Experimental Procedure and Statistical Analyses

Each female was used for only one experimental test. At the beginning of each test, the female was placed in a circular mesh cage (0.1 m in diameter × 0.05 m in height) located in the centre of the enclosure, and the alternative soundtracks were broadcast

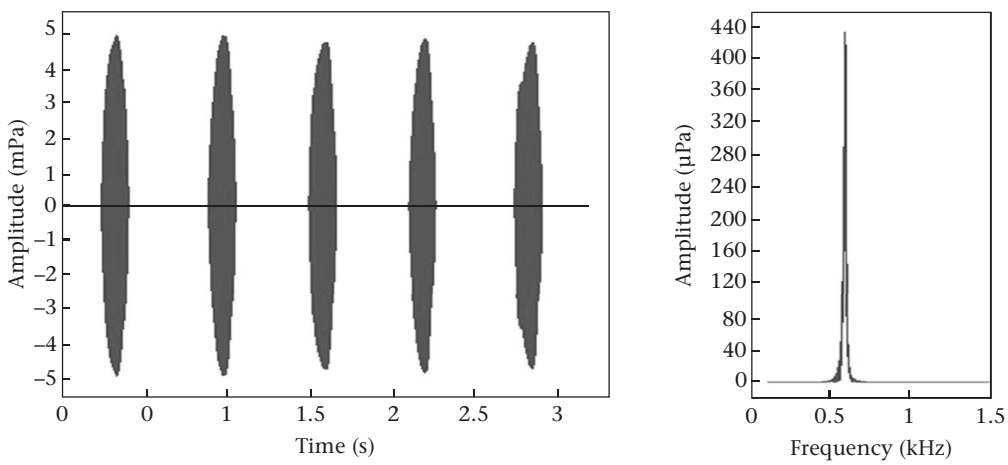

Figure 1. Main characteristics of the call sequence of *Bombina variegata* used during tests: on the left, an oscillogram showing the timing of five successive calls; on the right, the frequency of a call (Hamming windows, resolution 2.7 Hz).

antiphonally. After 5 min, the top of the cage was lifted remotely by pulling a string. The female's preference was scored as a 'choice' when she positioned herself in one of the two water bodies and remained there for at least 1 min. If no choice was made within 10 min, the test was discarded and the female was excluded from the experiments. In experimental situation A, we tested a female's preference in the situation in which both water bodies were of good quality (larvae-free). The female was exposed to the two acoustic signals (low and high fundamental frequency) whose position (left or right water body) was randomized between each tested female. Just after each female's first decision, the female was replaced in the circular mesh cage at the centre of the enclosure and the position of the two acoustic signals was then inverted. After 5 min, the female was released and allowed to express a second choice. Experiment B was performed as above, except that both ponds were of poor quality (containing larvae). In experiment C, we tested female choice when only one of the two water bodies contained larval competitors. The position of the water body (right or left) containing the larval competitors was randomized before each tested female. The low-frequency advertisement call was always associated with the poor-quality pond. As females clearly preferred the larvae-free pond associated with the high-frequency call during the first trial (see Results below), a second trial was not required in this experimental situation.

We used exact binomial tests (Siegel & Castelan, 1988) using the R program to examine female preference during each trial of each experiment. The same procedure was used to test whether a female consistently chose the same pond between the two successive trials within experiments A and B. The preference exhibited during the first trial was compared between experiments C–A, C–B and A–B using Fisher's exact tests. A similar test was used to examine whether the consistency of the two successive choices differed between experiments.

RESULTS

In experiments A and B, in which both ponds had the same level of quality, females exhibited a significant preference for low-frequency calls during the first trial (experiment A: $N = 15$, $P = 0.001$; experiment B: $N = 12$, $P = 0.04$; Fig. 2); the probability of a female choosing the pond where the low-frequency call was emitted was 0.87 (95% CI, 0.59–0.98) in experiment A and 0.83 (95% CI, 0.52–0.98) in experiment B. Thus, when the relative quality was kept identical between ponds, either at the upper or lower level of quality, females based their choice on call attractiveness. In contrast, in experiment C, in which larval competitors were introduced only in the pond associated with the low-frequency calls, females preferentially selected the pond free of larvae despite its association with high-frequency calls ($N = 20$, $P = 0.01$). As a result, the probability of choosing the pond associated with the low-frequency call was 0.2 (95% CI: 0.06–0.44; Fig. 2), which was diametrically opposed to the call preference exhibited in experiments A and B (Fisher's exact tests: experiments A versus C: $N = 35$, $P < 0.001$; experiments B versus C: $N = 32$, $P < 0.001$).

During the second trial of experiment A, females showed a significant preference for returning to the pond they previously visited despite the fact that the location of the acoustic signal was inverted between the two successive trials ($N = 13$, $P = 0.02$; Fig. 3): the probability of a female reselecting the pond she chose during the first trial was 0.85 (95% CI: 0.54–0.98). In contrast, in experiment B, females showed a significant preference for avoiding the pond they previously visited and preferred the unvisited pond, which was now associated with the low-frequency calls ($N = 12$, $P = 0.01$; Fig. 3): the probability of a female returning to the pond visited during the first trial was 0.08 (95% CI: 0.00–0.39). The consistency of pond preference exhibited during the two successive trials was diametrically opposed in the two experimental situations (Fisher's exact test: $N = 25$, $P < 0.001$; Fig. 3).

DISCUSSION

Overall, our results showed that females have a preference for low-frequency calls when prior information does not allow them to discriminate the relative quality of a pond. However, when prior

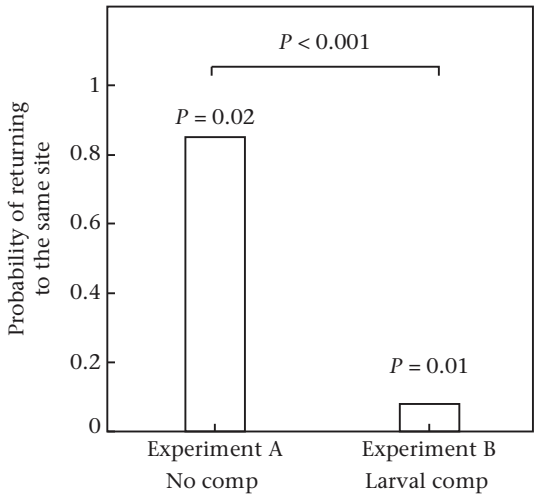

Figure 3. Pond preference consistency exhibited during the second trial (after the inversion of the two acoustic signals between ponds) in experiments A and B: experiment A, both ponds free of larvae ('No comp'); experiment B, both ponds containing larvae ('Larval comp').

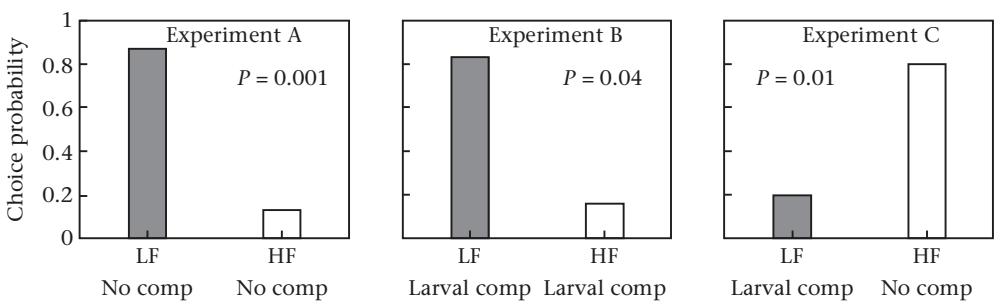

Figure 2. Female preference for call frequency (high frequency, 'HF': white bars; low frequency, 'LF': grey bars) in three experimental situations during trial 1: experiment A, absence of conspecific larval competitors ('Larval comp') in both ponds; experiment B, presence of conspecific larval competitors in both ponds; experiment C, presence of conspecific larval competitors in one pond (the pond associated with good call attractiveness, i.e. the low-frequency call).

information enables females to unambiguously determine pond quality, females appear to apply hierarchical decision making in which the quality of the pond prevails over call cues related to the quality of the male.

Females Prefer Low-frequency Calls When Pond Quality Is Uncertain

When the risk of larval competition was kept at the same level between the two ponds, our results show that females preferred to first visit the pond associated with low-frequency calls whatever the overall pond quality available in the enclosure (i.e. both ponds of good quality in experiment A or both of poor quality in experiment B). These results are congruent with previous studies showing female anurans' preference for low-frequency calls (Bosch & Márquez, 2005; Richardson et al., 2010) and for large males (Cayuela, Boualit et al., 2016; Wells, 1977; Wilbur, Rubenstein, & Fairchild, 1978). Since a low-frequency call correlates with large body size in anurans (Gerhardt, 1994), this could be a reliable indicator of caller quality. Indeed, several studies suggest that male body size may act as a condition-dependent signal of male genetic quality (Wells, 2010). Enhanced fitness of offspring sired by larger males has also been documented in several other organisms (Iyengar & Eisner, 1999; Reynolds & Gross, 1992). Nevertheless, it is yet to be demonstrated whether female preference for low-frequency callers is related to such indirect benefits in *B. variegata*. Furthermore, one cannot exclude the possibility that females rely on a male's ability to locate the most suitable pond when her prior information about pond quality is too uncertain.

Females Use Waterborne Chemical Cues to Evaluate Larval Competition Risks

In experiment C, in which good call attractiveness was associated with the poor-quality pond, females preferred the poor call attractiveness associated with the good-quality pond. This result cannot be explained by biased conditions in the enclosure since the location of the contrasting treatments (poor call attractiveness associated with a more valuable breeding resource) was regularly alternated between tested females. Comparing the females' response to call attractiveness observed in this situation to the one observed when both ponds were of the same quality (i.e. the first trial within experiments A and B) clearly revealed that females preferred the pond associated with the less attractive call frequency because it was the one that was free of larvae. This implies that females use environmental cues such as waterborne odours to discriminate the relative quality of ponds without having to visit them. This result is in line with our previous study showing that when both types of pond are available (as in experiment C), females no longer preferred mating with the heavier male, but repeatedly preferred mating in larvae-free ponds with the same male (Cayuela, Lengagne et al., 2016). Female amphibians are particularly sensitive to environmental factors that may strongly alter offspring fitness (Dillon & Fiaño, 2000; Halloy & Fiaño, 2000; Matsushima & Kawata, 2005; Resetarits & Wilbur, 1989), and sensitivity to both intraspecific and heterospecific waterborne odours is well documented (Schulte et al., 2011). Given the negative impact of intraspecific larval competition on *B. variegata* (Jasieński, 1988), it would therefore not be surprising if females can discern tadpole-free ponds at a distance of at least 1 m. However, our results do not allow us to assess whether direct cues enable females to accurately determine various levels of larval density; further investigations are also required to investigate the distance at which females can assess larval density within ponds.

Environmental Quality Overrides Male Quality in Female Decision Making

According to the results from experiment C, it seems clear that information guiding expectancy about pond quality prevails over information guiding expectancy about mate quality in female decision making. One might thus expect females to apply hierarchical decision making based on both sources of information. Such hierarchical decision making is not uncommon and has been evidenced in several organisms (Alatalo, Lundberg, & Glyn, 1986; Møller & Jennions, 2001). The choice exhibited during the first trial within each experimental situation is congruent with such a decision-making process. This is also the case of the successive choices made when both ponds were of poor quality (i.e. experiment B), since females consistently preferred low-call frequency in this scenario and changed ponds after the location of the call advertisements was inverted. However, one may ask why females preferred coming back to the first visited pond rather than the unvisited pond during the second trial in experiment A, since in this case both ponds were of good quality, and the most attractive call was associated with the unvisited pond during the second trial. In the situation where prior information indicated that both ponds were likely of good quality, the subsequent choice of which pond to visit was not influenced in the same way as in the situation where prior information indicated that both ponds were likely of poor quality. During the second trial in experiment A, females had to choose between a confirmed good-quality pond, likely occupied by a poor mate, versus an expected pond of identical quality (at best), likely occupied by a good mate. In experiment B, females had to choose between a confirmed poor-quality pond, likely occupied by a poor mate, versus an expected pond of identical quality (at worst), likely occupied by a good mate. That females significantly preferred to revisit the same pond in experiment A although both ponds were of good quality could be explained by the fact that, by returning to the same site, females can minimize the costs of searching for a new breeding site and potential mate, or reduce the risk of losing a good-quality pond. In experiment B, the females had less to lose as the quality of both sites was poor. Furthermore, the outcome difference revealed by experimental situations A and B strongly suggests that females updated their decision in the subsequent trial according to an accurate assessment of the pond they initially visited. This would imply that females had memorized spatial information (i.e. location) about the pond according to its quality and that the mechanisms underlying female decision making incorporate uncertainty assessment. As in other amphibian species (Daneri, Casanave, & Muzio, 2011; Pašukonis et al., 2016), spatial learning and memorization likely play a critical role in the localization of a breeding habitat in the yellow-bellied toad. More broadly, it is also probable that such spatial cognition capabilities would be involved in habitat- and mate-searching processes, especially in environmental contexts where the spatial availability of breeding ponds is highly unpredictable (Cayuela, Boualit et al., 2016).

These results cast some doubt on the benefit associated with female choosiness in regard to call attractiveness. Rather than being associated with an indirect benefit of mating, the possibility cannot be ruled out that female preference for low-frequency calls actually results from a sexual selection process for sensory exploitation (Arnqvist, 2006; Fuller, Houle, & Travis, 2005; Ryan, Fox, Wilczynski, & Rand, 1990; Sherman & Reeve, 1999). This involves the evolution in males of traits that exploit a pre-existing bias in the female's sensory system (as opposed to Fisherian runaway sexual selection or the good genes hypothesis, which predict that male traits and female preference coevolve). For example, in the anuran *Physalaemus pustulosus*, males produce a two-component call that includes a 'whine', which is necessary for

species recognition, as well as 'chucks', which increase their attractiveness to females (Ryan et al., 1990; Ryan & Rand, 1990, 1993). In this species, female basilar papilla is biased toward a lower-than-average frequency in the 'chuck' portion of the male's call, so lower-frequency calls might be perceived as more intense and more easily localizable than high-frequency signals, explaining female preference for low-frequency calls produced by larger males (Ryan, Perrill, & Wilczynski, 1992).

Conclusion

Overall, the results of our study indicate that *B. variegata* females apply hierarchical decision making in which environmental cues associated with pond quality prevail over a male's call attractiveness. However, further research is needed in order to disentangle the relative contributions of habitat and male quality to offspring fitness; this would allow a better understanding of the evolutionary consequences of complex individual decisions in the context of sexual selection.

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Testosterone levels and relatedness predict male mating success in a pond-breeding amphibian

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Abstract

Introduction

In many organisms, females are highly selective when they come to mate since they invariably invest more energy in their gametes than males do (Darwin 1871, Andersson 1994). Females may choose their mates on the basis of direct benefits (parental care, food, shelter or protection from predators) or indirect (i.e. genetic) benefits provided by males to the descent (Clutton-Brock 1991, Andersson 1994). In non-resource-based mating systems, females are expected to select their mates according to genetic benefits (Kirkpatrick & Ryan 1991, Tregenza & Wedell 2000 Kotiaho et al. 2001). When males differ in heritable traits, females are assumed to choose the one(s) bearing genes that will improve offspring genetic quality, which is affected by both additive and nonadditive genetic variation (Neff & Pitcher 2005).

The 'good gene' model of sexual selection fits into the framework of additive genetic variation. It predicts that females benefit from mating with males with 'good genes' because their offspring inherit allele or combination of alleles that provide a better fit than average (Mays & Hill 2004, Neff & Pitcher 2005). Accordingly, the fitness benefits of offspring are a function of the haploid contribution of male alone (i.e. additive genetic variation). Empirical studies have confirmed the link between mate preference and increased offspring fitness, while the fitness effects have been often highlighted in a reduced set of progeny traits (Petrie 1994, Welch et al. 1998, Hine et al. 2002; but see Head et al. 2005) and appear small at only few percent (reviewed by Neff & Pitcher 2005). In many species, female chooses 'good' mates using elaborate traits displayed by males (e.g. sexual ornament or calling) that advertise male genetic quality (Iwasa et al. 1991). For the female, the honesty of these signals is attested by the costs they incur to the male, expressed in the handicap principle (Zahavi 1975). In this context, the immunocompetence handicap hypothesis (Folstad & Karter 1992, Roberts et al. 2004, Rantala et al. 2012) postulates that there is a trade-off associated with androgen level wherein elevations in testosterone level promote the development and the expression of such elaborate traits but simultaneously could compromise the immune system (Hasselquist et al. 1999, Peters 2000, Muehlenbein & Bribiescas 2005). Testosterone-mediated courtship displays might thus expected to provide females with 'honest signals' when choosing mates because only males that bear 'good genes' and are resistant to pathogens would be able to afford all the costs due to bearing cumbersome sexual attributes that are susceptible to reduce ease of movement and increase predation risks. Furthermore, elevated androgen levels could lead physiological costs by inducing immunosuppressive effects (Zahavi 1975, Hamilton & Zuk 1982, Folstad & Karter 1992).

On the ground of non-additive genetic variation, the 'compatible gene' model of sexual selection assumes that females are susceptible to increase the genetic quality of their offspring by choosing mates on the basis of interactions between their own and paternal genomes (Zeh & Zeh 1996, Tregenza & Wedell 2000, Neff & Pitcher 2005, Pryke & Griffith 2009). While the 'good genes model' states that an allele increases offspring fitness regardless of the architecture of the remaining genome,

the 'compatible gene' hypothesis postulates that an allele increases fitness when paired with a specific homologue (dominance and overdominance) or an allele at another gene locus (epistasis); i.e. nonadditive genetic variation. Three predictions have been made regarding female choice: first, due to the risk of inbreeding depression (Charlesworth & Charlesworth 1987, Crnokrak & Roff 1999), females could benefit by mating with unrelated males since heterozygous offspring experience lower expression of recessive deleterious mutations (dominance) and are superior *per se* since they produce a great variety of gene products (overdominance) (Pusey & Wolf 1996, Kempenaers 2007, Szulkin et al. 2013). Second, it has been hypothesized that female should mate with closely related males (Edmands 1999, Szulkin et al. 2013) since "outbreeding depression" (or "hybrid breakdown") reduces offspring fitness due to disruptions in local adaptation (i.e. genotype × environment interactions; Templeton 1986), underdominance (Schierup & Christiansen 1996) or epistatic interactions (Lynch 1991). Third, since both small and large genomic differences can entail negative fitness consequences, it has been predicted that females should select males with an optimal level of outbreeding (Bateson 1983, Puurtinen 2011).

If the effect of genetic dissimilarity in mate choice is widespread in vertebrates (Kamiya et al. 2014), its relative influence compared to selection based on quality indicators has been deeply discussed (Mays and Hill 2004) and the question of the selective pressures that drive the evolution towards one or the other mode of sexual selection remains open. A tactic of mate choice based on compatible genes could be favored when their costs linked with gene incompatibility are heavy such as in populations with low genetic diversity or in populations exposed to high risks of infectious disease (Colegrave et al. 2002). The experimental approach conducted by Roberts and Gosling (2003) led to the conclusion that both tactics can coexist and can be nested hierarchically. Plasticity and context-dependence should determine which tactic would dominate under current conditions. Low genetic diversity for male quality within the population, a low sensitivity of sexual ornaments to current pathogens (Mays and Hill 2004) or a relatively low diversity at the MHC loci should favor mate selection based on genetic dissimilarity. The benefits are thus to avoid inbreeding depression, increase heterozygosity in face of unpredictable disease while avoiding risks of auto-immune disorders (Kaufman 1999). Environment variation such as water salinity for sticklebacks (Evans et al. 2013) or habitat fragmentation (McCairns et al. 2011) can also influence the dominance of a tactic over the other.

Finally, the 'genetic bet-hedging' model has been proposed to explain the evolution of multiple mating (reviewed by Yasui 1998) and states that, when fitness varies over time, natural selection should favor evolutionary strategies eliminating high intergenerational variance in fitness. 'Genetic bet-hedging' model includes two hypotheses: first, 'genetic bet-hedging' constitutes a strategy reducing the probability that all of a female's eggs are fertilized by a single male of a low genetic quality (Yasui 1998, 2001) and/or a genetically incompatible male (Jennions & Petrie, 2000, Tregenza & Wedell 2000, Zeh & Zeh 2001). Second, in a variable environment, genetic bet-hedging, through an increase in genetic diversity in offspring (Yasui 1998, Fox & Rauter 2003, Crean & Marshall 2009), reduces

the probability that all of a female's eggs are fertilized by a male whose the genotype is unsuitable for the current environmental conditions (i.e. genotype × environment interactions). Polyandry is not an alternative tactics since it can combine with both 'good genes' and 'compatible genes' tactics according to environmental stochasticity.

Despite having been detected in all vertebrate taxa including amphibians (Garner and Schmidt 2003), mate choice based on genetic dissimilarity appears to play a secondary role in this last group compared with other taxa (Kamiya et al. 2014). Hypothetically, the fragmentation of populations and the adaptation to local conditions could favor mating tactics that avoid outbreeding (Bos et al. 2009, Luo et al. 2015). Our aim in this paper is to contribute to that question in empirically examining 'good genes', 'compatibles genes' and 'genetic bet-hedging' models in the yellow-bellied toad (*Bombina variegata*), which deals with unpredictable breeding sites. First, according to the prediction of 'good genes' model, we tested whether male mating success was positively related to plasma testosterone levels. Second, in accordance to the 'compatibles genes' model, we examined the hypothesis that male mating success depends on male-female relatedness. Nevertheless, since both outbreeding and inbreeding depression can cause decrease in offspring fitness, we did not predict a specific sense regarding the relationship between male success and relatedness. Third, according to the 'bet-hedging genetic' model, we tested the hypothesis that female increases the genetic diversity in offspring and partition their brood between several males.

Materials and methods

Biological model

The yellow-bellied toad is an anuran reproducing in small temporary ponds including rocky pools, residual puddles, ruts, and ditches (Cayuela et al. 2014, 2015a, 2015b). Fecundation is external and males compete for access to females by emitting acoustic courtship signals and exhibiting fighting behaviors (Schneider et al. 1986). Males are also territorial and use hydrodynamic wave signals as intra-sexual territorial advertisements (i.e. wave communication, see Elepfandt & Simm 1985, Seidel et al. 1999, 2001). The presence of post-vitellogenic follicles throughout the breeding season allows females to perform egg-clutch fractionation (Guarino et al. 1998), which more specifically consists in sharing their egg capital into several clutches (up to seven); this behavior could have contributed to the evolution of polyandry in this species (Barandun et al. 1997, Buschmann 2002).

Toad captivity and experimental design

Yellow-bellied toads were collected in 2013 in a metapopulation located in Ardeche, France (GIS coordinates: 4° 30' 12.2" E, 44° 52' 50.4" N). In this metapopulation, toads breed in a set of 29 pond

archipelagoes (i.e aggregation of small rocky pools located on riverbank) located along a 12-km long river segment. Immediately after their arrival at the laboratory, adults were sized and weighted and DNA was collected by non-invasive buccal swabbing. Males were kept indoors in a licensed animal facility, in a climatic room with a light/dark cycle of 18:6, corresponding to the natural light/dark cycle in the study area. They were individually housed in covered plastic boxes (0.35 × 0.20 × 0.20 m) until breeding trial commenced. Boxes were kept at a slight angle with 300 ml of purified tape water and water was changed three times per week. Males were fed crickets (*Acheta domestica*) *ad libitum*.

Female were all kept outdoors together in an enclosure (4 × 8 × 0.5 m) mimicking the environmental conditions prevailing in non-breeding aquatic locations used by females before and between intra-seasonal breeding sequences. The common garden was placed in a cool shaded place in which shallow water bodies (4 × 4 × 0.5 m) with a large amount of plant litter and four terrestrial shelters (i.e. half-buried tiles) were provided. Although a large amount of invertebrates was naturally available inside the common garden, females were fed 150 crickets twice a week. Since female ovulation is synchronized with rainfall (Barandun et al. 1997), we simulated automated artificial rainfall once a day (~ 1 hour).

Breeding trials were performed in a set of 10 outdoor experimental enclosures (2 × 4 × 0.5 m). Enclosures were subdivided in two equal part (2 × 2 × 0.5 m) separated from each other by a fence. In each part, a small pond (mimicking the original breeding site, see Cayuela et al., 2011, 2013) and a shelter (i.e. a half-buried tile) were placed. Two egg-laying sites (i.e. a bundle of grass) were placed on the water surface at each end of the pond to facilitate egg collection. Artificial rainfalls were simulated once a day (~ 15 minutes at the end of the day) using a network of large rotary water sprayers.

For each breeding trial (n = 30), we used one male from the same pond archipelago than the female and while the other male came from another pond archipelago, in order to contrast *a priori* male–female relatedness levels. Since body length (i.e. snout-vent length) and body condition are involved in mate selection in amphibians (Wells 2010), we performed breeding trials in which males were size-matched for body length and body condition. To assess the paternity over the course of each breeding trial, the males were equipped with randomly-assigned white or red belts. The experiment began with a first breeding trial where the two males were randomly added in one of the two parts of the enclosure. After a 24-hours period of male acclimation, one female was added to each common garden, and toads were allowed to breed for a period of up to 168 hours. Each of the ten common gardens was checked every one-and-a-half hours (time frame inferior to the minimum duration of an amplexus) and the position of both males and female was recorded. As soon as females laid their eggs, eggs were collected and counted while males were removed and placed in the second part of the common garden. After a new 24-hours period of male acclimation, the female was added again for a second breeding trial. The experiment ended when eggs were laid or when the time limit of 168 hours was exceeded. From three to seven days following the end of the second trial, adults were removed from the animal facility, checked for identity, and returned to the wild.

Salivary testosterone concentrations

We evaluated testosterone levels in saliva, which is noninvasive method used for wild species steroid quantification including amphibians (Janin et al. 2012, Desprat et al. 2015). We followed the protocol proposed by Desprat et al. (2015) in another anuran with a similar body size, *Hyla arborea*. A dry cotton ball of known mass was directly introduced into the toad's mouth at the end of each breeding trial. The amount of sampled saliva was given by the increase in cotton ball mass after mouth wiping. Then saliva was extracted from the cotton ball with the addition of 150 µL of a phosphate buffer (1 M phosphate solution containing 1% BSA, 4 M sodium chloride, 10 mM EDTA and 0.1% sodium azide) followed by a centrifugation. The levels of testosterone were estimated in duplicate with a colorimetric 96-wells testosterone Enzymo-Immuno Assay kit (EIA, number 582701, Cayman Chemical) according to the instructions of the manufacturer. The mean testosterone concentration measured in male saliva was 3.73 pg/ml (SD = 3.56, min = 0.01, max = 14.64) during the first breeding trial (N = 52 males) and was 4.04 pg/ml (SD = 4.64, min = 0.01, max = 18.40) during the second breeding trial (N = 42 males).

Microsatellite markers development and coancestry analysis

We developed new microsatellites markers to quantify male-female relatedness. Total genomic DNA was isolated from 14 individuals collected in four populations located in France (Lambert 93; POP1: E 821007.00, N 6421004.10; POP2: E 799277.70, N 6404519.90; POP3: E 929465.90, N 6777261.20; POP4: E 855608.40, N 6486026.80). DNA was extracted from buccal swabs following standard digestion (proteinase K [75 µg] + 200 µl of TNES buffer [0.05 M Tris, 0.1 M NaCl, 0.01 M EDTA, 0.5% SDS]) and salt-chloroform purification (adapted from Nürnberger et al. 2003). Total genomic DNA was sent to GenoScreen, Lille, France (www.genoscreen.fr). 1µg was used for the development of microsatellites libraries through 454 GS-FLX Titanium pyrosequencing of enriched DNA libraries as described in Malausa et al (2011). Briefly, total DNA was mechanically fragmented and enriched for AG, AC, AAC, AAG, AGG, ACG, ACAT and ATCT repeated motifs. Enriched fragments were subsequently amplified. PCR products were purified, quantified and GsFLX libraries were then carried out following manufacturer's protocols and sequenced on a GsFLX PTP.

Appropriate microsatellite motifs with suitable priming sites were subsequently identified. Among these, 119 microsatellite loci were selected according to the length of their repeat tract (5 minimum). They were tested for amplification using a pool of four *B. variegata* individuals from the four

populations. Next, polymorphism of amplifiable loci was evaluated using 10 or 11 non-pooled individuals from the four populations. Amplification and polymorphism were tested on 3% agarose gels. We selected 13 loci that appear to be polymorphic when tested 3% agarose gels.

We then added 8 other microsatellite markers previously described (Bv11.7, Bv11.2, Bv24.12 developed by Nürnberger et al. 2003; Bobom5F, Bobom8A, Bobom9H, Bobom10F, Bobom12F developed by Hauswaldt et al. 2007) to constitute 3 sets of 7 markers for simplex or multiplex polymerase chain reaction (PCR) amplifications. PCR reactions were conducted using the Type-it TM Microsatellite PCR Kit (QIAGEN) in a 10-µl volume containing 5 µl of QIAGEN Type-it Multiplex PCR Master Mix, 1,5µl of Primer Mix (2 µM except 4µM for Bobom9H and 6µM for Bv24.12), and 2 µl of DNA from chelex extraction or 1µl of DNA from chloroform purification. Cycling conditions were as follows: (i) one step of initial denaturation (5 min) at 95°C, (ii) between 31 to 38 cycles with denaturation (30s) at 95°C, annealing (90s) at a temperature between 48 and 59°C, extension (30s) at 72°C, and (iii) one step of final extension (30min) at 60°C. The forward of each primer pairs was labeled with a fluorescent dye: 6FAM, HEX (Sigma Aldrich), ATTO550 and ATTO565 (Eurofins Genomics). The 3 mixes were genotyped on a 3730xl DNA Analyzer (Applied Biosystems) by the Gentyane genotyping platform of the INRA in Clermont-Ferrand.

Table 1. Eight microsatellite loci from Bombina variegata with PCR primers, repeat motifs, size ranges (bp: base pair) and accession number

Locus	Primer (5'-3')	Repeat motif	Size range (bp)	Accession number
Bomvar_DLWD0	F: CAGCTGTATGGGTTATTTGGC R: GAAATTGTAAATTCTGCCAGGG	AC(8)	89-125	####
Bomvar_Cons470	F: GGCACGAGATTTGTCTCAGCTG R: GTTTACAGCGCTACGGAATCTG	TTA(5)	234-246	####
Bomvar_CUSGH	F: TACATACTACCTACCAGCACACCC R: TCAGATGGAGAGTATAGCGTGAGC	AC(13)	86-96	####
Bomvar_DORC3	F: GTAATTCAGTGTGCCTTATACGC R: ATTACTAGACAGACAGGCAGATGG	CTAT(10)	191-223	####
Bomvar_DM3QM	F: TCTAGTTAAAAGAAGCCTATGGAG R: CGGCATCTATCTCCTCTACTC	TATG(7)	89-101	####
Bomvar_4EMX7J	F: CCAGAACCATTGGCAGAAATTG R: GAACATTGTGCTTATTCCTGTGG	CTAT(6)	226-238	####
Bomvar_CWL3Z	F: ATGACAAACTACACATGCCACGC R: TTGAGACCCTCACGGGTGATTAG	CTAT(8)	95-103	####

For each locus, alleles were scored independently by two operators with GENEMARKER v.1.95 (SoftGenetics), using GS600 LIZ size standard (Applied Biosystems). Among the 13 new markers, 2 were eliminated because their expression profile was unreliable and 3 others were excluded because they were actually monophormic. The eight remaining markers are presented in Table 1. The characteristics of the complete set of 15 loci tested in the 4 populations of yellow-bellied toads and used in the following analysis are provided in Table 2. Observed and expected heterozygosity were calculated using GENALEX (Peakall & Smouse 2006). The detection of null alleles as performed

using the program MICRO-CHECKER 2.2.3 (Oosterhout et al. 2004). The inbreeding coefficient *Fis* and the deviation of Hardy-Weinberg were assessed with GENEPOP 4.1 (Rousset 2008).

Male–female relatedness were obtained using the relatedness estimators implemented in the software COANCESTRY (Wang 2011) (ranging from −1 (least similar) to 1 (identical): Queller & Goodnight (1989), Li et al (1993), Lynch & Ritland (1999) and Wang (2002). Population allele frequencies were estimated on the basis of all genotyped adults involved the mating trials (N = 75) and 210 additional individuals genotyped in the same population. To evaluate the robustness of the pairwise relatedness metrics provided by the four estimators, we performed simulations in COANCESTRY following Wang's advice (2011). Our simulations showed that the estimator proposed by Lynch & Ritland (1999) was the best adapted to our genetic data. The frequency distribution of *r*-values between females and males used in our breeding trials is provided in Fig.1.

*Table 2. Characteristics of the microsatellite markers developed in this study (the eight first from the left) and those published by Nürnberger et al. (2003) (Bv11.7, Bv11.2, Bv24.12) and Hauswaldt et al. (2007) (Bobom5F, Bobom8A, Bobom9H, Bobom10F, Bobom12F) in four populations in France. Na = mean number of alleles per locus, Ne = effective number of alleles per locus, Ho = observed heterozygosity, uHE = unbiased expected heterozygosity, HWE = deviation of Hardy-Weinberg equilibrium (*** = significant, ns = non-significant), Fis = inbreeding coefficient, Null = probability of null allele presence.*

		Bomvar_DLWD0	Bomvar_Cons470	Bomvar_CUSGH	Bomvar_DORC3	Bomvar_DM3QM	Bomvar_4EMX7J	Bomvar_CWL3Z	Bomvar_4EGYJ3	bv11.7	bv11.2	Bv24.12	Bobom8A	Bobom12F	Bobom10F	Bobom5F	Bobom9H
POP 1	Na	2	2	2	4	2	3	2	3	3	2	2	3	8	6	3	6
	Ne	1.49	1.63	1.18	1.57	1.65	1.02	1.13	1.07	1.35	1.24	1.86	1.43	1.77	2.39	1.23	1.95
	Ho	0.26	0.27	0.12	0.31	0.29	0.01	0.09	0.02	0.17	0.13	0.29	0.26	0.34	0.52	0.18	0.33
	uHE	0.33	0.39	0.15	0.37	0.40	0.02	0.12	0.07	0.26	0.20	0.46	0.30	0.44	0.58	0.19	0.49
	HWE	***	***	ns	***	***	***	***	***	***	ns	***	***	***	ns	ns	***
	Fis	0.24	0.34	0.14	0.12	0.33	0.50	0.25	0.68	0.23	0.17	0.30	0.17	0.22	0.07	0.00	0.31
	Null	0.07	0.34	0.03	0.05	0.10	0.04	0.06	0.10	0.19	0.12	0.40	0.06	0.09	0.04	0.00	0.11
POP 2	Na	2	1	3	3	3	1	2	2	1	2	2	4	3	4	2	3
	Ne	1.03	-	1.32	2.48	1.02	-	1.01	1.98	-	1.44	1.13	2.21	1.13	1.90	1.01	2.01
	Ho	0.03	-	0.17	0.36	0.02	-	0.01	0.42	-	0.24	0.10	0.29	0.03	0.27	0.01	0.45
	uHE	0.03	-	0.25	0.60	0.02	-	0.01	0.50	-	0.31	0.11	0.55	0.11	0.48	0.01	0.50
	HWE	ns	-	***	***	ns	-	-	ns	-	ns	ns	***	***	***	-	ns
	Fis	-0.01	-	0.30	0.39	-0.00	-	-	0.15	-	0.21	0.13	0.48	0.71	0.42	-	0.12
	Null	0.00	-	0.11	0.17	0.00	-	-	0.05	-	0.26	0.10	0.18	0.13	0.14	-	0.03
POP 3	Na	4	2	2	7	2	4	3	4	2	4	2	5	8	6	6	6
	Ne	1.53	2.00	1.46	3.72	1.89	1.29	2.06	1.25	1.67	2.83	1.07	2.42	4.89	2.68	2.26	2.97
	Ho	0.33	0.54	0.28	0.74	0.49	0.19	0.50	0.18	0.40	0.67	0.06	0.52	0.78	0.66	0.58	0.64
	uHE	0.35	0.50	0.32	0.73	0.47	0.23	0.51	0.20	0.40	0.65	0.06	0.60	0.80	0.63	0.56	0.66
	HWE	ns	ns	ns	ns	ns	***	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Fis	0.04	-0.07	0.11	-0.00	-0.03	0.16	0.02	0.10	-0.01	-0.03	-0.03	0.11	0.02	-0.05	-0.03	0.03
	Null	0.05	0.48	0.03	0.03	0.00	0.06	0.12	0.03	0.27	0.00	0.00	0.08	0.01	0.00	0.02	0.03
POP 4	Na	2	2	2	5	3	2	4	3	1	4	2	4	5	5	3	4
	Ne	1.82	1.97	1.95	2.83	1.63	1.05	1.78	1.56	-	1.95	1.01	1.98	3.61	2.69	1.06	2.13
	Ho	0.49	0.39	0.44	0.62	0.42	0.04	0.32	0.38	-	0.51	0.01	0.55	0.75	0.49	0.03	0.50
	uHE	0.45	0.50	0.49	0.65	0.39	0.04	0.44	0.36	-	0.49	0.01	0.50	0.73	0.63	0.05	0.53
	HWE	ns	ns	ns	ns	ns	-	ns	ns	-	ns	-	ns	ns	ns	ns	ns
	Fis	-0.09	0.20	0.10	0.04	-0.07	-	0.28	0.05	-	-0.04	-	-0.10	-0.03	0.23	0.39	0.06
	Null	0.00	0.49	0.03	0.13	0.00	-	0.16	0.00	-	0.14	-	0.00	0.01	0.07	0.06	0.01

Statistical analysis

First, to investigate whether females partition their brood between males, we examined a potential negative correlation between male mating success at the first and the second trial using a Kendall test. Then, we first checked for colinearity between male-female relatedness and testosterone levels recorded during both the first and the second trial. In absence of significant colinearity between the two explanatory variables, we examined our assumptions within a single analysis. Generalized linear mixed models (GLMM) with logistic link were used to investigate the effect of testosterone levels and male-female relatedness on male mating success. The two variables were zero-centered to fit a normal distribution and were then incorporated as well as their interactive effect as explanatory terms in the fixed part of the model. If not significant, the interaction was then removed from the model. Since dyads of male experienced two breeding trials, trials were introduced as a random effect in the model. Models were fitted using restricted maximum likelihood optimization. The significance of fixed effects was based on *F* statistic tests (Type III tests) using the Kenward-Roger method to approximate the degree of freedom (Littell et al. 2006). We assessed model fit by examining graphically the normality of the residuals using a quantile-quantile plot.

Then, we investigated how male mating status (mating failure *vs.* mating success) can induce variation in plasma testosterone levels. For that purpose, we used the testosterone level recorded at the end of the first breeding trial as a base line measure. Using GLMM, we then examined how the difference between the testosterone levels recorded at the end of the second trial and the base line is influenced by male mating status. We used the same procedure as described previously to assess the significance of fixed effects and to evaluate model fit. The male mating status was included as an explanatory term in the fixed part of the model while male dyads were introduced as a random effect.

Results

We performed 30 experiments where 30 male dyads had to experience two consecutive breeding trials. Among these 30 experiences, 27 males dyads successfully performed the first breeding trial (the female spawned and the egg clutch was fertilized by one of the two males). Among these 27 dyads, 19 dyads successfully performed the second breeding trial. Male-female relatedness (mean = 0.12, SD = 0.29; see also Fig.1) was not correlated to testosterone levels (mean = 3.52, SD = 3.43) recorded in the first breeding trial (χ^2 = -0.4698, df = 36, P-value = 0.6413); as well male-female relatedness was related to testosterone levels (mean = 4.04, SD = 4.64) in the second breeding trial (χ^2 = -1.5143, *df* = 36, *P*-value = 0.1387).

The Kendall test indicates that females did not partition their brood among the two males but was rather consistent in their choice between the first and second trial (τ = 0.58, *P*-value < 0.001). Male mating success was positively correlated to testosterone levels ($F_{1,39.13}$ = 9.78, *P*-value = 0.003; see Table 2, Fig. 2) and male-female relatedness ($F_{1,27.67}$ = 6.75, *P*-value = 0.01; see Table 2, Fig. 3). The difference between pre-mating and post-mating testosterone levels is marginally positively affected by male mating success ($F_{1,18.70}$ = 3.14, *P*-value = 0.09; see Table 3).

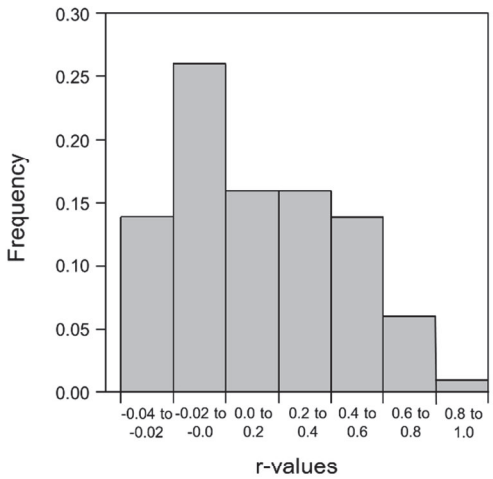


Fig.1. Frequency distribution of r-values between females (n = 27) and males (n = 54) in mating trials is biased towards high values.

Table 3. Male mating success in the yellow-bellied toad. Effects of testosterone levels and male-female relatedness on male mating success in the yellow-bellied toad, based on an ANOVA F-test type III, with degrees of freedom, and F and P values.

	Estimate	*Std* error	Residual *df*	*F*-value	*P*-value
Intercept	0.05	0.42	-	-	-
Testosterone	1.71	054	39.13	9.78	0.003
Relatedness	1.50	0.58	27.67	6.75	0.015

Table 4. Male mating success in the in the yellow-bellied toad. Effects of male mating status (mating failure vs. mating success) on the difference between the testosterone level recorded before and after the second breeding trial, based on an ANOVA F-test type III, with degrees of freedom, and F and P values.

	Estimate	*Std* error	Residual *df*	*F*-value	*P*-value
Intercept	0.14	0.22	-	-	-
Mating failure	-0.34	0.19	18.70	3.14	0.092

Fig.2. Male relative breeding success according to the relative plasma testosterone level (scaled values).

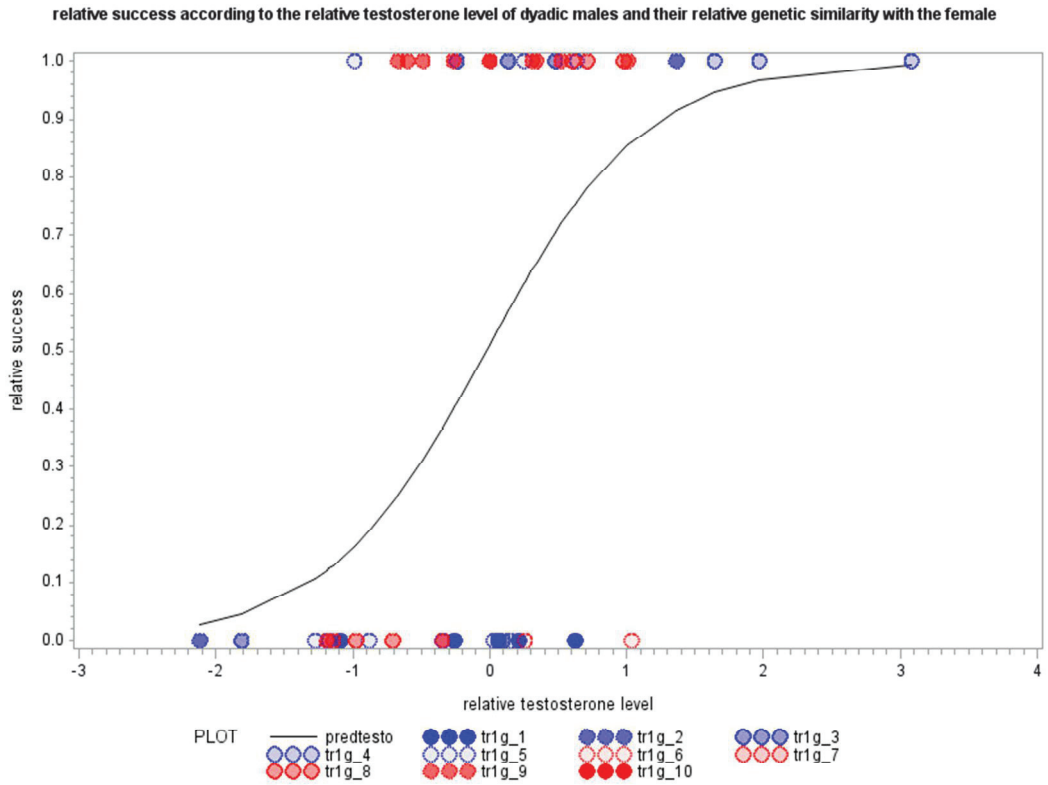
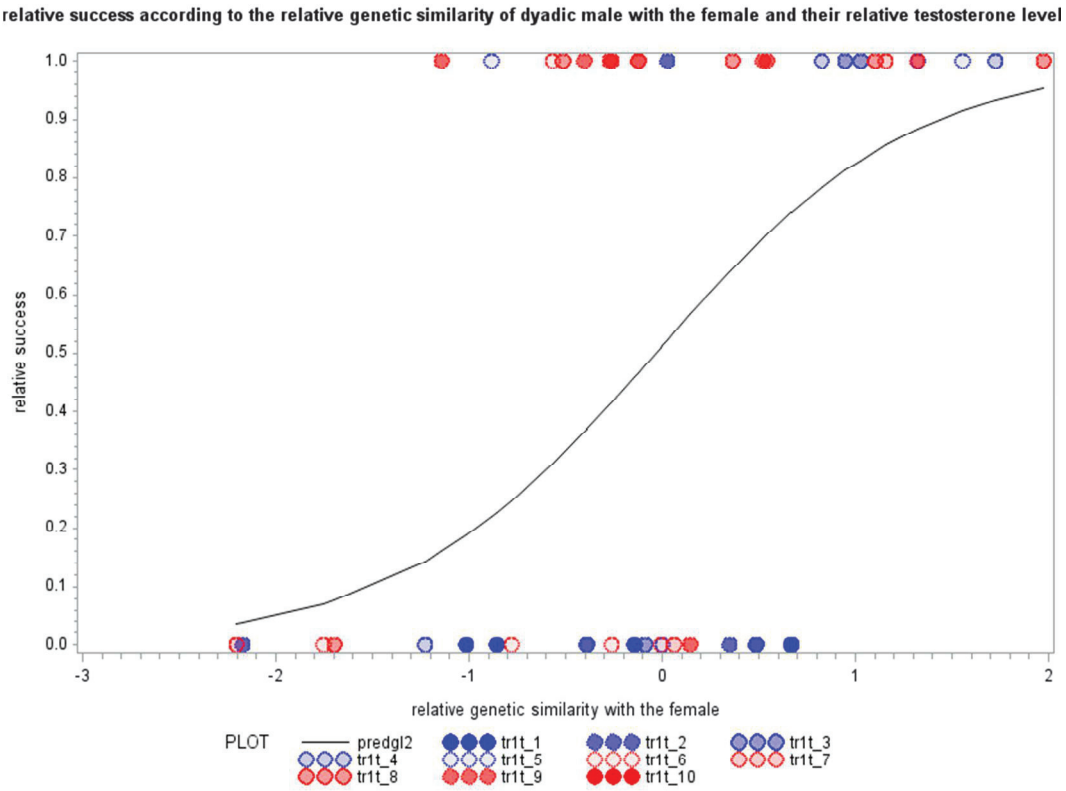


Fig.3. Male relative breeding success according to the relative genetic similarity (scaled values).



Discussion

We found no evidence that females increase offspring genetic diversity by partitioning their brood between different males. Our results indicated that male mating success was positively related to both testosterone levels and male-female relatedness levels. In addition, a statistically non-significant trend suggests that the difference between pre-mating and post-mating testosterone levels could be positively affected by male mating success.

No evidence of genetic bet-hedging

In amphibians, previous studies have shown that several male genotypes can provide a selective advantage to offspring in specific environmental conditions (Welch 2003), resulting from genotype × environment interactions. In the yellow-bellied toad, one might hypothesize that the broad spatio-temporal heterogeneity of environmental conditions prevailing during larval growth (Barandun & Reyer 1997, 1998, Cayuela et al. 2011) could lead to the evolution of genetic bet-hedging. Furthermore, in Bombinatorids, continuous production of oocytes during the breeding period and egg clutch fractionation allows sequential polyandry (Barandun et al. 1997, Guarino 1998, Buschmann 2002), which could facilitate the evolution of genetic bet-hedging (Byrne & Roberts 2012). Yet, we found no evidence that females increase offspring genetic diversity by partitioning their brood between different males. Rather, male mating success is better predicted by both plasma testosterone levels and male–female relatedness. However, in the field the fractionation of the clutch among different ponds should probably lead to a descent fathered by several males (Buschmann 2002). Our results nevertheless suggest that the mating rules that determine the female's choice do not vary from one pond to another.

Testosterone level influences male mating success

The relative difference in testosterone levels between males was a significant predictor of male mating success: the male with higher plasma testosterone concentration had a higher probability of siring offspring. In anurans, androgens, in combination with glucocorticoids, regulate the cycles of reproductive activity, as proposed in the energetic hormone-vocalization model (Emerson & Hess 2001). In particular, testosterone levels regulate reproductive behavior such as calling activity (Moore 1983, Marler & Ryan 1996, Moore et al. 2005, de Assis et al. 2012, Desprat et al. 2015), which is the best predictor of male mating success in many amphibian species (e.g. Ryan 1983, Gerhardt et al. 1987, Robertson 1990, Lopez & Narins 1991, Smith & Roberts 2003, Felton et al. 2006), including the

yellow-bellied toad (Schneider et al. 1986). Our results could thus be in line with the immunocompetence handicap hypothesis (Folstad & Karter 1992, Roberts et al. 2004), which states that as testosterone is responsible for the production of male secondary sexual traits influencing male fitness. However, further investigations are requested to clearly demonstrate that the cost of being able to express sexual acoustic signals lies in a decrease in the immune function in the yellow-bellied toad. In addition, because the amplexus behavior can cause significant increases in plasma gonadotropins (Gobbetti & Zerani 1999), differences in plasma androgens between sire and non-sire may be the result—rather than the cause—of the amplexus itself. Indeed, even if they are not statistically significant, our results also suggest that the difference between pre-mating and post-mating testosterone levels could be positively affected by male mating success. This trend is in accordance with previous studies showing that testosterone levels are higher in amplexing males than in non-amplexing males in anurans (Orchinik et al. 1988, Itoh & Ishii 1990, Gobbetti & Zerani 1999, Gramapurohit & Radder 2013).

Relatedness influences male mating success

The degree of male-female relatedness was also a significant predictor of male mating success. An abundant literature suggests that inbreeding avoidance is a common phenomenon in diverse taxa (e.g. Szulkin et al. 2009, Arct et al. 2010, Geffen et al. 2011, Lemaître et al. 2012), including amphibians (Waldman et al. 1992, Garner & Schmidt 2003, Jehle et al. 2007). However, in our study, outbreeding avoidance or inbreeding preference is the observed option. Observed levels of inbreeding depression widely vary in natural populations and theoretical studies showed that the magnitude of inbreeding depression the individuals should tolerate is often underestimated (Parker 1979, Lehmann & Perrin 2003, Kokko & Ots 2006) and strongly depends on the degree of iteroparity and the probability of mate encounter in each species (Kokko & Ots 2006). Furthermore, theoretical and empirical studies showed that outbreeding depression can also have negative fitness consequences such as risks of auto-immune diseases, and that there may be a substantial kin-selected benefit to mate with close relatives (LeBas 2002, Thünken et al. 2007, Szulkin et al. 2013). Genome rearrangements resulting from outbreeding may disrupt epistatic interactions that confer fitness advantages in specific environments (i.e. local adaptation, gene × environment interactions), as well as gene interactions that are independent of the environment. Three hypothesis could explain the pattern found in our study: first, stabilizing selection for optimal, intermediate genomic divergence has been documented in other species (Neff 2004) and could produce a pattern mimicking outbreeding avoidance if closely-related individuals are rare. However, this explanation is not likely in our focal population where the distribution of *r*-values among breeding adults is biased towards positive values (Fig.1). Alternatively, the presence of fine-scale population genetic structure associated with low dispersal rates among pond networks in our study area (Cayuela et al. in prep) may indicate that local adaptation and therefore

outbreeding avoidance are at least possible in our study system. Third, inbreeding avoidance is not a universal phenomenon and the yellow-bellied toad may simply be one exception among a handful of others that have already been described (e.g. Cohen & Dearborn 2004, Jennions et al. 2004, Thünken et al. 2007), including amphibians (Chandler & Zamudio 2008).

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DISCUSSION & PERSPECTIVES

Discussion générale et perspectives de recherches

Les acquis et les limites de cette thèse

De façon générale, ma thèse a montré que la variabilité spatio-temporelle de l'environnement du sonneur à ventre jaune constitue vraisemblablement une force sélective clé agissant sur la stratégie adaptative de cette espèce. Le sonneur à ventre jaune présente une tactique d'histoire de vie relativement lente, avec un fort degré d'itéroparité. Ceci constitue très probablement une réponse adaptative à une forte variance du succès reproducteur annuel due à la forte stochasticité des conditions de mise en eau de l'habitat de reproduction. Cette multiplication des occasions de reproduction est vraisemblablement corrélée à un processus de canalisation de la survie adulte, la composante de valeur sélective ayant le plus fort impact sur le taux d'accroissement démographique à long-terme chez les espèces longévives. Les sauts de reproduction (*breeding skipping*), déjà rapportées chez d'autres amphibiens (Muths et al. 2006, 2010, 2013, Church et al. 2007, Loman & Madsen 2010, De Lisle & Grayson 2011, Grayson et al. 2011, Price et al. 2012), constituent très probablement un trait comportemental impliqué dans ce mécanisme de réduction de la variance annuelle de la survie adulte. Ils semblent en particulier jouer un rôle important dans la limitation de l'impact des fluctuations météorologiques sur cette composante de la valeur sélective (Church et al. 2007). Si ces mécanismes démographiques sont bien connus chez les grands mammifères et les oiseaux (Gaillard et al. 1998, 2000, Gaillard & Yoccoz 2003, Boyce et al. 2006, Morris et al. 2008), ma thèse apporte à ce jour l'une des rares preuves empiriques de leurs existences chez les amphibiens. Elle met aussi l'accent sur la contexte-dépendance des effets météorologiques sur la dynamique des populations. Cependant, certaines limites posées par notre modèle biologique tempèrent la force de ces résultats. En particulier, notre incapacité à quantifier des paramètres démographiques aux cours des stades embryonnaires et larvaires constitue un frein dans l'utilisation de ce modèle, et du modèle amphibien de façon plus générale, pour traiter de questions démographiques.

Par ailleurs, nos analyses révèlent que la stratégie de longévité-itéroparité du sonneur à ventre jaune apparait relativement plastique. En effet, des fluctuations environnementales locales semblent conduire à des variations intraspécifiques des tactiques d'histoire de vie et à une régulation du positionnement des populations le long du *slow-fast continuum*. En particulier, ma thèse a permis de révéler qu'une augmentation du niveau d'imprévisibilité interannuelle des ressources de reproduction conduit à une accélération des cycles vitaux à l'échelle inter-populationnelle. Ces changements résultent probablement de modifications dans les schémas d'allocation de ressources entre les trois principaux postes de dépense énergétique que sont la maintenance, la croissance et la reproduction. De façon générale, les preuves de telles modifications des tactiques d'histoire de vie restent rares à l'échelle intraspécifique (Nilsen et al. 2009, Miller et al. 2011), ceci résultant plus vraisemblablement

de la rareté des données démographiques que de la faible fréquence de ces phénomènes. Malgré la confiance que nous plaçons dans nos résultats, reposant sur l'analyse de la démographie de cinq populations, nous encourageons de futurs travaux à confirmer ces conclusions en augmentant à la fois la profondeur des séries temporelles des données démographiques et le nombre de populations étudiées.

Dans notre système d'étude, la régulation de la vitesse des cycles vitaux est accompagnée par un syndrome de dispersion, impliquant une covariation entre la propension à disperser et certaines caractéristiques comportementales. Dans les environnements présentant un fort degré d'imprévisibilité interannuelle, les individus présentent une plus forte tendance à l'exploration et une plus faible timidité, deux traits comportementaux généralement reliés à la propension et/ou aux capacités dispersives individuelles (Clobert et al. 2009, Cote et al. 2010, Ronce & Clobert 2012) ; le patron inverse est mis en évidence chez les individus issus d'environnements présentant un fort degré de prévisibilité interannuelle. Nos élevages en *common garden* nous ont permis d'affirmer que ces traits résultent d'une transmission transgénérationnelle et ne constituent pas un simple produit de la plasticité phénotypique. Dans les métapopulations de sonneur à ventre jaune (au sens général du terme, i.e. populations spatialement structurées), ce syndrome se traduit par une augmentation drastique des taux de dispersion dans les environnements imprévisibles. Par ailleurs, ce syndrome est aussi associé à une réduction de la différentiation génétique au sein des métapopulations exposées à des environnements imprévisibles, résultant possiblement en une augmentation des flux de gènes. A notre connaissance, notre système d'étude constitue un des rares cas empiriques permettant d'établir des liens clairs entre des modifications des tactiques d'histoire de vie, l'émergence d'un syndrome de dispersion impliquant des traits comportementaux, ainsi que des modifications démographiques et génétiques à l'échelle des métapopulations. Néanmoins, les analyses présentées dans le manuscrit (article 3, Chapitre III) restent préliminaires en l'état actuel des choses. Par ailleurs, la portée de nos résultats est limitée par des verrous techniques et des contraintes liées au modèle biologique. Tout d'abord, en l'absence de mesures répétées après la métamorphose, il ne nous est pas possible de déterminer si les traits comportementaux mesurés dans les arènes sont exclusivement exprimés lors des phases de dispersion ou si ces comportements persistent dans différentes situations ou contextes et/ou cours de l'ontogénèse. En d'autres termes, il ne nous est donc pas possible de déterminer si ces traits comportementaux constituent des traits de personnalité animale (Bell et al. 2009, Stamps & Groothuis 2010), lesquels font l'objet d'un nombre grandissant de travaux chez les amphibiens (stade larvaire : Wilson & Krause 2012, Brodin et al. 2013, Carlson & Langkilde 2013 ; stade métamorphosé : Aragón 2011, Wilson & Krause 2012, Brodin et al. 2013, Maes et al. 2013, Candler & Bernal 2014, Gifford et al. 2014, Videlier et al. 2015). Ensuite, en l'absence de procédure de croisement entre des individus issus des différentes métapopulations, il ne nous est pas non plus permis de ségréguer dans ces traits comportementaux la part de variance explicable par des effets

maternels et celle liée à un déterminisme génétique. Enfin, s'il est tentant d'affirmer qu'un fort degré de différenciation génétique dans les métapopulations d'environnements prévisibles résulte d'une réduction des flux de gènes entre les sous-populations, il nous faut néanmoins rester prudent dans l'interprétation de ces patrons dans la mesure où il ne nous a pas été possible de tenir compte de la dérive génétique dans nos analyses. En effet, les mesures de différenciation génétique sont généralement impactées par la balance entre les effets homogénéisants des flux de gènes et les effets diversifiants de la dérive génétique qui interagissent généralement comme deux forces opposées (Prunier et al. 2015). Dans notre cas, il n'est pas possible d'écarter l'hypothèse alternative que des différences de taille de population effective soient la cause des divergences que nous avons détectées dans les degrés de différenciation génétique au sein des métapopulations étudiées.

Après avoir examiné comment le degré de prévisibilité interannuel des sites de reproduction et les conditions météorologiques affectent les traits d'histoire de vie et en particulier les décisions de reproduction, nous avons montré que la qualité des sites reproduction (i.e. risques de compétition au stade larvaire) exerce un fort impact sur la compétition entre mâles et sur les choix d'accouplement des femelles. En l'absence de compétiteurs larvaires dans les sites de reproduction, nos analyses révèlent que les femelles sélectionnent leurs partenaires sexuels en fonction de leur condition physique ainsi que de leurs caractéristiques de chants (i.e. fréquence fondamentale). Elles suggèrent aussi que, à taille et condition physique égales, les femelles préfèrent des mâles génétiquement plus apparentés. Ceci indique que, le choix d'accouplement des femelles étant condition-dépendant, la qualité génétique des jeunes pourrait bénéficier de variations génétiques additives et non-additives, en sélectionnant des mâles aux caractéristiques génétiques particulières. A ce titre, nos résultats sont en accord avec de précédents travaux mettant en évidence l'existence d'une sélection sexuelle biaisée par la condition physique des mâles (Castellano et al. 2009, Humfeld 2013) et les caractéristiques du chant (fréquences fondamental : Bosch & Márquez 2005, Burke & Murphy 2007, Richardson et al 2010 ; quantité de chant : Smith & Roberts 2003, Taylor et al. 2007 ; durée du chant : Castellano et al. 2000, Tarano & Herrera 2003) chez de nombreux anoures. Ils confirment aussi l'existence d'une sélection basée sur le degré de similarité-dissimilarité génétique entre partenaires sexuels chez les amphibiens (Garner & Schmidt 2003, Jehle et al. 2007, Chandler & Zamudio 2008, Bos et al. 2009, Caspers et al. 2014, Rausch et al. 2014, Rovelli et al. 2014, Luo et al. 2015 ; voir aussi Lampert et al. 2006). En cas de risque de compétition larvaire, les femelles présentent un choix hiérarchisé et donnent priorité à la qualité de l'environnement de développement larvaire s'il existe une discordance entre la qualité du site et celle du mâle. De façon générale, nos résultats confirment l'idée selon laquelle les fluctuations locales de l'environnement peuvent conduire à des changements dans la force, la forme et la direction de la sélection sexuelle en régulant la balance des coûts et bénéfices de valeur sélective dans les interactions mâle-femelle (Qvarnström 2001, Bussiere et al. 2008). A ce titre, ils pourraient laisser penser que différents régimes de sélection sexuelle sont susceptibles d'exister à l'échelle inter-

populationnelle, particulièrement si le degré de prévisibilité interannuel des sites de reproduction varie selon les populations. Néanmoins, nous ne disposons pas actuellement des données nécessaires pour examiner cette question. Les expériences réalisées par notre équipe de recherche ont utilisé des individus issus de populations exposées à différents régimes de stochasticité de l'habitat (environnements dits « prévisibles » *vs* « imprévisibles », chapitre II). Les expériences que j'ai conduites sur la contexte-dépendance et la hiérarchisation du choix d'accouplement des femelles en fonction du risque de compétition larvaire (article 1 et 2 du Chapitre II) ont impliqué des individus issus de métapopulations d'environnements imprévisibles. L'article 3 concernant l'influence des niveaux de testostérone plasmatique et du degré d'apparentement mâle-femelle sur le succès reproductif des mâles a, quant à lui, inclus des individus issus d'une population d'environnement « prévisible ». De futurs travaux devraient être entrepris pour évaluer si le degré de stochasticité de l'habitat est susceptible de constituer une force sélective agissant sur la compétition mâle-mâle et les règles de décision des femelles.

En résumé, la mise en œuvre pluridisciplinaire d'approches de suivi de terrain, d'analyse de patron de structuration et de diversité génétique, ainsi que de tests d'hypothèses en méso- et microcosmes m'ont permis d'échafauder un schéma conceptuel cohérent pour appréhender la stratégie adaptative de cette espèce d'amphibien originale dans des environnements contrastés, et par la même de contribuer aux réflexion nécessaires à sa conservation et à la gestion de ses habitats. De plus cette approche m'a permis d'établir les bases d'un programme de recherche dont je vais dans la dernière partie de cette discussion m'attacher à présenter les grands axes.

Les perspectives de recherche

Rôle des dommages oxydatifs dans la régulation des rythmes de vie dans des environnements au niveau de stochasticité contrasté

Nos résultats ont montré de nettes différences en termes de vitesse des cycles de vie en fonction du degré de stochasticité environnementale auquel les populations de sonneur à ventre jaune sont exposées. En particulier, nous avons mis en évidence que les individus provenant de populations dont les ressources pour la reproduction (i.e. archipels de pièces d'eau) sont instables et imprévisibles à l'échelle interannuelle présentent des durées de vie presque deux fois inférieurs, une fécondité réalisée (chez les femelles) deux fois supérieure et des taux de dispersion (de reproduction) près de 20 fois supérieurs aux individus issus de populations dans lesquelles les ressources reproductives sont stables et prévisibles dans le temps. Identifier et comprendre quels sont les mécanismes physiologiques impliqués dans la régulation des schémas d'allocation de ressources chez ces populations

constitueraient une contribution substantielle dans notre effort de connaissance des processus de vieillissement chez le vivant (Kirkwood & Austad 2000, Kirkwood 2002, Selman et al. 2012).

La théorie du « soma disponible » (*disposable soma theory*) est proposée pour la première fois par Kirkwood & Holliday (1979) pour expliquer l'évolution du vieillissement, c'est-à-dire l'accumulation de dommages cellulaires et moléculaires conduisant *ipso facto* à un déclin des fonctions biologiques et, par voie de conséquence, à un accroissement des risques de maladie et de mortalité à mesure que l'âge augmente. Cette théorie postule que l'investissement dans la croissance et la reproduction constitue un détournement de ressources (en particulier énergétiques) au détriment de la maintenance somatique ; la longévité serait déterminée au travers d'un compromis optimal entre la croissance et la reproduction d'une part et la maintenance somatique d'autre part. Ceci étant établi, un vieillissement accéléré et une durée de vie réduite sont donc fonctionnellement associés à des investissements en énergie eux-mêmes reliés au succès de la reproduction. Sur le plan physiologique, des dommages cellulaires causés par des espèces chimiques hautement réactives, sous-produits directs du métabolisme, constituent l'un des coûts impliqués par ces activités fortement demandeuses en énergie. La théorie des radicaux libres ou théorie du stress oxydatif (Rahman & MacNee 2002, Sies 2013) postule que des radicaux libres générés lors de l'oxydation phosphorylante dans les mitochondries (e.g. $ONOO^-$, $^{\cdot}O_2^-$ et $^{\cdot}RO$), entrainent des dommages chez différents composants cellulaires tels que les lipides, les protéines et les acides nucléiques (FIGURE 7). Un système sophistiqué de défenses anti-oxydantes enzymatiques et non-enzymatiques contrebalance et régule les niveaux généraux de radicaux libres pour maintenir l'homéostasie physiologique. Néanmoins, parce que ces défenses ne sont pas parfaitement effectives, les dommages oxydatifs induits par l'action des radicaux libres constituent très probablement un mécanisme métabolique clé jouant un rôle de régulateur dans les compromis d'histoire de vie (Harshman & Zera 2007, Dowling & Simmons 2009, Monaghan et al. 2009, Kim et al. 2010, Robert & Bronikowski 2010).

TABLEAU 3. *Prédiction concernant les mécanismes métaboliques régulant les compromis entre traits d'histoire de vie selon le degré de prévisibilité de l'environnement*

	Tactique d'histoire de vie rapide (environnements imprévisibles)	**Tactique d'histoire de vie lente** (environnements prévisibles)
Taux métabolique basal	+	-
Capacités oxydatives (*aerobic scope*)	+	-
Taux métabolique maximum	+	-
Production de radicaux libres	+	-
Ratio $\frac{ATP}{O_2}$	-	+
Détérioration ADN (somatique et germinal)	+	-
Détérioration protéines + lipides	+	-
Capacité de réparation ADN	+/-	+/-
Capacité de réparation protéines + lipides	+/-	+/-

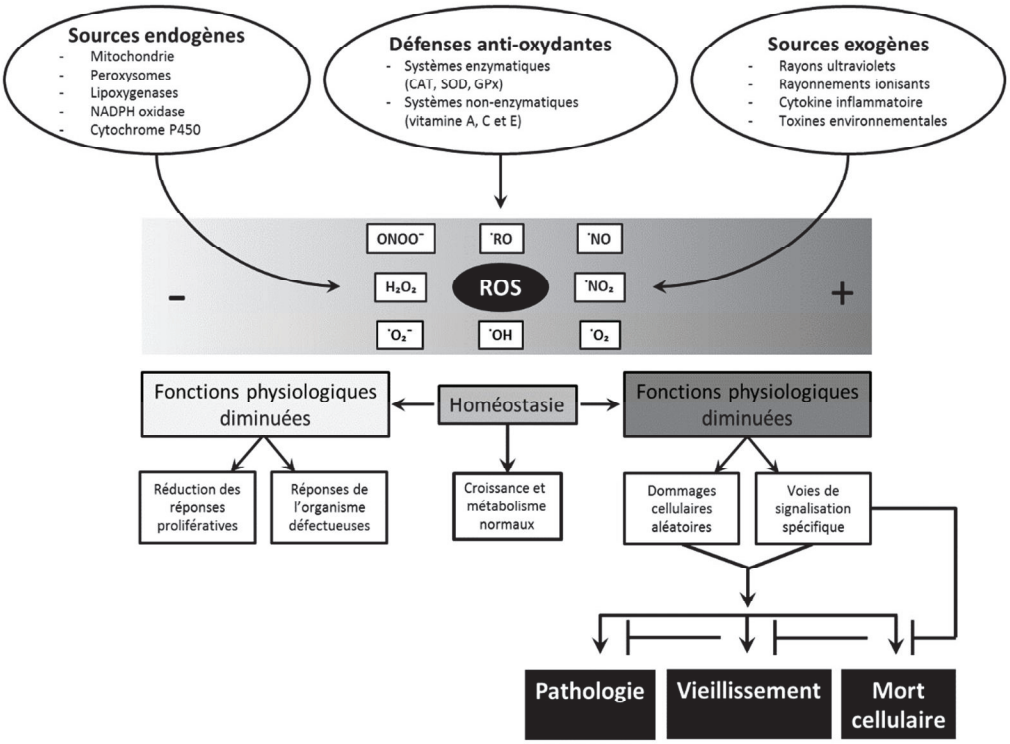

FIGURE 7. *Les oxydants constituent les sous-produits du métabolisme intracellulaire dans les mitochondries, les peroxysomes et dans les systèmes enzymatiques cytosoliques. La production de ROS (Reactive oxygen species ; ions oxygénés et peroxydes, rendus chimiquement très réactifs par la présence d'électrons de valence non appariés ; les radicaux libres sont un type de ROS) résulte aussi de multiples agents externes. Un système sophistiqué de défenses anti-oxydantes enzymatiques et non-enzymatiques contrebalance et régule les niveaux généraux de ROS pour maintenir l'homéostasie physiologique. Un abaissement de la production de ROS en-dessous du point d'homéostasie est susceptible d'interrompre le rôle physiologique des oxydants dans la prolifération cellulaire et la défense de l'hôte. De la même manière, un excès de ROS peut être délétère et conduire à un accroissement de la dégénérescence cellulaire, une accélération du vieillissement et le développement de pathologies liées à l'âge. Il est traditionnellement admis que les dégâts causés par une augmentation des ROS entrainent une détérioration des protéines, des lipides et des acides aminés. En plus de ces effets, un accroissement des niveaux de ROS peut aussi constituer un signal de stress activant des voies de signalisation spécifiques, sensibles aux réactions d'oxydoréduction. Une fois activées, ces diverses voies de signalisation peuvent avoir soit des effets dommageables soit des fonctions de protection. Adapté de Finkel & Holbrook (2000).*

Dans notre système d'étude, des prédictions quant aux mécanismes métaboliques régulant les compromis entre traits d'histoires peuvent être faites (**TABLEAU 3**). Chez les populations de sonneur à ventre jaune présentant une histoire de vie rapide et un syndrome du colonisateur, je fais l'hypothèse que les individus présentent des taux d'activité basaux et maximum (induit par un effort) ainsi que des capacités oxydatives plus importantes. Par voie de conséquence, je m'attends à une augmentation de la production de ROS, parmi lesquels des radicaux libres, qui devraient entrainer une augmentation des dommages sur les protéines, les lipides ainsi que sur l'ADN (à la fois nucléaire et mitochondrial) des lignées somatique et germinale. En revanche, aucune prédiction claire ne peut être raisonnablement faite à propos de capacités de réparation de l'ADN ainsi que des protéines et des lipides selon la tactique d'histoire de vie des individus.

Recherche de variation adaptative et de loci sous sélection dans des populations exposées à des environnements et à des niveaux de stochasticité contrastés

Nos résultats ont montré que le degré de stochasticité environnementale auquel sont exposées les populations de sonneur à ventre jaune régule la vitesse du cycle de vie ainsi que les taux dispersion. Nous avons aussi montré que des traits comportementaux reliés à la dispersion faisaient l'objet d'une transmission transgénérationnelle et que ces traits varient drastiquement selon le degré de stochasticité environnementale que subissent les populations, sans pouvoir néanmoins ségréger la part de variance explicable par des effets maternels de celle imputable à des effets génétiques. Une perspective de travail stimulante consisterait maintenant à montrer qu'il existe bien des variations adaptatives entre les populations exposées aux différents degrés de stochasticité. Puisque les caractères que confèrent les adaptations locales constituent généralement des traits quantitatifs polygéniques alors identifier des gènes candidats, évaluer leur implication dans les processus biologiques et analyser leur profil d'expression constituent une étape clé dans notre compréhension des réponses évolutives des populations à la variabilité de leur environnement.

Dans cette perspective, des marqueurs génétiques peuvent être utilisés pour rechercher l'existence de variations adaptatives entre les populations liées à des changements environnementaux et pour permettre d'évaluer la nature des processus sélectifs locaux (i.e. sélection directionnelle ou stabilisante) (voir le numéro spécial -22- de Molecular Ecology publié en 2013). Durant la dernière décade, des approches moléculaires tels que les micro-réseaux (i.e. microarrays) ou les méthodes de transcriptomique quantifiant des changements d'expression génique (Hoffmann & Willi 2008), les analyses QTL (quantitative trait loci, voir par exemple McKay & Latta 2002) ainsi que les approches de type genome-scan ont montré leur efficacité dans la détection de variations adaptatives inter-populationnelles et dans l'identification de loci candidats directement impliqués dans les réponses des populations aux changements environnementaux (Nosil et al. 2009).

Une première approche consisterait à rechercher des différences de polymorphisme et/ou de taux d'expression parmi des loci candidats connus et susceptibles d'être reliés à des différences phénotypiques observées dans les populations exposées à des degrés de stochasticité contrastés (voir par exemple Schwartz & Bronikowski 2013, Schwartz et al. 2015). Parce que des pertes hydriques et une hyperthermie peuvent constituer d'importants stress durant la phase de transfert de la dispersion chez les amphibiens (Wells 2010), les gènes HSP (trois familles de HSP chez les amphibiens ont été principalement étudiées : αA- et αB-crystallin, hsp30 et Bshsps ; voir Heikkila 2004) sont susceptibles de constituer des loci candidats dont le polymorphisme et les taux d'expression (constitutifs et inductibles) sont susceptibles de varier entre les populations de sonneur à ventre jaune différant par leurs taux de dispersion. Par ailleurs, puisque nos résultats montrent qu'il existe des différences de

type comportemental dans les populations selon le degré de stochasticité de l'habitat, des gènes reliés au comportement exploratoire (DRD4, e.g. van Oers & Mueller 2010) et d'agression (SERT, e.g. Müller et al. 2013) pourraient aussi constituer d'intéressants loci candidats. Enfin, on pourrait faire l'hypothèse que des gènes impliqués dans les capacités dispersives sont exprimés dans les tissus musculaires et interagissent de façon fonctionnelle avec des gènes liés au métabolisme enzymatique. Dans leur récente étude chez le crapaud buffle (*Rhinella marina*) en Australie, Rollins et al. (2015) ont identifié un groupe de loci candidats (KLF9, TDH, PSME4, PA200, CCNL2, UBE4B, SESN1, SLC6A6, TauT, KLF15, RASGEF1G, FAM134B et JK1) codant pour des enzymes métaboliques dont les taux d'expression varient entre les individus occupant le front d'invasion (avec une tactique d'histoire de vie *fast* et de fortes capacités dispersives) et ceux de la zone cœur de la distribution (tactique d'histoire de vie *slow* et faibles capacités dispersives).

Pendant longtemps, les comparaisons inter-populationnelles de patrons d'expression génique ont été limitées par la disponibilité des micro-réseaux (i.e. microarrays) chez les espèces non-modèles. Durant la dernière décennie, le développement des méthodes de séquençage massif (NGS) a permis de pallier ce problème chez les espèces non-modèles (Stapley et al. 2010, Orsini et al. 2013), puisque le comptage de séquences ESTs (séquences génomiques exprimées) renseigne sur la quantité d'information génique transcrite (Wolf 2013). A l'inverse de l'approche précédemment évoquée supposant une connaissance préalable de gènes candidats potentiels, une seconde consisterait à quantifier des différences dans l'expression du transcriptome (RNAseq) chez des individus élevés en conditions standardisées et issus de populations exposées à des environnements « prévisibles » ou « imprévisibles ». Cette approche permettrait d'identifier des loci candidats et d'appréhender leurs implications dans différents processus biologiques (voir par exemple, Lenz et al. 2013). Elle pourrait du reste être combinée à des approches de type QTL (quantitative trait locus, i.e. des zones du génome associées à une variation du trait quantitatif chez une progéniture issue de croisement génétique), lesquelles sont basées sur des analyses jointes de phénotypes et des génotypes dans le cadre de *design* de croisement.

En résumé, ces nouvelles perspectives devraient permettre de mieux comprendre les mécanismes physiologiques et génétiques sous-tendant les différences de traits comportementaux et d'histoire de vie mis en évidence dans ma thèse. Une première série d'expériences, visant notamment à quantifier des taux métaboliques chez des têtards élevés en *common garden* issus de différentes métapopulations de sonneur à ventre jaune, sera réalisée en 2016. La construction du transcriptome de référence de *B. variegata* est elle aussi programmée pour l'année 2016.

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ANNEXES

ANNEXE 1 : Matériel supplémentaire de l'article : Cayuela Hugo, Arsovski Dragan, Thirion Jean-Marc, Bonnaire Eric, Pichenot Julian, Boitaud Sylvain, Brison Anne-Lise, Miaud Claude, Joly Pierre, Besnard Aurélien. Contrasting patterns of environmental fluctuation contribute to divergent life histories among amphibian populations. Ecology 97:980-991. DOI: 10.1890/15-0693.1

Appendix A. Survey design and Environmental characteristics of the five studied populations of Bombina variegata.

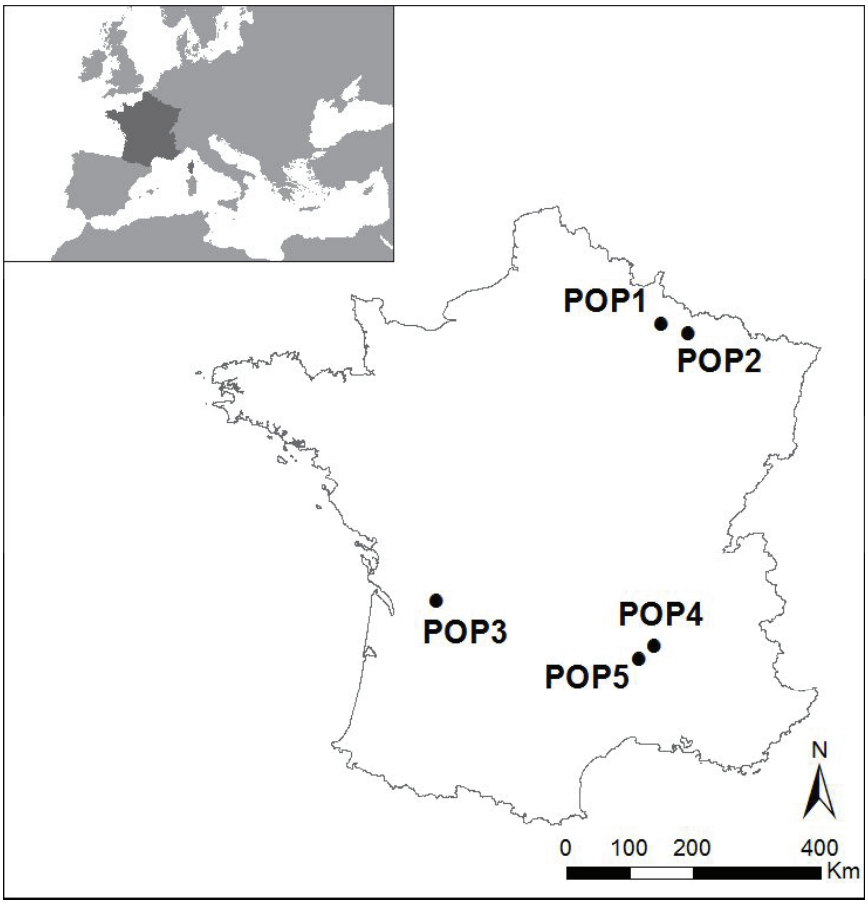


FIG. A1. Localization of the five studied population of *Bombina variegata*

TABLE A1. The five *B. variegata* populations studied and their main environmental characteristics. Weather characteristics were recorded during toad hibernation (October–March) and reproduction season (October–September). Precipitation and temperature values are given as the annual mean with the coefficient variation given as a percentage.

	Pond predictability	Pond origin	Hibernation		Reproduction	
			Precipitation	Temperature	Precipitation	Temperature
POP1	Unpredictable	logging, agriculture	69.27 (12.36%)	9.61 (17.24%)	69.12 (9.63%)	16.50 (14.22%)
POP2	Unpredictable	logging, agriculture	75.53 (20.36%)	7.73 (14.63%)	73.04 (10.93%)	14.65 (12.91%)
POP3	Unpredictable	logging, agriculture	79.98 (21.64%)	12.92 (6.88%)	69.05 (14.57%)	19.01 (7.88%)
POP4	Predictable	Natural erosion	110.12 (35.44%)	5.45 (25.05%)	99.62 (26.53%)	11.44 (18.10%)
POP5	Predictable	Natural erosion	114.24 (29.37%)	11.04 (12.73%)	104.65 (30.27%)	17.29 (12.99%)

TABLE A2. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP1.

POP 1					
	JUV	SUB	F	M	Number of secondary sessions
2000	39	4	39	36	6
2001	24	17	40	33	4
2002	2	7	36	34	4
2003	4	0	12	18	3
2004	0	1	5	10	1
2005	0	1	11	17	2
2006	60	25	32	23	9
2007	14	44	55	67	7
2008	61	33	75	74	9

TABLE A3. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP2.

POP 2					
	JUV	SUB	F	M	Number of secondary sessions
2008	828	1	495	472	3
2009	489	38	724	410	4
2010	335	131	669	593	4
2011	101	24	177	151	3
2012	471	127	576	590	3
2013	1093	465	483	455	3
2014	955	871	577	482	3

TABLE A4. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP3.

POP3					
	JUV	SUB	F	M	Number of secondary sessions
2005	0	8	18	21	5
2006	0	12	25	47	12
2007	0	12	28	31	11
2008	15	1	40	36	11
2009	48	22	44	36	12
2010	35	39	32	29	12
2011	25	23	25	34	13
2012	12	21	51	44	12
2013	35	3	49	46	12
2014	23	17	35	31	12

TABLE A5. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP4.

POP 4					
	JUV	SUB	F	M	Number of secondary sessions
2010	154	62	200	236	9
2011	52	124	174	214	9
2012	235	53	197	241	9
2013	56	177	170	214	6
2014	14	42	190	248	6

TABLE A6. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP5.

POP5					
	JUV	SUB	F	M	Number of secondary sessions
2010	145	8	109	155	9
2011	36	132	94	150	9
2012	60	35	109	177	6
2013	82	55	110	186	6
2014	31	52	139	221	6

Appendix B. Assessing a potential bias of vital rates resulting from the violation of the population closure assumption

Table B1. Number of 'extreme' sessions deleted each year to evaluate a potential bias of vital rates resulting from the violation of the population closure assumption in the five studied populations

	Year1	Year2	Year3	Year4	Year5	Year6	Year7	Year8	Year9	Year10
POP1	1	0	0	0	0	0	3	3	1	-
POP2	1	1	1	1	1	1	1	-	-	-
POP3	2	2	1	1	0	0	3	1	0	0
POP4	1	1	1	1	1	-	-	-	-	-
POP5	1	1	1	2	1	-	-	-	-	-

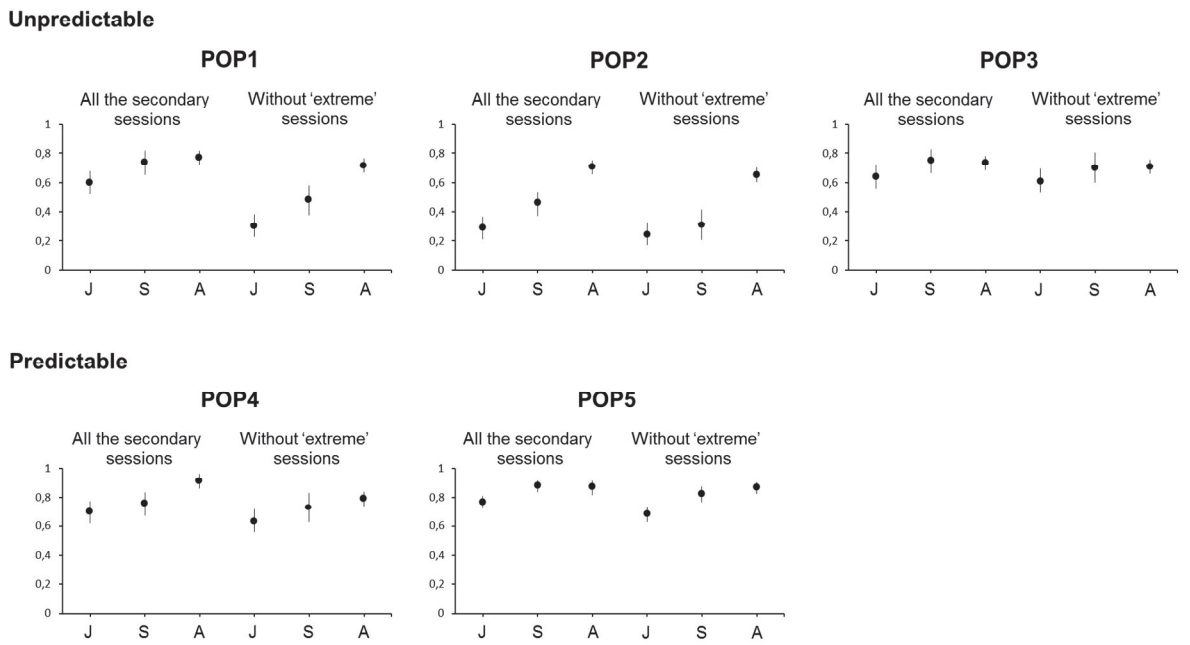


FIG B1. Comparison of survival variation at three ontogenetic stages (juvenile: J, subadult: S, adult: A) in the five studied populations of *B. variegata* with and without the removal of 'extreme' (i.e. few captured toads) secondary sessions. Because the violation of the closure assumption may bias survival estimates in robust-design like models? we evaluated the robustness of our analysis by removing secondary sessions during which few individual were encountered. Within a primary period, the secondary session during with the maximum number of encountered toads has been retained as the reference session for this year. For each primary period, we removed all the secondary sessions whose the number of captured toads was less than 50% below the number of toads encountered during the reference session. Then, we ran again the best-supported model using those new datasets. The mean estimates of survival (see figures below) are very close whether or not the extreme sessions are removed, except in POP1, in which juvenile and subadult survival is lower when extreme sessions are removed. The observed differences in the estimates in fact strengthen our conclusion that toad survival before sexual maturity is lower in 'unpredictable environments' than in 'predictable environments'.

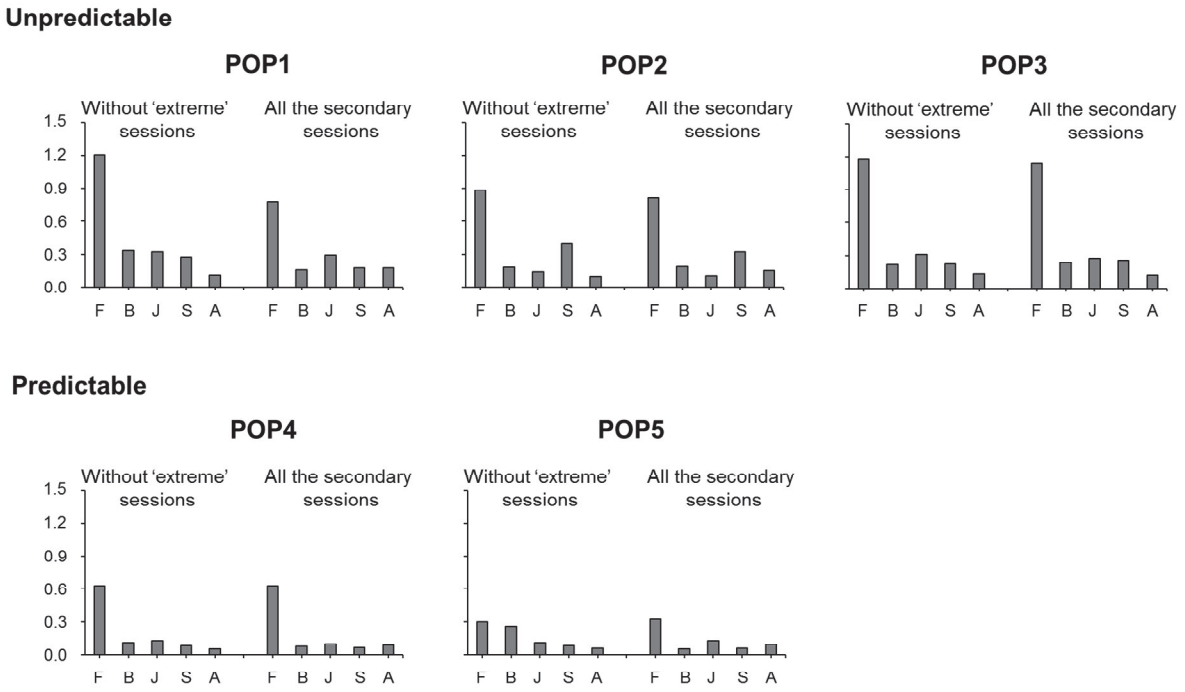


FIG B2. Comparison of demographic parameter variation (fecundity: F, breeding propensity: B, juvenile: J, subadult: S, adult: A) in the five studied populations of *B. variegata* with and without the removal of 'extreme' (i.e. few captured toads) secondary sessions. Because the violation of the closure assumption may bias survival estimates in robust-design like models, we evaluated the robustness of our analysis by removing secondary sessions during which few individual were encountered. Within a primary period, the secondary session during with the maximum number of encountered toads has been retained as the reference session for this year. For each primary period, we removed all the secondary sessions whose the number of captured toads was less than 50% below the number of toads encountered during the reference session. Then, we ran again the best-supported model using those new datasets. We examined whether or not the temporal variance of survival varies strongly when extreme sessions are removed. We found only marginal discrepancies that do not change our conclusion that temporal variation of vital rates is higher in 'unpredictable environments' than in 'predictable environments.

ANNEXE 2 . Matériel supplémentaire de l'article : Cayuela Hugo, Joly Pierre, Besnard Aurélien, Lengagne Thierry, Kaufmann Bernard, Bonnaire Eric, Pichenot Julian, Konecny Lara, Grolet Odile, Bellec Arnaud, Léna Jean-Paul. Habitat unpredictability shapes dispersal behavioral syndromes, dispersal dynamics and population genetic differentiation. Ecology, 97:2658-2670. DOI: 10.1002/ecy.1489

Appendix 1

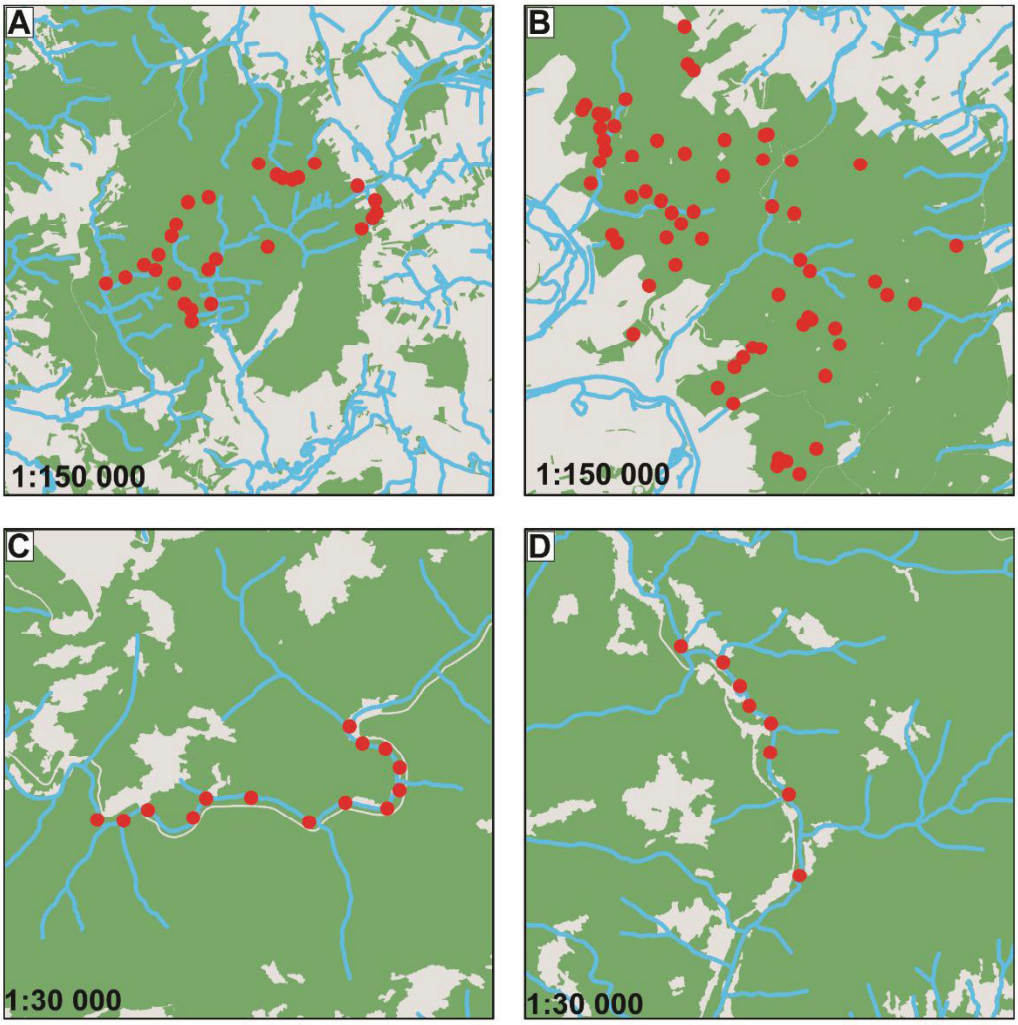


Figure 1A. Map showing the four studied metapopulations of *B. variegata*. Two of these metapopulations experience unpredictable environments (A, metapopulation BO; B, metapopulation VE) while the two other occur in predictable environments (C, metapopulation GL; D, metapopulation BG). In each metapopulation, toads were surveyed using capture-recapture method. The red points describe the pond archipelagoes occupied by *B. variegata* for breeding. The forest cover is shown in green and the rivers in blue.

Table 1A. Survey design characteristics for the four populations investigated in the study: study period, survey persistence, number of capture sessions performed during the survey period, total number of captures, number of individuals identified during the survey and the number of sampled pond networks.

Meta-population	Study period	Survey duration	Capture sessions	Number of captures	Number of individuals	Number of sampled pond networks
BO	2006–2008	3 years	9	638	305	28
VE	2012–2014	3 years	9	4587	2531	64
GL	2012–2014	3 years	9	2672	601	14
BG	2012–2014	3 years	9	1962	436	8

Table 1B. Environmental characteristics of the four studied populations: pond network persistence over years, pond origin (logging vs natural erosion), pond isolation (mean distance between two pond networks, and associated variation coefficient), pond network size (mean number of ponds within pond network and variation coefficient), climate characteristics during toad breeding season over the study period.

	pond network persistence	pond network origin	pond network isolation	pond network size
BO	1 to 10 years	logging activity	2864.50 (57%)	3.70 (70%)
VE	1 to 10 years	logging activity	4424.64 (53%)	5.64 (88%)
GL	>10 years	natural erosion	676.57 (61%)	4.52 (105%)
BG	>10 years	natural erosion	501.62 (61%)	4.71 (93%)

Appendix 2

We used the multievent capture-recapture model developed by Lagrange et al. (2014) to test the hypothesis that dispersal within metapopulations depends on the level of habitat unpredictability. This model allows to simultaneously estimating survival and dispersal probabilities among a large number of sites while accounting to recapture probabilities. Since heterogeneity of recapture probability has been already detected in previous studies on *B. variegata* (Cayuela et al. 2014), we modified the parameterization of Lagrange's model by including heterogeneity level states (see for instance Péron et al. 2010) to deal with this problem. The matrix of state-state transition and events has been modified as following:

Transition – step 1, survival probability

$$\begin{pmatrix}
\phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 1-\phi \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

Transition – step 2, site fidelity probability

$$\begin{pmatrix}
\alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

Transition – step 3, recapture probability

$$\begin{pmatrix} 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

Event – observation probability

$$\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix}$$

Table 2A. Model-averaging procedure for survival estimates. In the multi-events capture-recapture models, recapture probabilities always depend on an interaction between heterogeneity groups (HET) and time variation (TIME). Survival and dispersal probabilities can be constant (CST) or may vary between metapopulations (POP) and according to the level of environmental unpredictability (STATUS). Models are ranked according to AICc and relative AICc weights (*w*).

r	Model	w	AICc	S_{POP1}	S_{POP2}	S_{POP3}	S_{POP4}
1	$S_{(POP)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.68	19683.31	0.70 (0.04)	0.48 (0.01)	0.94 (0.02)	0.84 (0.02)
2	$S_{(POP)}, D_{(POP)}, P_{(HET \times TIME)}$	0.32	19684.83	0.70 (0.04)	0.48 (0.01)	0.94 (0.02)	0.84 (0.02)
3	$S_{(STATUS)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	19729.86	0.49 (0.01)	0.50 (0.01)	0.88 (0.01)	0.88 (0.01)
4	$S_{(STATUS)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	19731.38	0.49 (0.01)	0.50 (0.01)	0.88 (0.01)	0.88 (0.01)
5	$S_{(POP)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19828.78	0.70 (0.04)	0.48 (0.01)	0.94 (0.02)	0.84 (0.02)
6	$S_{(STATUS)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19875.34	0.49 (0.01)	0.50 (0.01)	0.88 (0.01)	0.88 (0.01)
7	$S_{(CST)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	20144.25	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)
8	$S_{(CST)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	20145.76	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)
9	$S_{(CST)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	20289.72	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)	0.69 (0.01)
	Model-averaged estimates			0.70 (0.04)	0.48 (0.01)	0.94 (0.02)	0.84 (0.02)

Table 2B. Model-averaging procedure for interannual dispersal estimates.

r	Model	w	AICc	D_{POP1}	D_{POP2}	D_{POP3}	D_{POP4}
1	$S_{(POP)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.68	19683.31	0.15 (0.02)	0.15 (0.02)	0.02 (0.00)	0.02 (0.00)
2	$S_{(POP)}, D_{(POP)}, P_{(HET \times TIME)}$	0.32	19684.83	0.19 (0.07)	0.14 (0.03)	0.01 (0.01)	0.02 (0.01)
3	$S_{(STATUS)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	19729.86	0.15 (0.02)	0.15 (0.02)	0.02 (0.00)	0.02 (0.00)
4	$S_{(STATUS)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	19731.38	0.19 (0.07)	0.14 (0.03)	0.01 (0.01)	0.02 (0.01)
5	$S_{(POP)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19828.78	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)
6	$S_{(STATUS)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19875.34	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)
7	$S_{(CST)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	20144.25	0.15 (0.02)	0.15 (0.02)	0.02 (0.00)	0.02 (0.00)
8	$S_{(CST)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	20145.76	0.19 (0.07)	0.14 (0.03)	0.01 (0.01)	0.02 (0.01)
9	$S_{(CST)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	20289.72	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)
	Model-averaged estimates			0.16 (0.04)	0.15 (0.02)	0.02 (0.01)	0.02 (0.01)

Table 2C. Model-averaging procedure for interannual dispersal estimates.

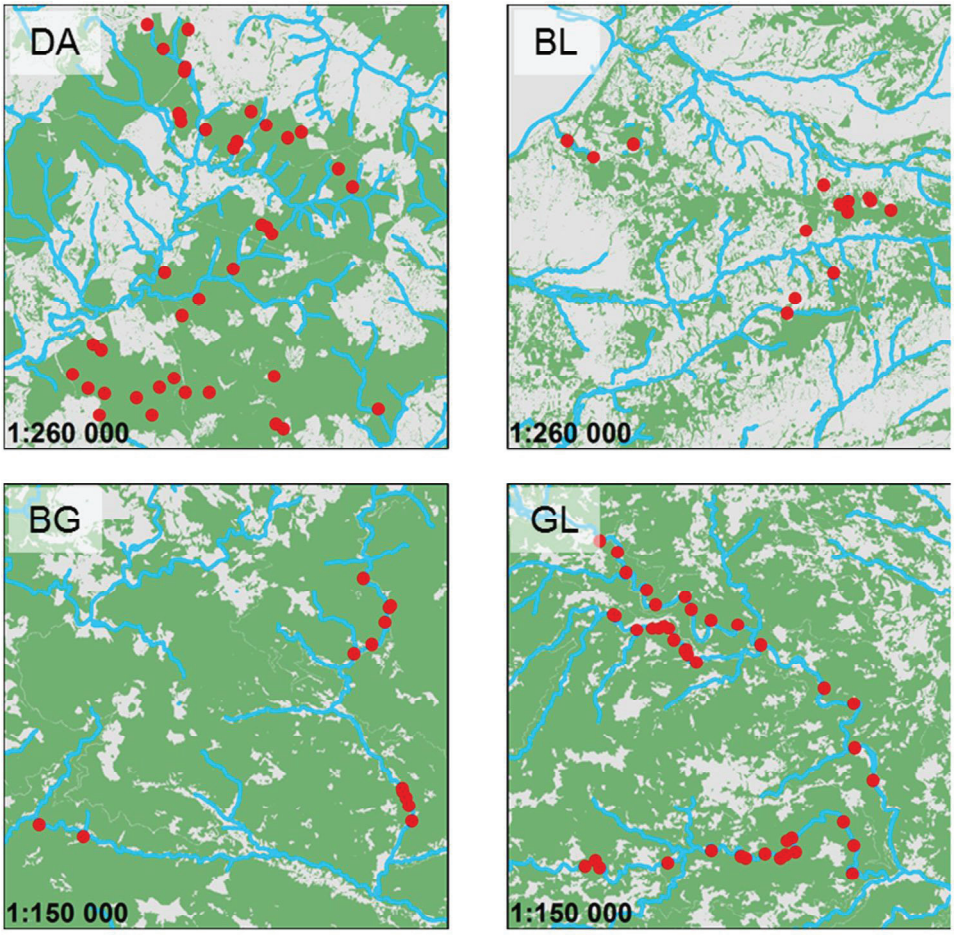
r	Model	w	AICc	D_{POP1}	D_{POP2}	D_{POP3}	D_{POP4}
1	$S_{(POP)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.68	19683.31	0.05 (0.01)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
2	$S_{(POP)}, D_{(POP)}, P_{(HET \times TIME)}$	0.32	19684.83	0.09 (0.02)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
3	$S_{(STATUS)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	19729.86	0.05 (0.01)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
4	$S_{(STATUS)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	19731.38	0.09 (0.02)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
5	$S_{(POP)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19828.78	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)
6	$S_{(STATUS)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	19875.34	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)
7	$S_{(CST)}, D_{(STATUS)}, P_{(HET \times TIME)}$	0.00	20144.25	0.05 (0.01)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
8	$S_{(CST)}, D_{(POP)}, P_{(HET \times TIME)}$	0.00	20145.76	0.09 (0.02)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)
9	$S_{(CST)}, D_{(CST)}, P_{(HET \times TIME)}$	0.00	20289.72	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)
	Model-averaged estimates			0.06 (0.02)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)

Appendix 3

Table 3A. Characteristics of the microsatellite markers developed in Cayuela et al. (submitted) (the eight first from the left) and those published by Nürnberger et al. (2003) (Bv11.7, Bv11.2, Bv24.12) and Hauswaldt et al. (2007) (Bobom5F, Bobom8A, Bobom9H, Bobom10F, Bobom12F) in metapopulations experiencing unpredictable environments (BG and GL) and predictable environments (BL and DA). Na = mean number of alleles per locus, Ne = effective number of alleles per locus, Ho = observed heterozygosity, uHE = unbiased expected heterozygosity, HWE = deviation of Hardy-Weinberg equilibrium (*** = significant, ns = non-significant), Fis = inbreeding coefficient, Null = probability of null allele presence.

		Bomvar_DLWD0	Bomvar_Cons470	Bomvar_CUSGH	Bomvar_DORC3	Bomvar_DM3QM	Bomvar_4EMX7J	Bomvar_CWL3Z	Bomvar_4EGYJ3	bv11.7	bv11.2	Bv24.12	Bobom8A	Bobom12F	Bobom10F	Bobom5F	Bobom9H
BG	Na	2	2	2	4	2	3	2	3	3	2	2	3	8	6	3	6
	Ne	1.49	1.63	1.18	1.57	1.65	1.02	1.13	1.07	1.35	1.24	1.86	1.43	1.77	2.39	1.23	1.95
	Ho	0.26	0.27	0.12	0.31	0.29	0.01	0.09	0.02	0.17	0.13	0.29	0.26	0.34	0.52	0.18	0.33
	uHE	0.33	0.39	0.15	0.37	0.40	0.02	0.12	0.07	0.26	0.20	0.46	0.30	0.44	0.58	0.19	0.49
	HWE	***	***	ns	***	***	***	***	***	***	ns	***	***	***	ns	ns	***
	Fis	0.24	0.34	0.14	0.12	0.33	0.50	0.25	0.68	0.23	0.17	0.30	0.17	0.22	0.07	0.00	0.31
	Null	0.07	0.34	0.03	0.05	0.10	0.04	0.06	0.10	0.19	0.12	0.40	0.06	0.09	0.04	0.00	0.11
GL	Na	2	1	3	3	3	1	2	2	1	2	2	4	3	4	2	3
	Ne	1.03	-	1.32	2.48	1.02	-	1.01	1.98	-	1.44	1.13	2.21	1.13	1.90	1.01	2.01
	Ho	0.03	-	0.17	0.36	0.02	-	0.01	0.42	-	0.24	0.10	0.29	0.03	0.27	0.01	0.45
	uHE	0.03	-	0.25	0.60	0.02	-	0.01	0.50	-	0.31	0.11	0.55	0.11	0.48	0.01	0.50
	HWE	ns	-	***	***	ns	-	-	ns	-	ns	ns	***	***	***	-	ns
	Fis	-0.01	-	0.30	0.39	-0.00	-	-	0.15	-	0.21	0.13	0.48	0.71	0.42	-	0.12
	Null	0.00	-	0.11	0.17	0.00	-	-	0.05	-	0.26	0.10	0.18	0.13	0.14	-	0.03
BL	Na	4	2	2	7	2	4	3	4	2	4	2	5	8	6	6	6
	Ne	1.53	2.00	1.46	3.72	1.89	1.29	2.06	1.25	1.67	2.83	1.07	2.42	4.89	2.68	2.26	2.97
	Ho	0.33	0.54	0.28	0.74	0.49	0.19	0.50	0.18	0.40	0.67	0.06	0.52	0.78	0.66	0.58	0.64
	uHE	0.35	0.50	0.32	0.73	0.47	0.23	0.51	0.20	0.40	0.65	0.06	0.60	0.80	0.63	0.56	0.66
	HWE	ns	ns	ns	ns	ns	***	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Fis	0.04	-0.07	0.11	-0.00	-0.03	0.16	0.02	0.10	-0.01	-0.03	-0.03	0.11	0.02	-0.05	-0.03	0.03
	Null	0.05	0.48	0.03	0.03	0.00	0.06	0.12	0.03	0.27	0.00	0.00	0.08	0.01	0.00	0.02	0.03
DA	Na	2	2	2	5	3	2	4	3	1	4	2	4	5	5	3	4
	Ne	1.82	1.97	1.95	2.83	1.63	1.05	1.78	1.56	-	1.95	1.01	1.98	3.61	2.69	1.06	2.13
	Ho	0.49	0.39	0.44	0.62	0.42	0.04	0.32	0.38	-	0.51	0.01	0.55	0.75	0.49	0.03	0.50
	uHE	0.45	0.50	0.49	0.65	0.39	0.04	0.44	0.36	-	0.49	0.01	0.50	0.73	0.63	0.05	0.53
	HWE	ns	ns	ns	ns	ns	-	ns	ns	-	ns	-	ns	ns	ns	ns	ns
	Fis	-0.09	0.20	0.10	0.04	-0.07	-	0.28	0.05	-	-0.04	-	-0.10	-0.03	0.23	0.39	0.06
	Null	0.00	0.49	0.03	0.13	0.00	-	0.16	0.00	-	0.14	-	0.00	0.01	0.07	0.06	0.01

Figure 3A. Map of the four studied metapopulations of *Bombina variegata* experiencing unpredictable (DA and BL) and predictable environments (BG and GL).



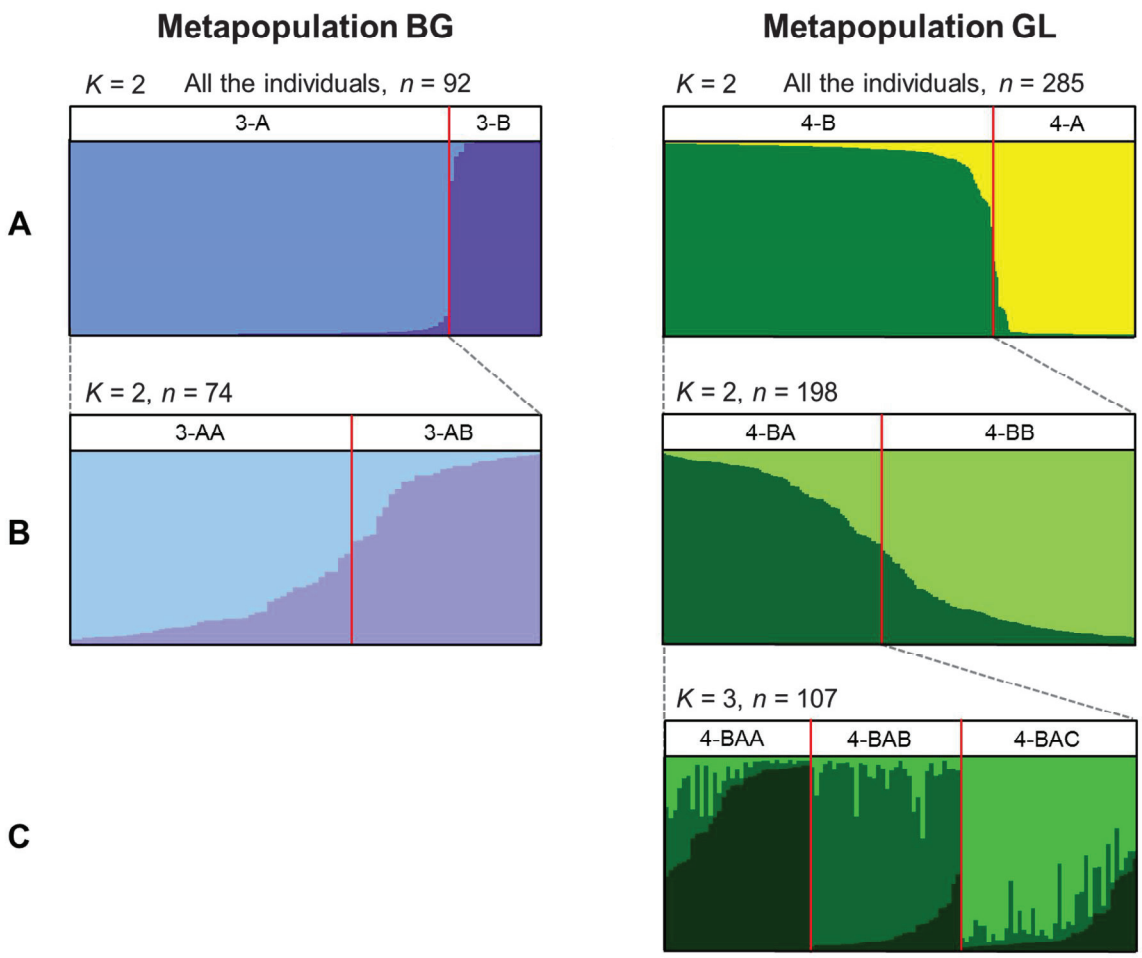


Figure 3B. Bar plots showing the results of hierarchical STRUCTURE analyses in the two metapopulations of *Bombina variegata* where genetic structuring was detected, i.e. BG and GL experiencing unpredictable environments. Each vertical line represent one individual: coloured segment indicate the estimated membership of that individual in each inferred genetic cluster. In metapopulation BG, two genetic clusters (K = 2) were initially inferred and hierarchical analysis revealed further genetic substructure for cluster 3-A in which two nested clusters (K = 2) were inferred, i.e. 3-AA and 3-ABB. In metapopulation GL, two clusters (K = 2) were initially identified, i.e. cluster 4-A and 4-B, and hierarchical analysis then highlighted further substructure within cluster 4-B (K = 2), i.e. 4-BA and 4-BB. Further genetic substructure was then identified within the cluster 4-BA (K = 3) and three new clusters were thus inferred, i.e 4-BAA, 4-BAB and 4-BAC.

ANNEXE 3. Matériel supplémentaire de l'article : Cayuela Hugo, Arsovski Dragan, Thirion Jean-Marc, Bonnaire Eric, Pichenot Julian, Boitaud Sylvain, Miaud Claude, Joly Pierre, Besnard Aurélien. Demographic responses to weather fluctuation are context dependent in a long-lived amphibian. Global Change Biology, 22:2076-2087. DOI: 10.1111/gcb.13290

Appendix S1. *Survey design and additional information regarding capture-recapture data in the five studied populations of Bombina variegata.*

Table 1. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP1.

	POP 1				
	JUV	SUB	F	M	Number of secondary sessions
2000	39	4	39	36	6
2001	24	17	40	33	4
2002	2	7	36	34	4
2003	4	0	12	18	3
2004	0	1	5	10	1
2005	0	1	11	17	2
2006	60	25	32	23	9
2007	14	44	55	67	7
2008	61	33	75	74	9

Table 2. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP2.

	POP 2				
	JUV	SUB	F	M	Number of secondary sessions
2008	828	1	495	472	3
2009	489	38	724	410	4
2010	335	131	669	593	4
2011	101	24	177	151	3
2012	471	127	576	590	3
2013	1093	465	483	455	3
2014	955	871	577	482	3

Table 3. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP3.

POP3					
	JUV	SUB	F	M	Number of secondary sessions
2005	0	8	18	21	5
2006	0	12	25	47	12
2007	0	12	28	31	11
2008	15	1	40	36	11
2009	48	22	44	36	12
2010	35	39	32	29	12
2011	25	23	25	34	13
2012	12	21	51	44	12
2013	35	3	49	46	12
2014	23	17	35	31	12

Table 4. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP4.

POP 4					
	JUV	SUB	F	M	Number of secondary sessions
2010	154	62	200	236	9
2011	52	124	174	214	9
2012	235	53	197	241	9
2013	56	177	170	214	6
2014	14	42	190	248	6

Table 5. Annual variation in numbers of secondary sessions and yellow-bellied toads in all ontogenetic stages (JUV juveniles, SUB subadult, F female, M male) in POP5.

POP5					
	JUV	SUB	F	M	Number of secondary sessions
2010	145	8	109	155	9
2011	36	132	94	150	9
2012	60	35	109	177	6
2013	82	55	110	186	6
2014	31	52	139	221	6

Appendix S2. *Complete selection model procedure for the five studied populations of Bombina variegata.*

Table 1. Model selection procedure for the first three populations of *B. variegata* (POP1, POP2, POP3) considered in the study: *r* model rank, *k* = number of model parameters, Dev. = deviance, QAICc = Akaike information criterion adjusted for a small sample size and their derivate quantities, AGE = age-specific variation (three ontogenetic stages considered: juvenile, subadult, adult), CST = constant, SEX = gender-specific variation, YEAR = year-specific variation, TXES = spring temperature, RRES = spring precipitation.

r	Model definition				*k*	Dev.	QAICc
	Survival	Breeding	Recruitment	Recapture			
POP1							
1	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	36	12,023.63	12,097.10
2	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	36	12,096.35	12,099.83
3	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	33	12,046.74	12,113.98
4	AGE	CST	YEAR	AGE × SEX + YEAR	31	12,064.59	12,127.69
5	AGE	SEX	YEAR	AGE × SEX + YEAR	33	12,063.77	12,131.01
6	CST	CST	YEAR	AGE × SEX + YEAR	29	12,076.41	12,135.37
7	RRES	SEX	YEAR	AGE × SEX + YEAR	31	12,073.26	12,136.35
8	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	36	12,065.90	12,139.37
9	AGE	RRES	YEAR	AGE × SEX + YEAR	32	12,076.65	12,141.81
10	CST	CST	YEAR	AGE+YEAR	28	12,086.06	12,142.95
11	TXES	SEX	YEAR	AGE × SEX + YEAR	31	12,081.05	12,144.15
12	CST	SEX	YEAR	AGE × SEX + YEAR	30	12,084.01	12,145.03
13	CST	CST	YEAR	AGE × SEX	21	12,718.52	12,761.03
14	CST	CST	YEAR	AGE	20	12,723.85	12,764.31
POP2							
1	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	32	127,945.92	128,010.03
2	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	32	128,097.73	128,161.84
3	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	30	128,150.22	128,210.32
4	TXES	SEX	YEAR	AGE × SEX + YEAR	28	128,254.72	128,310.81
5	RRES	SEX	YEAR	AGE × SEX + YEAR	28	128,310.43	128,336.52
6	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	33	128,271.37	128,337.50
7	AGE	RRES	YEAR	AGE × SEX + YEAR	29	128,345.08	128,403.17
8	AGE	CST	YEAR	AGE × SEX + YEAR	27	128,393.80	128,447.88
9	AGE	SEX	YEAR	AGE × SEX + YEAR	29	128,399.44	128,457.54
10	CST	CST	YEAR	AGE + YEAR	24	128,422.89	128,470.96
11	CST	SEX	YEAR	AGE × SEX + YEAR	27	128,430.35	128,484.43
12	CST	CST	YEAR	AGE × SEX + YEAR	25	128,438.80	128,488.87
13	CST	CST	YEAR	AGE × SEX	19	130,103.96	130,142.01
14	CST	CST	YEAR	AGE	18	130,116.44	130,152.48
POP3							
1	AGE	CST	YEAR	AGE × SEX + YEAR	33	19,703.59	19,770.20
2	AGE	SEX	YEAR	AGE × SEX + YEAR	35	19,699.57	19,770.26
3	AGE	RRES	YEAR	AGE × SEX + YEAR	35	19,699.64	19,770.33
4	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	38	20,064.71	20,141.52
5	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	38	20,095.56	20,172.37
6	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	37	20,122.99	20,197.77
7	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	35	20,131.52	20,202.21
8	TXES	SEX	YEAR	AGE × SEX + YEAR	34	20,147.56	20,216.21
9	RRES	SEX	YEAR	AGE × SEX + YEAR	34	20,151.08	20,219.73
10	CST	SEX	YEAR	AGE × SEX + YEAR	32	20,202.25	20,266.82
11	CST	CST	YEAR	AGE + YEAR	30	20,307.14	20,367.64
12	CST	CST	YEAR	AGE × SEX + YEAR	30	20,307.14	20,367.64
13	CST	CST	YEAR	AGE × SEX	22	20,718.04	20,762.31
14	CST	CST	YEAR	AGE	21	21,093.23	21,135.48

Table 2. Model selection procedure for the two last populations of *B. variegata* (POP4, POP5) considered in the study.

r	Model definition				*k*	Dev.	QAICc
	Survival	Breeding	Recruitment	Recapture			
POP4							
1	AGE × RRES	RRES	YEAR	AGE × SEX + YEAR	28	42,179.06	42,235.20
2	AGE × TXES	TXES	YEAR	AGE × SEX + YEAR	28	42,182.74	42,238.88
3	AGE	RRES	YEAR	AGE × SEX + YEAR	25	42,190.37	42,240.47
4	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	29	42,186.29	42,244.43
5	AGE × TXES	CST	YEAR	AGE × SEX + YEAR	26	42,202.66	42,254.78
6	AGE	CST	YEAR	AGE × SEX + YEAR	23	42,215.52	42,261.61
7	AGE	SEX	YEAR	AGE × SEX + YEAR	25	42,212.74	42,262.84
8	CST	CST	YEAR	AGE × SEX + YEAR	21	42,251.96	42,294.04
9	CST	SEX	YEAR	AGE × SEX + YEAR	23	42,248.42	42,294.51
10	RRES	SEX	YEAR	AGE × SEX + YEAR	24	42,229.87	42,277.97
11	TXES	SEX	YEAR	AGE × SEX + YEAR	24	42,236.14	42,284.24
12	CST	CST	YEAR	AGE + YEAR	20	42,309.33	42,349.40
13	CST	CST	YEAR	AGE × SEX	17	42,395.88	42,429.93
14	CST	CST	YEAR	AGE	16	42,456.78	42,488.83
POP5							
1	AGE × RRES	SEX × RRES	YEAR	AGE × SEX + YEAR	32	27,024.37	27,088.64
2	AGE × TXES	AGE × TXES	YEAR	AGE × SEX + YEAR	32	27,027.58	27,091.85
3	AGE × TXES	SEX	YEAR	AGE × SEX + YEAR	28	27,037.20	27,093.40
4	AGE	SEX × RRES	YEAR	AGE × SEX + YEAR	29	27,050.11	27,108.33
5	AGE	RRES	YEAR	AGE × SEX + YEAR	25	27,065.11	27,115.27
6	AGE	SEX	YEAR	AGE × SEX + YEAR	25	27,077.89	27,128.05
7	AGE	CST	YEAR	AGE × SEX + YEAR	23	27,088.06	27,134.20
8	RRES	SEX	YEAR	AGE × SEX + YEAR	24	27,093.66	27,141.81
9	TXES	SEX	YEAR	AGE × SEX + YEAR	24	27,095.60	27,143.75
10	CST	SEX	YEAR	AGE × SEX + YEAR	23	27,098.05	27,144.19
11	CST	CST	YEAR	AGE × SEX + YEAR	21	27,105.61	27,147.73
12	CST	CST	YEAR	AGE + YEAR	20	27,233.17	27,273.28
13	CST	CST	YEAR	AGE × SEX	17	27,239.64	27,273.72
14	CST	CST	YEAR	AGE	16	27,361.51	27,393.58