

Density-dependent life history and the dynamics of small populations

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Summary

1. Small population dynamics depend importantly on the strength and shape of density dependence. Unfortunately, the lack of reliable life-history data often prevents to make accurate demographic predictions for populations regulated by density dependence.

2. We created a gradient from low to high densities in small experimental populations of common lizards (*Zootoca vivipara*) and investigated the shape and strength of the density dependence of life-history traits during a yearly cycle. We then analysed stochastic population dynamics using one-sex and two-sex age-structured matrix models.

3. Body growth and reproductive performances decreased with density, yearling and adult survival and body size at birth were density-independent, and juvenile survival increased with density. The density dependence of reproduction was partly explained by positive effects of body size on age at first reproduction and clutch size.

4. Parturition date decreased with density in sparse populations and then increased, providing one of the first empirical evidence of a component Allee effect in the phenology of reproduction.

5. Population growth rate (λ) was most affected by variations in juvenile and yearling survival. However, density at equilibrium was most affected by juvenile access to reproduction and yearling clutch size.

6. Stochastic simulations revealed that negative density dependence buffers the effects of initial density on extinction probability, has positive effects on the persistence of sparse populations and interacts with sex ratio fluctuations to shape extinction dynamics.

7. This study demonstrates that negative density dependence modifies the dynamics of small populations and should be investigated together with Allee effects to predict extinction risks.

Key-words: age-structured population models, Allee effects, life-history variation, negative density dependence, population dynamics, small populations

Introduction

Density-dependent mechanisms are important drivers of population dynamics (Brook & Bradshaw 2006; Courchamp, Berec & Gascoigne 2008). Negative density dependence arises from intraspecific competition for limited resources and can affect individuals through consumptive (i.e. resources-based) and nonconsumptive (i.e.

social-based) effects (White 2001; Edeline *et al.* 2010). On the other hand, positive density dependence or Allee effects can arise from a reduced cooperation between conspecifics at low densities, from inbreeding depression or from a sex ratio bias (Courchamp, Berec & Gascoigne 2008). Population models demonstrate that negative density dependence can stabilize a population at low densities where the risk of extinction remains high (Morris & Doak 2002; Lande, Engen & Saether 2003), while the demographic Allee effect implies an unstable equilibrium below which deterministic extinction occurs (Courchamp,

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Berec & Gascoigne 2008). Unfortunately, density dependence is often ignored in models used to predict small population dynamics and is difficult to estimate in natural populations (but see Grant & Benton 2000; Henle, Sarre & Wiegand 2004; Zabel *et al.* 2006). Yet, even in small populations, density can be locally high and limit population growth (Grant & Benton 2000 and references therein). In addition, small populations are more prone to Allee effects caused by demographic stochasticity and sex ratio fluctuations (Legendre *et al.* 1999; Engen, Lande & Saether 2003; Bessa-Gomez, Legendre & Clobert 2004).

A wide range of functions has been proposed to describe the shape of density dependence (reviewed in Henle, Sarre & Wiegand 2004 and Courchamp, Berec & Gascoigne 2008). For instance, the θ -logistic model allows to model linear, concave or convex shapes of negative density dependence by changing the parameter θ (e.g. Saether, Engen & Matthysen 2002; Sibly *et al.* 2005). Different shapes of density dependence can either increase or decrease the extinction probability of populations (e.g. Morris & Doak 2002; Runge & Johnson 2002; Henle, Sarre & Wiegand 2004). However, in reality, the relationship between density and population growth is determined by the sensitivity of life-history traits to population density (Gilpin & Ayala 1973; Fowler 1981; Saether, Engen & Matthysen 2002; Courchamp, Berec & Gascoigne 2008). Therefore, a full understanding of density dependence and population dynamics requires a good knowledge of life-history responses to population density (Runge & Johnson 2002; Henle, Sarre & Wiegand 2004; Bassar *et al.* 2010). In general, demographic rates affecting the most the population growth rate should be the least affected by an increase in density (Eberhardt 1977, 2002). Yet, the most influential demographic rates for population growth rate in density-independent models are not necessarily those that influence the most density at equilibrium in density-dependent models (Grant & Benton 2000, 2003). Moreover, patterns of density dependence can be complicated by differences between sexes and stages in their sensitivity to density (e.g. Massot *et al.* 1992; Grant & Benton 2000; Coulson *et al.* 2001). Stage-specific and sex-specific life-history data are therefore often needed to produce realistic dynamics of structured populations regulated by density dependence (Coulson *et al.* 2001; Zabel *et al.* 2006).

Here, we used a realistic field experiment to investigate the relationship between density, life-history traits (including body growth, survival and reproductive traits), population growth and predicted extinction dynamics of the common lizard (*Zootoca vivipara*, Jacquin 1787). The common lizard is currently not endangered but populations at warm margins of the range are put at higher risks of extinction by climate warming (Massot, Clobert & Ferriere 2008). In order to characterize the shape and strength of the density dependence, we seeded outdoor enclosures with small populations of common lizards

following a gradient from low to high densities and we monitored experimental populations during a yearly cycle. Negative density dependence is an important regulatory mechanism in natural populations of common lizards because several components of population growth decrease with density (e.g. individual growth rate, body size, reproduction and dispersal, Massot *et al.* 1992; Lecomte *et al.* 1994, 2004; Le Galliard *et al.* 2006; Meylan, Clobert & Sinervo 2007). Adult survival is lower in males than in females, and the adult sex ratio is in average female-biased with significant spatial and temporal variation (Le Galliard *et al.* 2005). Therefore, a shortage of mates could also impact population growth in small populations.

We developed one-sex and two-sex age-structured population models parameterized with estimates of demographic rates obtained from experimental data. Two-sex models incorporated a mating function to investigate the potential interactions between density dependence and stochastic fluctuations in sex ratios and mating pair formation. Such stochastic fluctuations can arise from the interplay between demographic stochasticity, sex-specific survival rates and mating system and are crucial to consider in small populations but rarely accounted for (Legendre *et al.* 1999; Engen, Lande & Saether 2003; Bessa-Gomez, Legendre & Clobert 2004). This study advances our understanding of the density-dependent regulations of small populations. First, we provided a complete description of the sex- and age-specific patterns of the density dependence of life history, allowing us to detect for the first time in this species a component Allee effect in reproduction and juvenile survival. In addition, our models highlight the importance of negative density dependence in stochastic population dynamics and demonstrate that density dependence can interact with sex ratio fluctuations to give rise to a demographic Allee effect.

Material and methods

MODEL SPECIES

The common lizard is a small (adult snout-vent length, SVL: 50–75 mm) ovoviviparous species from humid habitats across northern Eurasia. It is characterized by a short life expectancy (3–4 years), a continuous growth and a polygynandrous mating system. Females produce one clutch per year with one to six genetic mates whereas males can successfully mate with up to fourteen females (Fitze *et al.* 2005). Natural populations can be divided into three age classes: juveniles (<1 year old), yearlings and adults (≥ 2 years old). In our study site (CEREPEP, Saint-Pierre-lès-Nemours, France), age at first reproduction varies between 1 and 3 years old (see Mugabo *et al.* 2010) and individuals reach about 85% of their asymptotic size by the age of 2 years (Fitze & Le Galliard 2008). SVL strongly influences age at first reproduction and clutch size in this species (Le Galliard, Marquis & Massot 2010; Mugabo *et al.* 2010). In natural populations from where individuals originate (Mont Lozère, southern

France), mean density ranges from 200 to 2000 adults and yearlings per ha (Massot *et al.* 1992). In our experimental system, the prebreeding equilibrium density is estimated around 2000 yearlings + adults per ha (Lecomte *et al.* 2004).

MANIPULATION OF POPULATION DENSITY

We manipulated the initial density of 24 experimental populations maintained in outdoor enclosures (see Lecomte *et al.* 2004 for a description of outdoor enclosures). Populations were established postbreeding following five density levels. The density level 1 had 1 adult male, 2 adult females, 2 yearling males, 2 yearling females, and 5–6 and 4–5 juvenile males and females, respectively (i.e. initial density N_0 equivalent to 700 adults + yearlings per ha). Density levels 2–5 differed from density level 1 by a multiplicative factor of 2–5, respectively, and had similar age- and sex-structures (i.e. density gradient from N_0 to $5N_0$). Initial age- and sex-structures fall within the range seen in the natural populations from where the lizards originated (proportion of adults range = 0.35–0.57, mean = 0.47 ± 0.09 SD Massot *et al.* 1992; adult sex ratio (ASR) range = 0.20–1, mean = 0.18 ± 0.18 SD, Le Galliard *et al.* 2005). The number of enclosures per treatment was adjusted to reach a similar sample size per treatment (density level 1: $N = 10$, level 2: $N = 5$, level 3: $N = 4$, level 4: $N = 3$, level 5: $N = 2$). Enclosures were randomly assigned to treatments.

Adults and yearlings were captured in May 2008, and all newborns were obtained from the captured gravid females. Individuals were marked by toe clipping, sexed, measured for SVL to the nearest mm and weighted to the nearest 0.01 g. Adults ($n = 162$) and yearlings ($n = 216$) were randomly assigned to experimental populations. Juveniles ($n = 549$) were released according to a split-clutch design such that juveniles from the same clutch were equally distributed among treatments and enclosures. At the start, treatment groups did not differ in SVL and body condition (estimated from an analysis of covariance of the log-transformed body mass including log-transformed SVL as a covariate; ANOVA, all $P > 0.34$). Adult and yearling males and nonreproductive females were released in outdoor enclosures on the 12th and 13th of June whereas postreproductive females and their juveniles were released right after parturition (from the 11th of June to the 23rd of July). Experimental populations were then monitored during 1 year.

MEASUREMENTS OF LIFE-HISTORY TRAITS

Life-history data were collected during two successive capture sessions carried out in 'August 2008' (from the 25th of August to the 11th of September, $n = 763$) and in 'May 2009' (from the 11th of May to the 14th of June, $n = 321$). Growth rates were calculated as the change in SVL divided by the time interval as defined in Mugabo *et al.* (2010). Annual survival probabilities were estimated from recapture data in May 2009, after the mating period, when the catchability is close to one. In May 2009, all reproductive females ($n = 104$) were kept in the laboratory until parturition to assess clutch size (total number of eggs), date of parturition, body condition after parturition and the SVL at birth of their viable offspring. Contrary to older females, not all females born in 2008 were sexually mature in late spring 2009. We therefore estimated the proportion of breeders within the group of released juveniles.

STATISTICAL ANALYSES

We investigated the relationship between population density and life-history traits using three alternative shapes of density dependence. For each trait we ran three sets of statistical models including a step function (density level as a factor), a linear regression or a quadratic regression. The best supported shape of density dependence was assessed using an information-theoretic approach based on Akaike Information Criterion (Burnham & Anderson 2002) as described below.

Density dependence in growth rates, body size, parturition date and postpartum body condition was assessed with hierarchical mixed-effects linear models in R 2.15.2 (<http://cran.r-project.org/>) following Pinheiro & Bates (2000) and Fox (2002). Density dependence in survival, proportion of breeding females among juveniles and clutch size was assessed with mixed-effects generalized linear models including a logit link function and binomial error terms for the two former and a log link function and Poisson's error terms for the latter following Bolker *et al.* (2009). All models included a random effect of enclosure identity and models of SVL at birth included a clutch identity effect nested in the enclosure effect. In addition, models describing juveniles' traits included a random effect of clutch identity to test for differences among families. Family reaction norms of annual growth rates and survival in response to density were quantified by including an interaction between the clutch identity random effect and the density effect following Nussey *et al.* (2005). The significance of random effects was tested with likelihood ratio tests (LRT).

The fixed part of all models included a treatment effect (i.e. a step, linear or quadratic function), a sex effect and their first-order interaction and the additive effect of release date. Whenever necessary, models also included an additive effect of age class and its first-order interaction with treatment effect. Additional fixed effects were (i) a linear effect of initial SVL when analysing growth rates to control for decelerating growth curves, (ii) a linear effect of recapture date when analysing SVL at recapture, and (iii) a clutch size effect corrected for female SVL (residuals of a linear regression) and a date of birth effect when analysing SVL at birth of offspring. These covariates were included because we already demonstrated that they can explain significantly life-history variation among individuals (Mugabo *et al.* 2010, 2011). All covariates were centred.

All models with normally distributed responses and nested random effects were fitted using a maximum likelihood (ML) approach in the *lme* procedure. Otherwise, models were fitted using a Laplace approximation of the ML in the *lmer* procedure. Assumptions of normality were fulfilled but Bartlett tests revealed significant variance heterogeneity between groups that we accounted for with a *varIdent* function in *lme* (not shown). For non-normally distributed responses, data did not show evidence of under or over dispersion (see Appendix S1, Supporting information).

For each studied trait, the best supported models were selected using an information-theoretic approach (Burnham & Anderson 2002) based on Akaike Information Criterion corrected for small sample size [(Q)AIC_c]. We calculated $\Delta(Q)AIC_c$ [difference with (Q)AIC_c of the best model] and (Q)AIC_c weight (w_i , a measure of the degree of support relative to the set of alternative models tested). First, we used a backward selection process starting from the full models to select the best supported model with the smallest number of parameters. Second, the total support of each

scenario of density dependence (linear, quadratic, step function or density independence) was calculated as the sum of (Q)AIC_c weights of all models based on this scenario (see Table 1). The scenario with the highest sum of (Q)AIC_c weights was considered as best supported. Model averaging was used whenever possible to obtain estimates of fixed effects from the set of models including the best supported scenario (*modavg* procedure, see Appendix S1, Supporting information for more details). For normally distributed responses, estimates were obtained by model averaging using a restricted maximum likelihood approach (REML).

Since age at first reproduction and clutch size are influenced by SVL in this species (Le Galliard, Marquis & Massot 2010; Mugabo *et al.* 2010), we further estimated the direct effects of density on juvenile access to reproduction and clutch size and indirect effects through density dependence of body growth using path analyses in the *sem* procedure. Path analyses also included all the explanatory variables accounted for in model averaging (Appendix S2, Supporting information).

POPULATION MODEL

Population dynamics were investigated using an age-classified matrix projection model with three age classes (juveniles, yearlings and adults). The model assumed a postbreeding census and a birth pulse reproduction (Caswell 2001). We analysed eight versions of this model (see Appendix S3, Supporting information for further details). First, we parameterized deterministic one-sex models with and without density dependence of demographic rates, and estimated the elasticity for each demographic rate (Grant & Benton 2000). Second, we developed a deterministic density-dependent two-sex model to predict the sex-structures at equilibrium and a deterministic density-independent two-sex model. Third, we developed four stochastic versions of the deterministic models listed above by including demographic stochasticity on all demographic rates and running individual-based simulations during 50 years (Appendix S3, Supporting information). Stochastic simulations were used to investigate the consequences of initial population density for the extinction risk (Legendre *et al.* 1999). Two-sex models assumed a male and

female coupled life cycle and a polygynous mating system with an unrestricted harem size (i.e. a single breeding male can inseminate all breeding females from the same population) or a harem size of 4 (i.e. a single male mates on average with four females). Model parameters and density dependence were estimated from our data (Appendix S3; Table C1, Supporting information), and initial age- and sex-structures were similar to the ones in our experiment. Calculations and simulations were carried out using ULM (Legendre & Clobert 1995).

Results

GROWTH RATE AND BODY SIZE

Density had negative short-term and long-term effects on body growth and body size (SVL) in all age classes (Appendix S1, Supporting information). During the summer, juvenile growth rate and SVL decreased quadratically with density (quadratic function best supported, Table 1), and density dependence was similar in males and females (total support of models without an interaction between density and sex = 0.73 and 0.87 for growth rate and SVL in 2008, respectively, Appendix S1; Tables A1–2, Supporting information). On the long-term, annual growth rate and SVL in May 2009 of juveniles also decreased quadratically with density (Table 1), but density effects were stronger in females than in males (total $w_i = 0.99$ and 1 for growth rate and SVL in 2008, respectively; Appendix S1; Tables A3–4, Supporting information, Fig. 1). Summer and annual growth rates and SVL varied between clutches (LRT, all $P < 0.02$). The analysis of reaction norms of annual growth rate revealed no significant differences in plasticity among families (clutch slope on density and correlation clutch intercept – clutch slope on density: LRT, all $P > 0.73$).

In adults and yearlings, short-term and long-term density dependence in growth and SVL differed between

Table 1. Total support [sum of (Q)AIC_c weights, ranging between 0 and 1] of the three scenarios of density dependence (DD, i.e. linear, quadratic or step function shape) and a density-independent scenario in the statistical models fitted for each life-history trait. Statistical models tested for each life-history trait are listed in Appendix S1 (Supporting information). The scenario with the best total support is bolded

Life-history trait	Linear DD	Quadratic DD	Step function	No DD
Summer growth in juveniles	0.39	0.50	0.11	0
Juvenile body size in August 2008	0.39	0.52	0.09	0
Annual growth in juveniles	0.03	0.90	0.07	0
Juvenile body size in May 2009	0.04	0.82	0.14	0
Summer growth in yearlings and adults	0.17	0.83	0	0
Yearling and adult body size in August 2008	0.59	0.41	0	0
Annual growth in yearlings and adults	0.75	0.25	0	0
Yearling and adult body size in May 2009	0.85	0.15	0	0
Juvenile annual survival	0.43	0.37	0.01	0.19
Yearling and adult annual survival	0.37	0.23	0.01	0.39
Juvenile access to reproduction	0.55	0.40	0.05	0
Parturition date	0.02	0.84	0.12	0.02
Clutch size	0.64	0.26	0.10	0
Postpartum body condition	0.69	0.14	0.06	0.11
Body size at birth	0.34	0.04	0.02	0.60

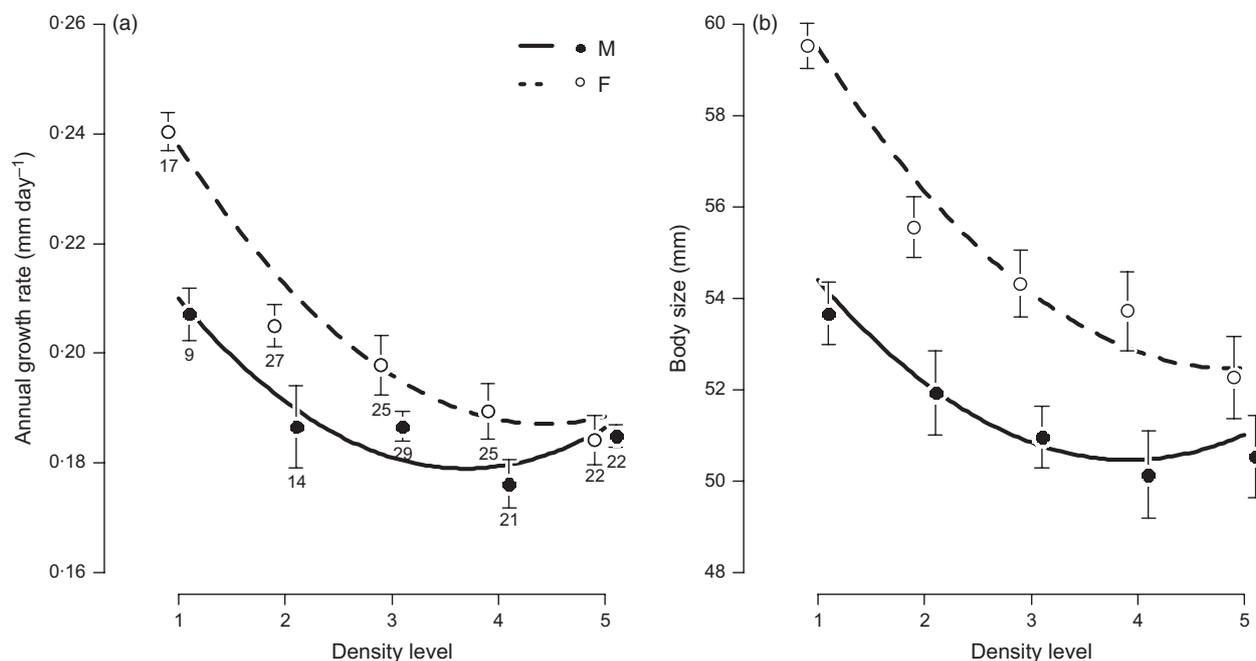


Fig. 1. Density dependence of annual body growth (a) and of snout-vent length (SVL) after 1 year (b) in juveniles. Estimates of regression lines were obtained by model averaging (Appendix S1, Supporting information). Data are given as mean \pm SE. F: females, M: males. Numbers indicate sample size in each treatment. Total numbers of individuals released per population ranged from 17, 34, 51, 68 and 85. Piecewise regression models in the *segmented* procedure showed that the significant quadratic effect for body growth was due to the existence of an inflection point at intermediate density levels. For body growth, inflection point was at a density level of 2.0 [(1.5, 2.6) 95% CI] in females and 2.1 [(1.3, 2.8) 95% CI] in males. For SVL, inflection points was at 2.0 [(1.1, 2.9) 95% CI] in females and 2.6 [(0.9, 4.3) 95% CI] in males.

sexes and age classes (all total $w_i > 0.91$ except for SVL 2008 where total $w_i = 0.35$ for models including an interaction between density and age class; Appendix S1; Tables A5–8, Supporting information). Body growth and SVL in males were not significantly affected by density (*post hoc F* tests, all $P > 0.09$), but our sample size at the end of the experiment was small ($n = 30$). In females, growth rate during the summer decreased quadratically with density, whereas annual growth rate and SVL decreased linearly with density (Table 1 and Appendix S1; Tables A5–8, Supporting information). Density dependence was stronger in yearlings than in adults. On the short-term, growth rate decreased slightly more linearly with density in yearlings than in adults (Appendix S1; Table A5, Supporting information; quadratic slope for yearlings = 0.0038 ± 0.0003 , adults = 0.0046 ± 0.0024). On the long-term, the linear decrease of growth rate and SVL was much stronger in yearlings than in adults (growth rate: Appendix S1; Table A7, Supporting information, slope for yearlings = -0.0070 ± 0.0014 , adults = 0.0020 ± 0.0018 ; SVL: Appendix S1; Table A8, Supporting information: slope for yearlings = -1.22 ± 0.23 , adults = -0.46 ± 0.26).

ANNUAL SURVIVAL

In juveniles, the linear scenario of density dependence was slightly more supported than the quadratic scenario

(Table 1 and Appendix S1; Table A9, Supporting information, Fig. 2). Juvenile survival tended to increase linearly with density, and males and females were similarly affected (total $w_i = 0.53$ for models not including an interaction between density and sex, Appendix S1; Table A9, Supporting information). Clutches of juveniles had similar annual survival (LRT < 0.01 , $P = 0.99$) and did not differ in their response to density (clutch slope on density and correlation clutch intercept – clutch slope on density: LRT, all $P > 0.90$). Yearling and adult annual survival was little influenced by density as the density-independent scenario received slightly more total support than the linear and quadratic scenarios (Table 1, Fig. 2). Annual survival was lower in males than in females in all age classes and was lower in adults than in yearlings (Appendix S1; Tables A9–10, Supporting information, Fig. 2).

REPRODUCTION

The proportion of breeding females among released juveniles decreased linearly with density on the logit scale (Table 1 and Appendix S1; Table A11, Supporting information; Fig. 3a). Path analysis revealed significant 'direct' density dependence for breeding (61% of total effect) and significant 'indirect' density dependence caused by body growth (39%; Appendix S2, Supporting information). Parturition dates varied quadratically with density (Table 1), but in different ways according to age class (total $w_i = 0.55$

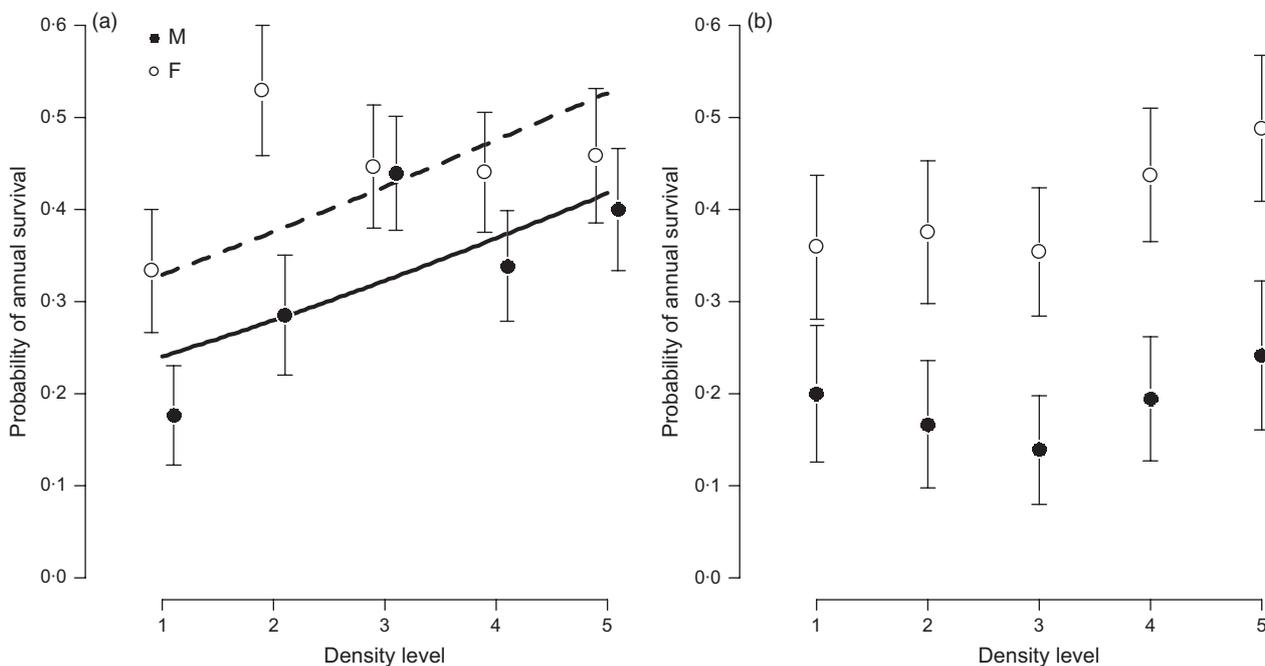


Fig. 2. Probability of annual survival in juveniles (a) and in yearlings and adults (b). Estimates of regression lines were obtained by model averaging (Appendix S1, Supporting information). Data are given as mean \pm SE. M: males, F: females.

for models including an interaction between density and age class, Appendix S1; Table A12 (Supporting information); Fig. 3). In juveniles and yearlings, parturition date was lowest at an intermediate level of density and highest in dense populations (Fig. 3c). In adults, parturition date decreased more linearly with density and was lowest at high density (Fig. 3d). Clutch size decreased linearly with density (Table 1, Fig. 3b, log slope = -0.13 ± 0.03). Age classes responded similarly to density (total $w_i = 0.43$ for models including an interaction between density and age class) but juveniles produced fewer eggs than yearlings and adults (total $w_i = 1$ for models including age effects, Appendix S1; Table A13, Supporting information; Fig. 3b). Path analysis revealed that 27% of total density dependence of clutch size could be attributed to 'indirect' effects through body growth (Appendix S2, Supporting information). Postpartum body condition also decreased linearly with density (Table 1). Density dependence was similar in all age classes (total $w_i = 0.93$ for models without an interaction between density and age class, Appendix S1; Table A14, Supporting information). The size at birth of viable offspring was not affected by density (Table 1 and Appendix S1; Table A15, Supporting information).

POPULATION DYNAMICS AND EXTINCTION RISK

The density-dependent deterministic model predicted a stable equilibrium (N_{eq}) of 43 lizards including 28 juveniles, six yearling females, four yearling males, four adult females and one adult male. Elasticity analyses indicated that the asymptotic growth rate λ was most affected by a change in juvenile survival, followed by yearling survival

(Table 2). Contrary to λ , N_{eq} was highly affected by a change in fecundity at 1 year old (fec_1) followed by fecundity at 2 years old (fec_2). High elasticities for fecundity were due to a high elasticity of the proportion of breeders at 1 year old (γ_1) and of clutch size at 2 years old (f_2 , Table 2). N_{eq} was less affected by changes in juvenile and yearling survival and was weakly affected by a change in the slopes of density dependence (Table 2).

The observed population growth rate after a yearly cycle decreased nonlinearly with density. Density dependence was steepest at an intermediate density and shallowest at low and high densities (Appendix S4; Fig. D1, Supporting information). Stochastic simulations demonstrated that density-independent models provided a poor fit of the relationship between observed population growth rate and density. The density-dependent one-sex model provided a very good fit of the observed population growth rates at high densities (density levels 4–5) but overestimated population growth at the lowest density (Appendix S4; Fig. D1, Supporting information). The density-dependent two-sex models provided the best fit of the shape of the relationship between the observed population growth and density but underestimated population growth, especially with a harem size of 4 (Appendix S4; Fig. D1, Supporting information).

Stochastic simulations further demonstrated that negative density dependence buffers differences in extinction probabilities among populations starting at different densities. In the one-sex density-independent model, the extinction probability gradually decreased with initial population density (Fig. 4a). In the density-dependent model, extinction probabilities were lower for all initial

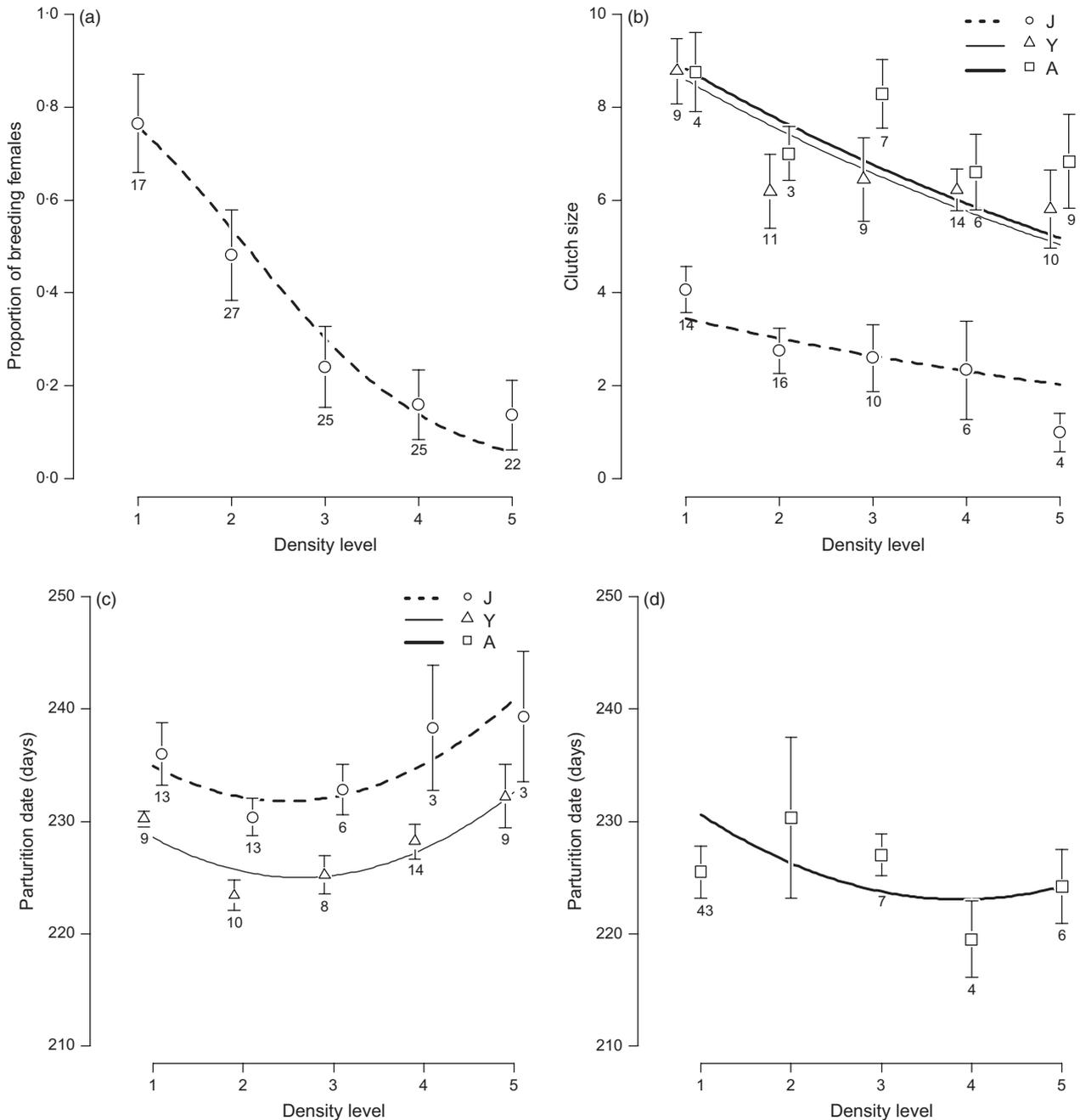


Fig. 3. Density dependence of the proportion of 1-year old breeding females (a, $n = 116$), clutch size (b, $n = 132$) and parturition date (c in juveniles and yearlings, $n = 88$ and d in adults, $n = 24$). Estimates of regression lines were obtained by model averaging (Appendix S1, Supporting information) Data are given as mean \pm SE. J: juveniles, Y: yearlings, A: adults. Piecewise regression models (see legend of Fig. 1) indicated a threshold for density dependence at a density level of 2.1 [(0.8, 3.4) 95% CI] and 2.2 [(1.5, 2.8) 95% CI] in juveniles and yearlings, respectively.

densities and more similar among populations except for the populations starting at low densities (Fig. 4b). As expected, accounting for sex ratio fluctuations and mating pair formation increased importantly the extinction probability, though this effect was much stronger in density-dependent models and interacted with density dependence (Fig. 4c,d, for an unrestricted harem size). Accounting for density dependence decreased the predicted extinction probability of initially sparse populations

(levels 1–2) but increased it importantly in initially dense populations (levels 4–5). Restricting the harem size to 4 (Appendix S4; Fig. D2, Supporting information) produced similar patterns but further increased extinction probabilities. To understand this interaction between density dependence and sex ratio fluctuations, we ran simulations of two-sex models with a harem size of 4 but no sex bias in yearling and adult mortality. Increasing male survival produced patterns similar to those predicted by

Table 2. Elasticities of the asymptotic growth rate (λ) and density at equilibrium (N_{eq}) for each demographic rate. Estimates of elasticities of λ and of N_{eq} are, respectively, from the density-independent one-sex model and the density-dependent one-sex model. For density-dependent demographic rates, elasticity of N_{eq} was also estimated for the strength of density dependence (see Appendix S3, Supporting information). Values between brackets give the ratio of the elasticity of demographic rates to the highest elasticity

Demographic rates	Elasticity of λ	Elasticity of N_{eq}
Annual juvenile survival	0.47 (1)	1.58 (0.20)
Slope of the density dependence of s_1	–	0.99 (0.12)
Annual yearling survival	0.38 (0.80)	2.57 (0.32)
Annual adult survival	0.16 (0.34)	1.08 (0.13)
Juvenile fecundity ($fec_1 = \gamma_1 \times f_1 \times hs_1 \times sr_1$)	0.09 (0.19)	8.07 (1)
Proportion of breeders (γ_1)	0.09 (0.19)	6.27 (0.78)
Slope of the density dependence of γ_1	–	–0.91 (0.11)
Total clutch size (f_1)	0.09 (0.19)	0.73 (0.09)
Slope of the density dependence of f_1	–	–0.20 (0.02)
Hatching success (hs_1)	0.09 (0.19)	0.58 (0.07)
Primary sex ratio (sr_1)	0.09 (0.19)	0.58 (0.07)
Yearling fecundity ($fec_2 = \gamma_2 \times f_2 \times hs_2 \times sr_2$)	0.26 (0.55)	4.69 (0.58)
Proportion of breeders (γ_2)	0.26 (0.55)	1.79 (0.22)
Total clutch size (f_2)	0.26 (0.55)	4.68 (0.58)
Slope of the density dependence of f_2	–	–0.62 (0.08)
Hatching success (hs_2)	0.26 (0.55)	1.79 (0.22)
Primary sex ratio (sr_2)	0.26 (0.55)	1.79 (0.22)
Adult fecundity ($fec_3 = \gamma_3 \times f_3 \times hs_3 \times sr_3$)	0.11 (0.23)	1.06 (0.13)
Proportion of breeders (γ_3)	0.11 (0.23)	0.78 (0.10)
Total clutch size (f_3)	0.11 (0.23)	1.07 (0.13)
Slope of the density dependence of f_3	–	–0.27 (0.03)
Hatching success (hs_3)	0.11 (0.23)	0.78 (0.10)
Primary sex ratio (sr_3)	0.11 (0.23)	0.78 (0.10)

one-sex models (Appendix S4; Fig. D2(C,D), Supporting information).

Discussion

PATTERNS AND MECHANISMS OF NEGATIVE DENSITY DEPENDENCE

Growth rate, body size and reproductive rates decreased linearly or weakly quadratically with density depending on the season, sex and age class. In a previous study, we demonstrated that effects of food availability on life history were strongly influenced by age class, sex and asymmetric social interactions between birth cohorts (Mugabo *et al.* 2010, 2011). Adult male common lizards are socially dominant over conspecifics and asymmetric competition for food between age and sex classes has been observed in the wild (Massot *et al.* 1992; Lecomte *et al.* 1994; Mugabo *et al.* 2010, 2011). Here, we found that negative density dependence was stronger in juveniles than in yearlings and adults and was stronger in females than in males, with adult males being little affected by density. These results are in accordance with previous observations and point to asymmetric trophic and/or social interactions.

Negative density dependence can be triggered by consumptive (resource-based) and nonconsumptive (social-based) effects (White 2001; Edeline *et al.* 2010). In

crowded environments, competition for food can reduce the amount of energy available for structural growth and reproduction (White 2001; Amundsen, Knudsen & Klemetsen 2007). In addition, a decelerating density dependence on body growth is classically explained by a curvilinear density dependence of feeding rates (e.g. Jenkins *et al.* 1999; Grant & Imre 2005; Amundsen, Knudsen & Klemetsen 2007). Our growth and reproduction data thus suggest that population density decreased feeding rates in juveniles over the year, as well as summer feeding rates in yearling and adult females. A previous analysis of prey consumption indeed showed that feeding rates are weakly affected by prey density and that lizard abundance has a negative effect on the biomass of preferred preys (González-Suárez *et al.* 2011). In addition, social stress due to crowding can induce direct physiological responses that reduce the amount of energy allocated into body growth or reproduction (Edeline *et al.* 2010 and references therein). These effects are mediated by the activation of the hypothalamic-pituitary-adrenal (HPA) axis in response to aggressive social interactions and may also occur in the common lizard (Meylan, Clobert & Sinervo 2007). Therefore, trophic and social interactions may both contribute to the observed density dependence for growth and reproduction.

Access to reproduction at the age of 1 year, clutch size and postparturition body condition decreased linearly

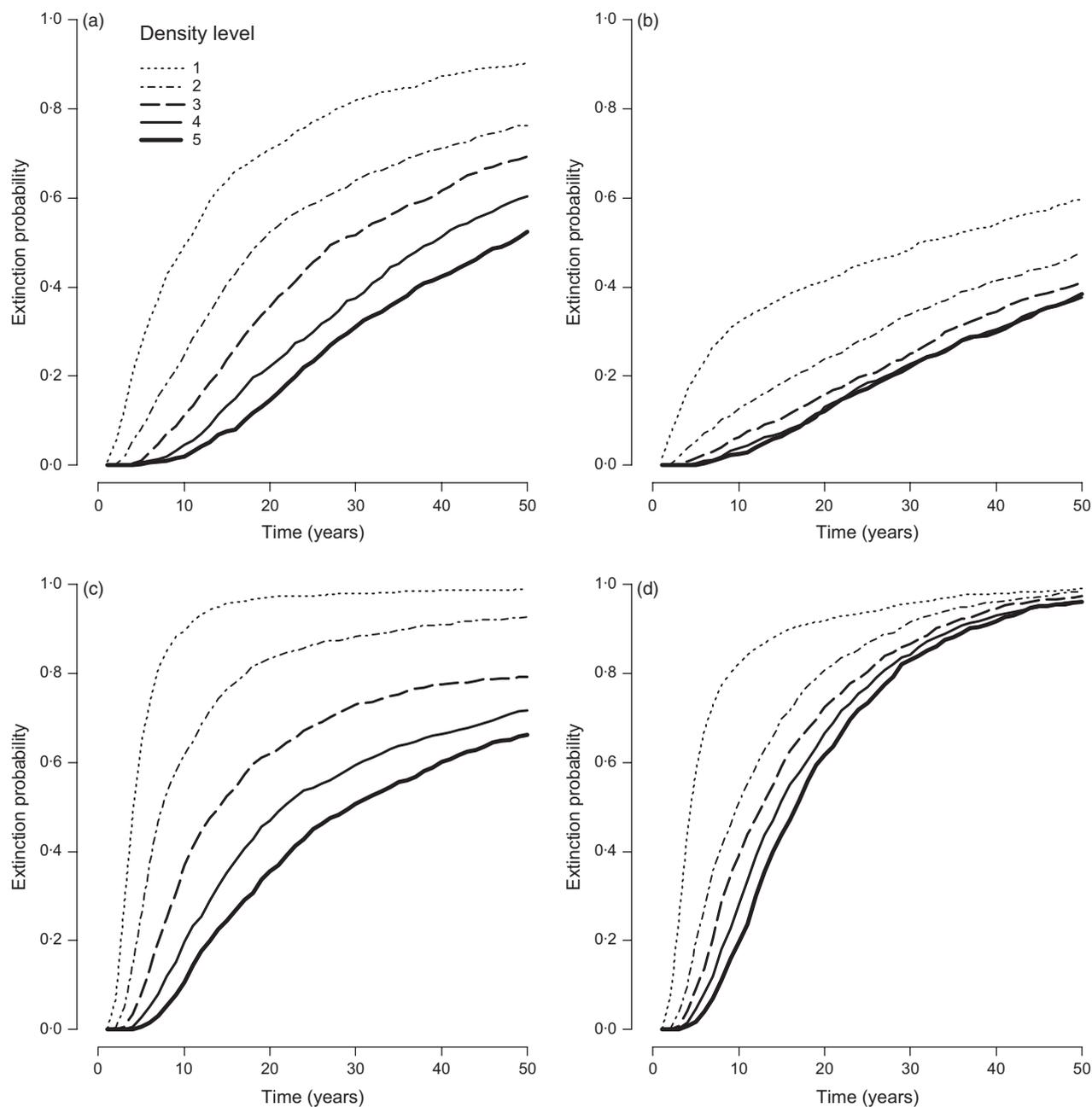


Fig. 4. Cumulated extinction probability over time according to initial density level predicted by stochastic simulations of (a) a density-independent one-sex model, (b) a density-dependent one-sex model, (c) a density-independent two-sex model and (d) a density-dependent two-sex model. Two-sex models assumed an unrestricted harem size. Results are from Monte Carlo simulations of 1000 trajectories (see Appendix S3, Supporting information).

with density. The reduced energy storage (body condition) at high densities could further diminish future female survival and reproduction. Female common lizards indeed fuel future survival and reproduction by a mixture of long-term energy stores and energy acquired during vitellogenesis (i.e. income breeding, Mugabo *et al.* 2011). Altogether, these results are expected life-history responses in species with a plastic age at sexual maturation and a plastic reproductive effort, such as the common lizard (see review by Bassar *et al.* 2010). Density dependence of reproduction was partly driven by positive

effects of body size on age at first reproduction and clutch size. These results contrast with those of a field experiment by Massot *et al.* (1992) where increased density had little effects on body size of breeding females but strong effects on their fecundity. At high altitude (as in Massot *et al.* 1992), structural growth is more constrained by climate conditions and seasonality than at our low altitude study site. Females therefore reach maturity at an older age and adult body growth is much lower and less sensitive to a change in the competitive environment (Massot *et al.* 1992; Sorci & Clobert 1999 and references

therein). Thus, density in altitude populations may influence primarily reproduction through energy allocation into body reserves and physiological trade-offs rather than through body growth.

PATTERNS AND MECHANISMS OF POSITIVE DENSITY DEPENDENCE

Parturition dates showed evidences of an Allee effect at low density and of negative density dependence from moderate to high densities in juveniles and yearlings. To our knowledge, only one other study in a colonial seabird reported positive density dependence in breeding dates (Votier *et al.* 2009). The delayed breeding in small colonies was explained by a social stimulation of reproduction and a social facilitation of foraging (Votier *et al.* 2009). Common lizards are not cooperative breeders or foragers, but a limited access to sexually receptive males at low densities could delay the onset of reproduction in females. At high densities, the timing of reproduction may be further constrained by food intake (González-Suárez *et al.* 2011) and aggressive social interactions (see e.g., Le Galliard *et al.* 2005). Adult female common lizards are socially dominant over young females (Lecomte *et al.* 1994), which could explain why juveniles and yearlings but not adults displayed delayed parturition dates at higher densities. In addition, variation in survival probabilities could also have contributed to the pattern of parturition dates by affecting density during the breeding season (Fig. 2b). In the common lizard, hatching dates are negatively correlated with body growth during the first year of life (Le Galliard, Marquis & Massot 2010), but also with juvenile survival and clutch size at first reproduction (M. Mugabo, O. Marquis, S. Perret & J.-F. Le Galliard, unpublished data; respectively Wald- $Z = -3.17$, $P = 0.001$ and $F_{1,25} = 9.28$, $P = 0.005$). Therefore, the density dependence of parturition dates could substantially affect offspring fitness.

Juvenile survival was also positively affected by density. A linear response to density was best supported. However, uncertainties remained about the shape of density dependence since the quadratic scenario also received substantial support (Table 2). Inconsistent effects of density are seen for juvenile survival in natural populations of common lizards. In a first study, juvenile survival was lower in a population with experimentally increased density than in a population with decreased density (Massot *et al.* 1992), while in a second study, female juvenile survival was lower in two populations with experimentally decreased density than in two control populations (males were unaffected, Meylan, Clobert & Sinervo 2007). These and our results suggest that density-dependent juvenile survival interacts with environmental factors and individual characteristics, such as climate conditions, habitat quality or individual behaviour, that remain to be identified (Coulson *et al.* 2001; Zabel *et al.* 2006; Meylan, Clobert & Sinervo 2007). Here, positive density depen-

dence of juvenile survival could be due to a dilution of predation from avian predators (e.g. Foster & Treherne 1981) or changes in activity behaviour of juveniles associated with faster growth but more predation risks (e.g. Sorci & Clobert 1999).

DENSITY-INDEPENDENT LIFE HISTORY

Yearling and adult survival probabilities were little affected by population density (Fig. 2). However, uncertainties remained about the shape of density dependence, as demonstrated by the similar support received by the density-independent, the linear and, to a lesser extent, the quadratic scenarii (Table 2). A weak density dependence of survival rates could reflect an environmental canalization of the most influential demographic rates for population growth (here juvenile and yearling survival, Eberhardt 1977, 2002; Gaillard & Yoccoz 2003). Low variation in adult survival could also result from selective mortality of juveniles leading to less phenotypic variation in adults (Gaillard & Yoccoz 2003). In addition, the absence of response of the body size at birth of the first generation of offspring to density observed in our study is consistent with previous studies where the 'quality' at birth of offspring common lizards was density-independent (Massot *et al.* 1992; Meylan, Clobert & Sinervo 2007). Thus, female common lizards compromised the quantity but not the 'quality' of offspring at high density. This allocation strategy is expected in species with a variable clutch size, a trade-off between offspring numbers and size at birth, and a positive directional selection on body size at birth.

In addition, we found a substantial interindividual variation independent of variation in population density, age or sex. Genetic, parental and environmental factors could have all contributed to generate individual heterogeneity in our study. Heterogeneity among individuals plays a central role in evolutionary and ecological dynamics, including extinction dynamics of small populations (Lande, Engen & Saether 2003). For example, heterogeneity in resource partitioning between competing individuals influences density-dependent population dynamics and population stability (omnicki 1978, 1980). In general, however, the demographic consequences of individual differences arising from genetic, parental or environmental effects are difficult to predict (Vindenes, Engen & Saether 2008).

DYNAMICAL CONSEQUENCES OF DENSITY DEPENDENCE

The deterministic two-sex density-dependent model produced smooth dynamics towards a stable equilibrium and predicted a stable density that agrees with previous long-term observations in the same experimental set-up (Lecomte *et al.* 2004). The (ASR = proportion of females) shifted from 0.67 in initial populations to 0.81 at equilib-

rium and the proportion of adults changed from 0.43 to 0.34. This equilibrium age- and sex-structure also falls within the range of variations observed in natural populations from where lizards originated (Massot *et al.* 1992; Le Galliard *et al.* 2005; Meylan, Clobert & Sinervo 2007). These results suggest that following populations during a yearly cycle was enough to produce realistic predictions of the deterministic dynamics. A replication of the experiment over several years would further allow testing for the effects of climate factors that might interact with density dependence (Coulson *et al.* 2001; Zabel *et al.* 2006).

We combined elasticity analyses with stochastic simulations to investigate the consequences of density dependence for small population dynamics. Elasticity analyses of density-independent models are often used to determine the most influential life stages of a species and manage small populations (Caswell 2001). Elasticity analyses revealed that the asymptotic growth rate λ was influenced most by juvenile and yearling survival, while the density at equilibrium N_{eq} was influenced most by juvenile and yearling fecundity. Thus, elasticities of λ and N_{eq} pinpointed the same most influential life stages but different critical demographic rates. In addition, N_{eq} was little affected by the strength of density dependence. Therefore, uncertainties on the form of the density dependence of demographic rates should have limited effects on the predictions drawn from population models. These results confirm the need to account for density dependence to draw accurate conclusions about the most influential life stages and demographic rates for population dynamics (Grant & Benton 2000, 2003).

Density-dependent stochastic models provided a better fit to the observed relationship between population growth rates during a yearly cycle and population density than density-independent models. The density-dependent one-sex model provided the best fit at high densities but overestimated population growth rates at the lowest densities, whereas the density-dependent two-sex models provided the best fit of the shape of density dependence but underestimated population growth rates. These results suggest that population growth was influenced by a shortage of reproductive males at low densities and by the negative density dependence acting on reproduction at high densities. The underestimation of population growth by two-sex density-dependent models suggests that access to reproduction of 1-year old males and/or male survival were higher than estimated and that males were able to fertilize more than four females in average (Fitze *et al.* 2005).

Long-term stochastic simulations yielded three other major results. First, accounting for density dependence buffered the effects of initial density on predicted extinction probabilities. Second, accounting for density dependence alone had positive effects on predicted extinction probabilities. In general, the influence of demographic stochasticity on the time to extinction in density-dependent populations depends on (i) the upper limit on population density causing the negative density dependence, (ii) the long-term

stochastic population growth rate, and (iii) the shape of density dependence (Lande 1993; Lande, Engen & Saether 2003). The linear negative density dependence acting on maturation and fecundity included here implies that reproductive rates increase in declining populations and thus act as a rescue effect allowing sparse populations to rapidly move away from a zone of high extinction risks (Morris & Doak 2002; Henle, Sarre & Wiegand 2004). Third, density dependence interacted with sex ratio fluctuations to shape the extinction dynamics of populations. In accordance with previous studies (e.g., Legendre *et al.* 1999; Engen, Lande & Saether 2003; Bessa-Gomez, Legendre & Clobert 2004), demographic stochasticity raised substantially the risk of extinction of small populations by increasing the probability of a shortage of males. More interestingly, the comparison of one-sex and two-sex models showed that negative density dependence acting on reproduction combines with sex ratio fluctuations to generate higher extinction risk in initially dense populations, while initially sparse populations are less at risks of extinction from density dependence compared with unregulated populations. This unexpected result is the consequence of a higher probability that no breeding male survived to inseminate breeding females in initially dense populations regulated by negative density dependence around a stable equilibrium than in unregulated populations. In initially sparse populations, increased reproductive rates allowed regulated populations to reach densities with lower risks of extinction due to a shortage of males faster than unregulated populations (Appendix S4; Fig. D1, Supporting information).

Conclusions

Our combination of experimental and modelling data demonstrates the importance of the density dependence of life history for the dynamics of small populations influenced by demographic stochasticity. In addition to the patterns reported here, it is known that density dependence can also interact with the mating system and sex ratio fluctuations through density-dependent effects on intrasexual and intersexual competition (Kokko & Rankin 2006 and references therein). Interactions between population density, the mating system and small population dynamics are therefore likely to be more general than those found in this study and should be considered when attempting to predict the probability of extinction of endangered populations.

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Supporting Information

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

Appendix S1. Selection results of models exploring each studied trait based on Akaike Information Criteria [(Q)AIC_C].

Appendix S2. Path analyses.

Appendix S3. Age-structured projection matrix model.

Appendix S4. Consequences of density for the persistence of populations.