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RESEARCH ARTICLE

The costs of living on the coast: Reduction in body size and size-specific reproductive output in coastal populations of a widespread amphibian

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Abstract

1. Body size is a critical component of organismal biology. Body size is known to be influenced by a plethora of environmental conditions, among which exposure to large scale variations of salinity has been comparatively overlooked. Yet, exposure to salinity is known to affect energetic allocation toward growth and reproduction.
2. In this study, we investigated the morphological differences between inland and coastal individuals of spined toads (*Bufo spinosus*) in Western France.
3. We measured adult morphology both outside and during the reproductive season on 190 individuals, and assessed reproduction in pairs originating from inland ($N=20$) and coastal ($N=30$) environments.
4. Overall, we found that adult coastal toads were smaller and lighter than inland individuals. Reproductive correlates of these differences included lower fecundity and smaller egg size (but higher egg density) in coastal females. Interestingly, these differences were not allometric correlates of body size, as coastal females invested proportionally less in all components of reproduction (fecundity, egg size and egg protection).
5. These results suggest altered resource allocation to growth and reproduction in coastal amphibians, which may be related to the marked spatial gradient of salinity (measured in reproductive ponds) and the associated costs of osmoregulation (higher osmolality in coastal individuals), for which local adaptation and higher tolerance to salinity remains to be tested.

KEYWORDS

amphibians, fecundity, inland, morphology, reproduction, salinity

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1 | INTRODUCTION

Variation in body size among individuals in a population and among different populations is associated with many other biological traits. For instance, body size can influence large scale interactions such as trophic interactions, population dynamics and can affect both the structure and functioning of communities (Brown et al., 2004; Cohen et al., 1993; Elton, 1927; Hildrew et al., 2007; Jobling, 1997). At the individual scale, body size can influence most (if not all) life history traits such as metabolic rates (Brown et al., 2004; Kleiber, 1947; Nagy, 2005), growth rates (Davidowitz & Nijhout, 2004), susceptibility to predation (Hart & Bychek, 2011; Margulies, 1989), foraging and resource acquisition (Brown et al., 1993; Greenleaf et al., 2007; Mittelbach, 1981), age at maturity (Bluweiss et al., 1978; Roff, 2001), survival and longevity (Badwan & Harper, 2021; Smith, 2002).

Body size is also a critical determinant of fitness through its influences on reproduction. Indeed, a larger body size can increase reproductive success (Berglund & Rosenqvist, 1990; Bosch & Vicens, 2006) through effects on mate selection (assortative mating; Crespi, 1989; Han & Fu, 2013; Shine et al., 2001), fecundity (Honěk, 1993; Pincheira-Donoso & Hunt, 2017), and egg and/or offspring size (Ito, 1997; Marshall et al., 2000; Moran & McAlister, 2009). Body size often governs the amount of resources that individuals can invest during a reproductive event (George, 1994). This amount of resources will affect fecundity (Briegel, 1990; Calvo & Molina, 2005; Honěk, 1993) and egg and/or offspring size (Ito, 1997; Marshall et al., 2000; Moran & McAlister, 2009), two reproductive parameters that are known to trade-off against each other (Lasne et al., 2018; Smith & Fretwell, 1974). In turn, larger eggs have higher hatching success (Metz et al., 2010; Xu et al., 2019), produce larger offspring (Pepin et al., 1997) and overall result in better offspring fitness (Xu et al., 2019). Importantly, egg and/or offspring size can also be adjusted by the parents based on the expected offspring performances under a given set of environmental conditions (Fox et al., 1997; Marshall et al., 2008), emphasizing the importance of environmental characteristics in shaping individuals' body size.

Although body size has been shown to influence tolerance to fluctuating environmental conditions (Brown & Sibly, 2006; Preziosi et al., 1996), body size itself can also be influenced by environmental conditions (Moran & McAlister, 2009). Differences in size can be observed between populations of a same species (Mousseau & Roff, 1989; Vitasse et al., 2009) because, throughout the range of a species, individuals are likely to experience different sets of environmental conditions (Frederiksen et al., 2005). Accordingly, geographic variation in body size has often been related to latitude or altitude (Loeschcke et al., 2000; Vinarski, 2014; Vitasse et al., 2009) because of the resulting clines in temperature. Temperature is a strong determinant of individual body size, with body size and egg/offspring size decreasing with increasing average temperature (Gardner et al., 2011; Moran & McAlister, 2009; Sheridan & Bickford, 2011; Skadsheim, 1989), a process which has been linked to the temperature size rule (Atkinson, 1994; Sentis et al., 2017).

Among the various environmental parameters which may influence body size, large scale variations of salinity have been comparatively overlooked. Coastal habitats are constantly exposed to salinity (Hobohm et al., 2021; McLean et al., 2001), a pattern which can be attributed to landward transport of sea-spray (Benassai et al., 2005) or seawater infiltration (Gopinath et al., 2015), both in aquatic (Hoque et al., 2016; Little et al., 2022) and terrestrial (Su et al., 2020; Szabo et al., 2016) habitats, thereby inducing a strong contrast with inland environments. Salinity is an important factor, as most organisms (e.g. numerous invertebrates, vertebrates but also plants) have to osmoregulate in order to survive (i.e. osmoregulators) (Bradley, 2009; Munns & Tester, 2008). Facing fluctuating salinity osmoregulators rely on physiological and behavioural mechanisms to regulate hydric and ionic fluxes in order to maintain homeostasis (Evans & Kültz, 2020; Schultz & McCormick, 2012). These mechanisms are metabolically costly, and energetic allocation to fuel these expensive mechanisms trade-off with resources available to growth and reproduction in a large variety of organisms including fishes, freshwater invertebrates, plants and microbes (Alkhamis et al., 2022; Cañedo-Argüelles et al., 2013; Herbert et al., 2015; Munns & Tester, 2008; Pinder et al., 2005; Stearns, 1989). As a consequence, salinity has been shown to influence development rates, growth and ultimately body size in a wide variety of freshwater taxa (Hopkins et al., 2013, 2014; Lambret et al., 2021; Pinder et al., 2005).

Amphibians are one such taxa known to be susceptible to environmental variations due to their low dispersal abilities (Wells, 2007), permeable skin, eggs without shell and complex life cycle (López-Alcaide & Macip-Ríos, 2011). They have limited abilities to maintain their homeostasis relative to the environment (Katz, 1989), and they have been shown to be particularly susceptible to salinity (see e.g. Lorrain-Soligon et al., 2021; Lorrain-Soligon, Bichet, et al., 2022), even in terrestrial habitats (Lorrain-Soligon, Robin, et al., 2022; Traversari, 2021; Vegso et al., 2022). However, some amphibian species can persist in brackish habitats (Greenwald, 1972; Hopkins & Brodie, 2015), highlighting variable tolerances between species (Hopkins & Brodie, 2015) and/or populations (e.g. populations originating from brackish water being more tolerant than populations originating from freshwater; Gomez-Mestre & Tejedo, 2003; Hopkins et al., 2016, 2017; Licht et al., 1975). These differences among populations have been useful to demonstrate phenotypic selection (Gomez-Mestre & Tejedo, 2003) and variable gene expression associated with local salinity in amphibians (Albecker et al., 2021). In terms of morphology, the size of individuals has been shown to increase when distance to the ocean increases (decreasing exposure to salinity) at a very short spatial scale (<1 km; Lorrain-Soligon, Robin, et al., 2022) but neither variations of adult morphology on a larger spatial scale, nor their consequences for reproductive effort have been tested to date (but see Marangoni et al., 2008).

In this study, we investigated the morphological differences between inland and coastal individuals of spined toads (*Bufo spinosus*). We verified salt-exposure by measuring salinity in coastal and inland sites and osmolality in coastal and inland toads. We quantified adult morphology (body size, body mass, body condition, sexual size

dimorphism) both outside and during the reproductive season on 190 individuals. We further quantified reproduction in pairs originating from inland ($N=20$ pairs) and coastal environments ($N=30$ pairs) and assessed investment in reproduction as well as fecundity and egg size. We expected differences between coastal and inland populations, as exposure to salinity should alter resource allocation, and, in individuals originating from coastal environments, we predicted (1) reduced body size of adults in response to exposure to salinity (Lorrain-Soligon, Robin, et al., 2022), (2) reduced fecundity and egg size in response to the smaller size of adults (Ito, 1997; Marshall et al., 2000; Moran & McAlister, 2009) and (3) a comparatively smaller investment in reproduction linked to increased costs of osmoregulation (Herbert et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study species

The spined toad (*Bufo spinosus*) is the largest toad species in western Europe, with females being larger than males (Speybroeck et al., 2018). This species is terrestrial during most of its annual cycle, except during late winter–early spring when adults converge to water bodies to reproduce (Brischoux et al., 2018). During this aquatic reproductive period, males clasp females in an axillary amplexus until egg laying. The species is largely distributed across Europe and found both in coastal and inland habitats (Speybroeck et al., 2018).

2.2 | Study sites and field procedures

We captured by hand coastal and inland individuals during two different time periods, in Western France (Figure 1). Three coastal

ponds (distance to coastline 0.54 ± 0.24 SE [Standard Error] km) and four inland ponds (distance to coastline 52.94 ± 6.13 SE km) were prospected (see Figure 1) to collect amplexant pairs during the reproductive period (16/02/2022 to 02/03/2022) when individuals are readily available at reproductive ponds. Various sites were chosen in order to capture the first arriving amplexant pairs at each site and to avoid any site effect. Salinity measured (Pocket Salt Meter PAL-ES2, Atago) at these reproductive sites confirmed that coastal sites were salt-exposed (mean salinity: 2.67 ± 0.69 gL⁻¹, range 1.8–3.9 gL⁻¹) while inland sites were not exposed to salt (salinity: 0.0 gL⁻¹).

Outside the reproductive period (08/09/2022 to 01/11/2022) when individuals resumed activity after aestivation, we prospected various coastal (distance to coastline 0.82 ± 0.44 SE km, Figure 1) and inland areas (distance to coastline 43.84 ± 7.18 SE km, Figure 1). These non-reproductive individuals were opportunistically captured on roads, which induced relatively dispersed captures across wide coastal and inland areas. As a consequence, for these individuals, we could not define specific capture ‘sites’ (see Figure 1 and statistical analyses below).

During the reproductive period, we captured 30 coastal amplexant pairs (60 individuals in amplexus) and 20 inland amplexant pairs (40 individuals in amplexus). Amplexant pairs were captured by hand, placed in a transport box (14 × 16 × 9 cm) and brought to the laboratory (thermally controlled room with air temperature set at 17° and photoperiod set at 12 h dark–12 h light) immediately after field sessions for further measurements (see below). During the non-reproductive period, we captured 45 individuals (23 males and 22 females) from various coastal areas, and 45 individuals (22 males and 23 females) from inland areas. Individuals were captured by hand, placed in a transport box (14 × 16 × 9 cm) and brought to the laboratory (thermally controlled room with air temperature set at 17°C and photoperiod set at 12 h dark–12 h light) immediately after field sessions for further measurements (see below).

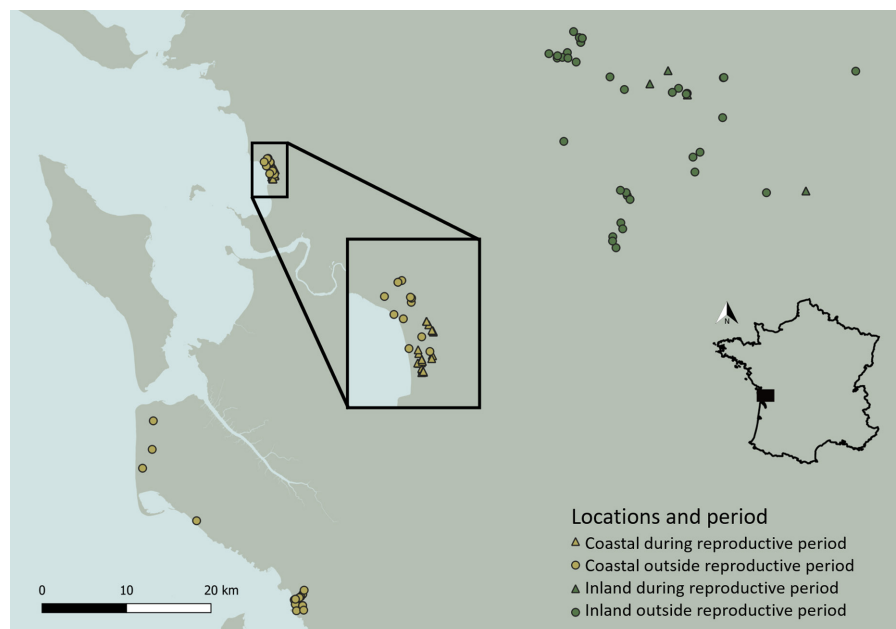


FIGURE 1 Locations of the coastal and inland sites where reproductive and non-reproductive individuals were captured in Western France.

To confirm that salt exposure in coastal toads induced osmotic consequences, we collected blood (via cardiocentesis) from 10 coastal males (originating from one coastal pond: salinity = 2.80 g L⁻¹, distance to the ocean = 811.65 m), and 10 inland males (originating from one inland pond: salinity = 0.00 g L⁻¹; distance to the ocean = 50,371.30 m) on 08/03/2023 (different animals as than those described above). Osmolality was computed only in males because during the reproductive period, males are more easily captured than females. Only individuals weighing more than 15 g were sampled and we collected 100 µL of blood (representing no more than 10% of blood volume). The blood was centrifuged for 7 min at 2000g, plasma was separated and stored at -20°C. Plasma osmolality (mOsmol kg⁻¹) was measured from 10 µL aliquots on a Vapro2 osmometer (Elitech Group). Plasma osmolality in coastal individuals was significantly higher than plasma osmolality in inland individuals (linear model [LM]: Estimate = 8.500, SE = 3.855, $t_{1,5} = 2.205$, p -value = 0.041; 231.3 ± 2.906 mOsmol kg⁻¹ in coastal individuals, and 222.8 ± 2.533 mOsmol kg⁻¹ in inland individuals).

2.3 | Measurements

At the laboratory, all individuals were measured (snout-vent length, SVL) using a calliper (± 1 mm) and weighed using an electronic balance (± 0.1 g). Amplexing individuals collected during the reproductive season were temporarily separated for these measurements and shortly reunited to further quantify reproduction (see below). A body condition index (BCI) was computed as the residuals of the linear regression between $\log(\text{SVL})$ and $\log(\text{body mass})$.

2.4 | Reproductive effort

Separated amplexant pairs (for measurements, see above) reformed systematically as soon as the partners were brought back into contact. Once the amplexant pairs were reunited, each pair was placed in a plastic container (35 × 55 × 26 cm) containing freshwater (~20 L, salinity: 0.3 g L⁻¹) as well as branches for laying support. Amplexant pairs were left in these tanks until egg laying (mean duration before egg laying: 66 ± 0.75 h, range 10–175 h). Once egg laying was completed, individuals were again weighed to calculate loss in body mass.

The clutch of bufonid toads is formed by egg strings containing ~3000–10,000 eggs (Miaud & Muratet, 2018). In order to assess fecundity, each egg string was placed in a container (35 × 20 × 25 cm) containing 2 cm of dechlorinated tap water and a scale (graph paper). A picture was taken from above in order to measure the total length of the egg string using ImageJ software (Schneider et al., 2012). For each clutch, we randomly selected 6 segments of 10 cm long and individually counted the number of eggs within each segment. The mean number of eggs per 10-cm segment was calculated and used to assess fecundity (number of eggs) for each clutch based on the length of the egg strings. We also calculated egg density as the

number of eggs divided by the length of the egg strings. Finally, on a subsample of 100 randomly selected eggs in each egg strings, we measured egg diameter.

Adult individuals as well as eggs strings were then released at their site of capture.

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Population	Population (coastal or inland)	105 individuals from coastal populations (53 males and 52 females) and 85 individuals from inland locations (42 males and 43 females), as well as 30 clutches from coastal individuals and 20 clutches from inland individuals

2.6 | Statistical analyses

For all statistical analyses, locations represent the difference between coastal and inland environments, while sites represent the different sites or ponds prospected within each location. Descriptive summaries of these data are given in Appendix S1.

All data analyses were performed using R 3.6.3 (R Core Team, 2020) and Rstudio v1.1.419.

2.6.1 | Adult morphology

As individuals captured during the breeding season had a larger body size (SVL) than those captured after the breeding season, both in coastal (during the breeding season: $70.28 \text{ mm} \pm 1.38 \text{ SE}$; after the breeding season: $64.53 \pm 1.04 \text{ SE}$; LM: Estimate = 5.750, SE = 1.826, $t_{1,103} = 3.149$, p -value = 0.002) and in inland (during the breeding season: $83.95 \text{ mm} \pm 1.54 \text{ SE}$; after the breeding season: $73.64 \pm 1.54 \text{ SE}$; LMs: Estimate = 10.306, SE = 2.186, $t_{1,83} = 4.715$, p -value < 0.001) locations, we investigated differences in SVL between coastal and inland locations separately for the two periods (during the breeding season or outside the breeding season).

For individuals captured during the breeding season, we tested for the existence of assortative mating, either in coastal or inland populations, by running Pearson correlation tests between male and female body size (SVL). We tested for the effect of location (coastal or inland) on individuals' body size (SVL), body mass and body condition (BCI), separately for males and females. These effects were assessed by computing linear mixed models (LMMs, packages *lme4* [Bates et al., 2015] and *lmerTest* [Kuznetsova et al., 2017]) with location as an explanatory covariate and the site as a random effect.

For individuals captured outside the breeding season, we tested for the effect of location (coastal or inland) on individuals' body size (SVL), body mass and body condition (BCI), separately for males and females. These effects were assessed by computing LMs with location as an explanatory covariate.

2.6.2 | Reproduction

Fecundity and egg size

We tested for the differences in egg string length (mm), clutch size (number of eggs), egg density (number of eggs/mm) and egg diameter (mm), between locations by computing LMMs with location as an explanatory variable and site as a random effect. We also tested for the correlation between egg density or egg diameter and egg number by using a LMM with egg density or egg diameter as a dependent variable, clutch size, location and their interaction as covariates, and site as a random effect. These variables were selected by top-down selection, and only the retained variables are presented in the final models.

Adults' investment in reproduction

We tested for the effect of location (coastal or inland) on individuals' variations in mass (Δ mass, computed as the difference in mass between time at capture and after laying, as a proportion of mass at capture [%]), separately for males and females. These effects were assessed by computing LMMs with location as an explanatory covariate, and the site as a random effect.

We tested for the differences in laying time (time elapsed between capture and laying) between locations by computing LMMs with location as an explanatory variable and site as a random effect.

We tested for the effects of females' body size (SVL), females' body mass, and females' variations in mass (Δ mass, computed as the absolute difference in mass between time at capture and after laying [g]) on clutch size, by computing LMMs with clutch size as a dependant variable, and females SVL, mass or Δ mass as well as their interaction with location (coastal or inland) as explanatory variable, and site as a random effect. In order to understand if these effects (location and females' SVL, mass or Δ mass) were additive or interactive, we performed a top-down selection procedure to retain significant effects.

3 | RESULTS

3.1 | Body size between coastal and inland populations

For individuals captured during the reproductive season, the body size (SVL) and mass of females and males were higher in inland population compared to coastal ones (Table 1; Figure 2a). BCI of females was higher in inland locations compared to coastal ones but did not vary in males (Figure 2b; Table 1).

Across amplexant pairs, male and female SVL were not correlated in coastal populations ($r=0.115$, 95% CI=[-0.256, 0.456], $t=0.611$, $df=28$, p -value=0.546), but we found a marginally non-significant correlation in inland amplexant pairs ($r=0.442$, 95% CI=[-0.001, 0.740], $t=2.093$, $df=18$, p -value=0.051).

For individuals captured during the non-reproductive period, SVL and mass were higher in inland populations compared to coastal ones, both in males and females (Table 1; Figure 2c). BCI was higher in males in inland compared to mainland populations but did not vary in females according to location (Table 1; Figure 2d).

3.2 | Reproductive effort between coastal and inland populations

Egg strings were longer in inland individuals (Estimate=2011.003, SE=605.112, $t_{1.6}=3.323$, p -value=0.017). Accordingly, clutch size (number of eggs) was higher in inland locations (Estimate=2749.442, SE=613.069, $t_{1.5}=4.485$, p -value=0.007, Figure 3a). However, egg density (number of eggs divided by egg string length) was higher in coastal populations (Estimate=0.206, SE=0.088, $t_{1.48}=-2.348$, p -value=0.023, Figure 3b). Indeed, egg density was negatively related to clutch size across locations (Estimate<0.001, SE<0.001, $t_{1.48}=-3.420$, p -value<0.001). Egg diameters varied according to clutch size (Estimate<0.001, SE<0.001, $t_{1.46}=2.786$, p -value=0.007), location (Estimate=-0.522, SE=0.183, $t_{1.46}=2.849$, p -value=0.006), and their interaction (Estimate<-0.001, SE<0.001, $t_{1.46}=-2.527$, p -value=0.015; Figure 4). Eggs were larger in inland populations but egg diameter increased with clutch size in coastal clutches (Estimate<0.001, SE<0.001, $t_{1.25}=2.375$, p -value=0.025; Figure 4) while it remained constant across clutch size in inland clutches (Estimate<0.001, SE<0.001, $t_{1.18}=-0.881$, p -value=0.390; Figure 4).

Body mass change during reproduction differed according to location both in males and females (Table 1; Appendix S2). Within sexes, inland males have gained mass, while coastal males have lost mass (Table 1; Appendix S2). Coastal females have lost less mass compared to inland ones (Table 1; Appendix S2).

Latency between capture and egg-laying was slightly shorter in coastal individuals, but this difference was not significant (respectively $57.81\text{ h} \pm 8.83$ SE and $78.49\text{ h} \pm 9.25$ SE; Estimate=22.499, SE=14.540, $t_{1.5}=1.547$, p -value=0.180).

We showed that clutch size was highly dependent on female morphological traits (namely body size [SVL], body mass, and loss in mass), location and their interaction (Figure 5a; Table 1). Indeed, clutch size increased with female SVL (Figure 5a; Table 1) but this relationship was steeper in inland individuals (Estimate=177.41, SE=29.68, $t_{1.18}=5.978$, p -value<0.001) compared to coastal ones (Estimate=93.81, SE=11.36, $t_{1.28}=8.255$, p -value<0.001). Clutch size was also positively related to female body mass but the interaction between location and body mass was not significant (Table 1). In addition, clutch size was negatively related to female loss in mass, but the interaction between location and body mass loss was not significant (Figure 5b; Table 1).

TABLE 1 Model outputs for individuals captured during breeding season [concerning body size (SVL), body mass, body condition (BCI), Δ body mass and clutch size] or outside breeding season [concerning body size (SVL), body mass and body condition (BCI)]. Only variables retained during the selection procedures are shown.

Period	Dependent variable	Selected covariates	Estimate	SE	t-value	df (num.den)	p-value	
During breeding season	Females SVL (mm)	Location (Inland-Coastal)	15.095	3.928	3.843	1.6	0.008	
	Males SVL (mm)	Location (Inland-Coastal)	13.940	2.271	6.139	1.4	0.004	
	Females mass (g)	Location (Inland-Coastal)	47.303	12.235	3.866	1.4	0.007	
	Males mass (g)	Location (Inland-Coastal)	22.235	2.768	8.033	1.4	0.001	
	Females BCI	Location (Inland-Coastal)	0.026	0.011	2.254	1.2	0.029	
	Males BCI	Location (Inland-Coastal)	0.019	0.013	1.455	1.5	0.152	
	Female delta mass (%)	Location (Inland-Coastal)	-5.339	2.036	-2.623	1.7	0.012	
	Male delta mass (%)	Location (Inland-Coastal)	3.973	1.485	2.676	1.5	0.010	
	Clutch size	Female SVL (mm)	Location (Inland-Coastal)	93.81	12.51	7.497	1.46	<0.001
			Location (Inland-Coastal)	-6548.4	2616.5	-2.503	1.46	0.016
	Clutch size	Female SVL:Location	Location (Inland-Coastal)	83.6	29.13	2.87	1.46	0.006
			Location (Inland-Coastal)	42.476	4.267	9.955	1.47	<0.001
	Clutch size	Female body mass (g)	Location (Inland-Coastal)	699.628	264.04	2.65	1.47	0.011
			Location (Inland-Coastal)	-112.061	17.882	-6.267	1.47	<0.001
Clutch size	Female loss in mass (g)	Location (Inland-Coastal)	1370.648	477.4	2.871	1.7	0.023	
		Location (Inland-Coastal)	11.698	2.828	4.136	1.43	<0.001	
Outside breeding season	Females SVL (mm)	Location (Inland-Coastal)	11.698	2.828	4.136	1.43	<0.001	
	Males SVL (mm)	Location (Inland-Coastal)	6.103	1.274	4.788	1.43	<0.001	
	Females mass (g)	Location (Inland-Coastal)	28.669	7.169	3.999	1.43	0.002	
	Males mass (g)	Location (Inland-Coastal)	10.343	1.824	5.672	1.43	<0.001	
	Females BCI	Location (Inland-Coastal)	0.008	0.022	0.374	1.43	0.711	
	Males BCI	Location (Inland-Coastal)	0.022	0.013	1.765	1.43	0.085	

Abbreviations: BCI, body condition index; SVL, snout-vent length.

4 | DISCUSSION

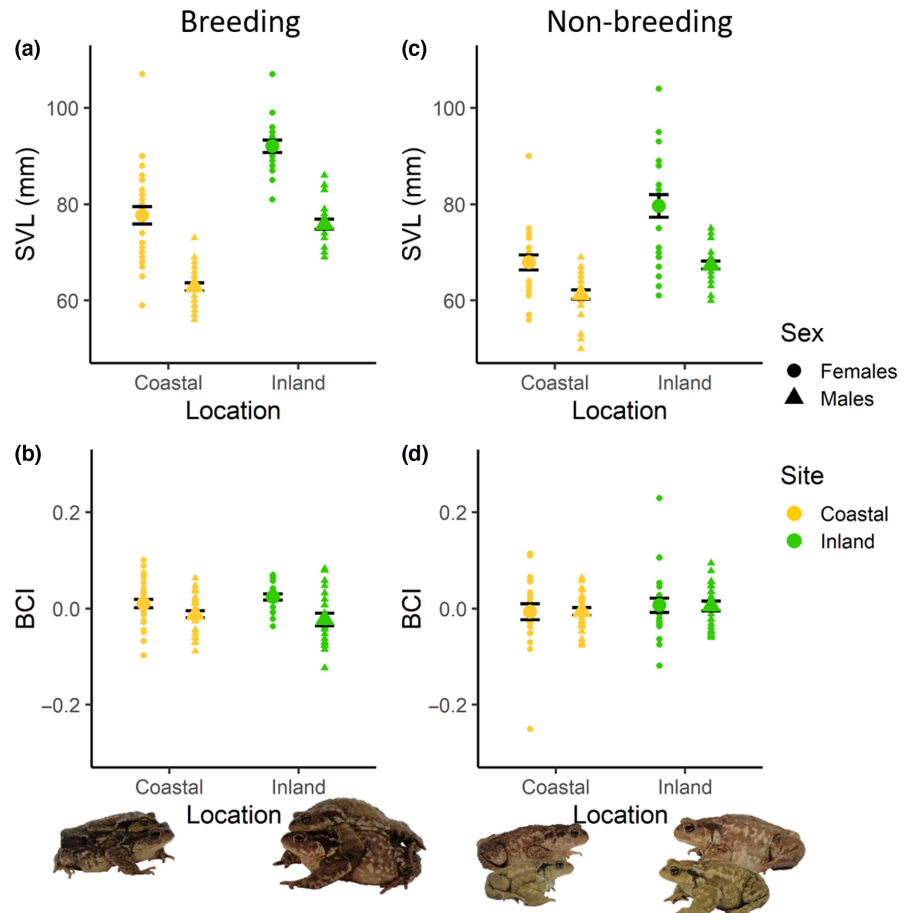
Overall, we found that coastal toads were smaller and lighter than inland individuals, both during and outside the reproductive season. Reproductive correlates of these morphological differences included lower fecundity and smaller egg size, but higher egg density, in coastal females as compared to inland individuals. Interestingly, these differences were not mere allometric correlates of smaller body size in coastal individuals, as coastal females produced proportionally smaller clutches than their inland counterparts. In

combination with fecundity-dependent body mass loss and egg density, these results suggest altered resource allocation to growth and reproduction in coastal amphibians.

4.1 | Smaller body size in coastal toads

Individuals from coastal populations were smaller and lighter than their inland counterparts, suggesting that coastal habitats altered resource allocation to growth in these individuals. Coastal

FIGURE 2 Body size (snout-vent length [SVL]; a, c) and body condition (body condition index [BCI]; b, d) according to location and sexes, for individuals captured during the breeding season (left column) or outside the breeding season (right column). Means \pm SE and raw data points.



environments are constantly exposed to salt, notably due to the effect of landward sea-spray (Benassai et al., 2005) inducing a spatial gradient of salinity from the seashore both in aquatic (Lorrain-Soligon, Bichet, et al., 2022; Lorrain-Soligon, Robin, et al., 2022; Santoro et al., 2006, see also our salinity recordings) and terrestrial environments (Angiolini et al., 2013; Canfora et al., 2014). As a result, direct salt exposure or salt exposure resulting from individual's diet (Nagy et al., 2021) affected osmotic balance in coastal individuals (higher plasma osmolality; see also Lorrain-Soligon, Bichet, et al. (2022); Lorrain-Soligon, Robin, et al. (2022) for another species of coastal amphibian), further suggesting that these individuals experienced higher osmotic costs, which can trade-off with energetic allocation toward growth (Herbert et al., 2015; Munns & Tester, 2008). These costs could involve increased energetic expenditures linked to osmoregulation or alternatively, other costs linked to an increased tolerance to higher osmolality, and future studies should investigate the mechanisms underlying these osmotic costs. Importantly, such osmoregulatory constraints may affect coastal individuals throughout their life. During larval development, tadpoles exposed to salinity express a stunted growth (Gomez-Mestre et al., 2004; Hopkins et al., 2013, 2014; Lukens & Wilcoxon, 2020), which can carry-over after metamorphosis (Lewis et al., 2021). During juvenile and adult (terrestrial) stages, exposure to salted substrates may also influence energetic allocation between osmoregulation and growth (Herbert et al., 2015). Interestingly, Marangoni et al. (2008) highlighted the

same pattern of body size reduction near the coast in two anurans species (*Pelobates cultripes* and *Epidalea calamita*) and attributed this pattern to osmotic consequences of highly desiccating sandy substrates, and Hyeun-Ji et al. (2020) highlighted dwarfism in *E. calamita* populations exposed to drier and warmer climatic conditions. These hypotheses indicated that other component of coastal environments, such as desiccating substrate or possibly desiccating winds, also linked to hydric stress, can lead to decreased body size similarly to our study. These studies dovetail relatively well with our hypothesis related to osmotic stress. Indeed, dehydration and salt exposure trigger similar mechanisms of water and ionic regulations (Bentley, 2002; Hazon & Flik, 2002; Shoemaker & Nagy, 1977) and, in addition to energetic costs of osmoregulation, both affect activity levels (Feder & Londos, 1984; Lorrain-Soligon, Bichet, et al., 2022; Titon Jr et al., 2010) and thus resource acquisition (Feder & Londos, 1984; Yuqing et al., 2021).

Alternatively, but not exclusively, other ecological characteristics of coastal habitats could also explain the results we found. For instance, weaker predation pressure (Velasco et al., 2019) and lower competition (most amphibians being intolerant to salt, Hopkins & Brodie, 2015) in coastal habitats could affect growth rates and individual body size (Relyea, 2001; Van Buskirk & Yurewicz, 1998). Similarly, growth rates and individual body size are highly dependent on resource types and availability (Dmitriew, 2011; Dunham, 1978; Festa-Bianchet et al., 2004). For instance, species diversity and

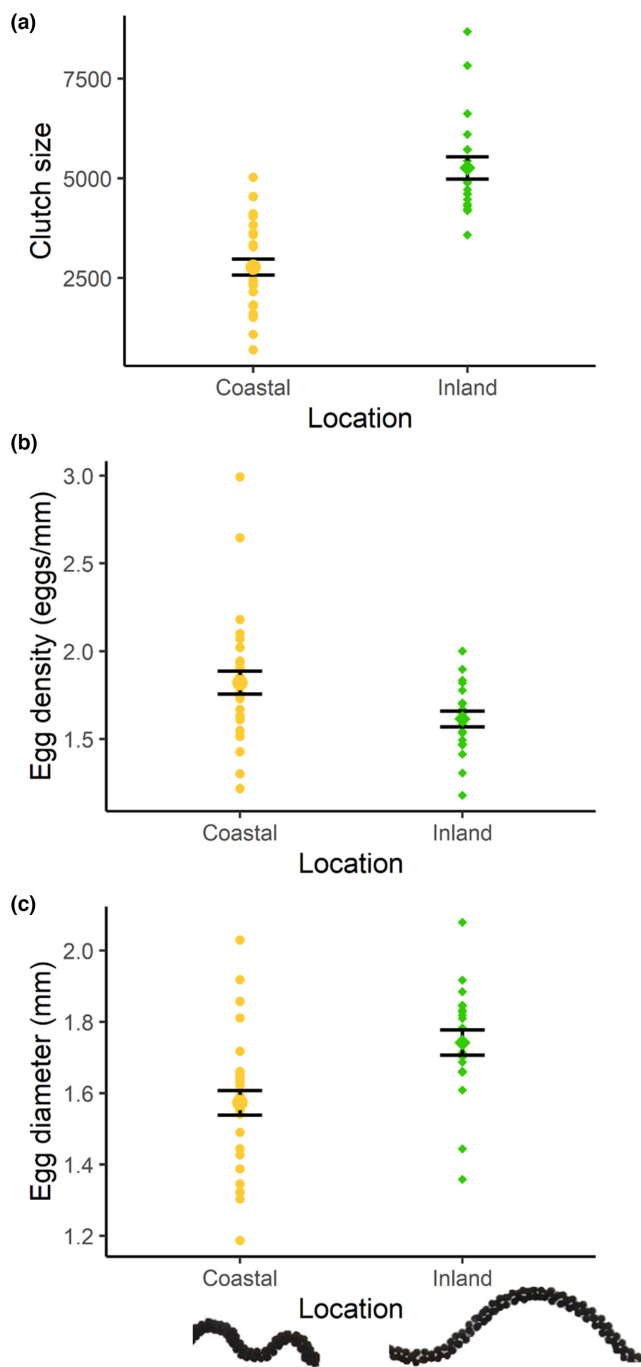


FIGURE 3 Clutch size (number of eggs, a), egg density (b) and egg diameter (c), according to location (coastal [$N=30$] and inland [$N=20$]), for individuals captured during the breeding season. Means \pm SE and raw data points.

especially invertebrates diversity and abundance are known to decrease with increasing salinity (Cunillera-Montcusí et al., 2022; Ersoy et al., 2022; Finlayson et al., 2013; González-Sansón et al., 2022; Kendall et al., 2022; Pinder et al., 2005). However, coastal habitats are also known to be highly productive interface environments (Hobohm et al., 2021) and arthropod (one of the main food source of toads, Wells, 2007) diversity and abundances have been shown to be relatively high in coastal habitats (Barrett et al., 2005; Brunbjerg

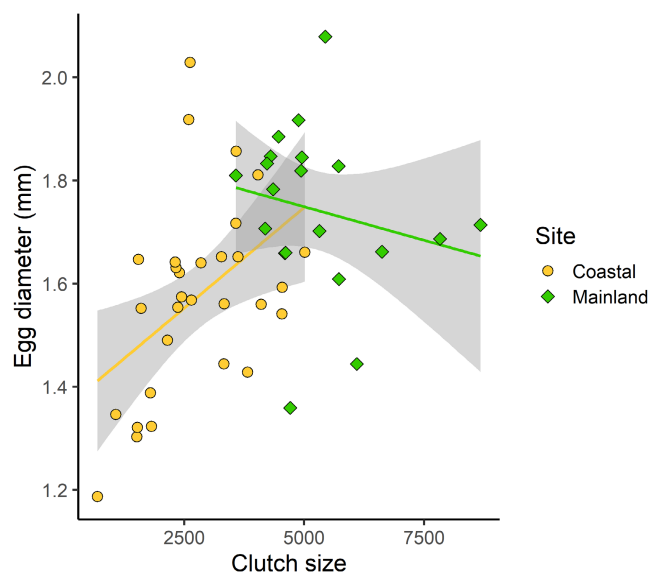


FIGURE 4 Relationships between eggs diameter (mm) and clutch size (number of eggs) according to location (coastal [$N=30$] and inland [$N=20$]). Means \pm SE and raw data points.

et al., 2015; Polis & Hurd, 1996), notably because of the positive effects of both terrigenous and marine sources of nutrients on trophic webs (Polis & Hurd, 1996). Thus, the size reduction in coastal population is unlikely to be related only to a reduction in resources abundance. This hypothesis seems supported by the fact that coastal toads are smaller and lighter than their inland counterpart but have overall (except for females during reproductive period) similar body condition (an index of body reserves; Schulte-Hostedde et al., 2005).

Complementarily, although we did not investigate the physiological contrasts between coastal and inland toads, it is likely that specific physiological mechanisms mediate the link between environmental constraints and body size. In this respect, corticosterone, a pleiotropic mediator involved in energetic allocation (Crespi & Warne, 2013), osmoregulation (McCormick & Bradshaw, 2006) and stress response (including osmotic stress; Hopkins et al., 2016; Tornabene, Hossack, et al., 2021), as well as aldosterone (involved in ionic and water regulations in amphibians; Hillyard et al., 2008; Tornabene et al., 2022), may be key parameters to consider in order to investigate the mechanistic bases of the differences we found. Finally, although some of the data we collected may have included juvenile individuals (i.e. sampling outside the reproductive season), our data gathered on reproductive individuals clearly show that the pattern we found is attributable to smaller adult body size in coastal individuals. Interestingly, these data show that sexual maturity is attained at smaller body size in coastal individuals (i.e. 59 and 56 mm SVL, respectively, for the smallest female and male involved in an amplexus) as compared to inland individuals (i.e. 81 and 69 mm SVL, respectively, for the smallest female and male involved in an amplexus). Such results may indicate that the age-size relationship in toads (characterized by indeterminate growth; Duellman & Trueb, 1994) may be altered in coastal environments. This may further suggest that coastal individuals may reproduce at younger

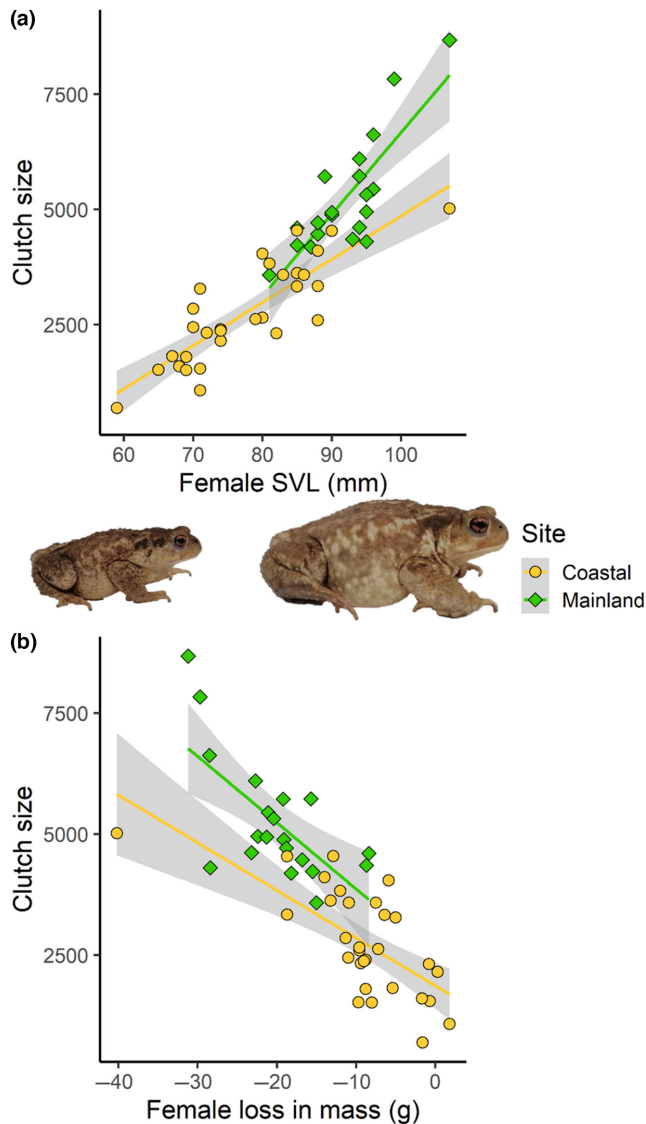


FIGURE 5 Relationships between (a) female body size and (b) female Δ body mass and clutch size (number of eggs) according to location (coastal [$N=30$] and inland [$N=20$]), for individuals captured during the breeding season. Means \pm SE and raw data points.

age than inland ones, a potentially major shift in life-history strategy linked to lower survival in sites exposed to salt (Hall et al., 2020; Lorrain-Soligon, Bichet, et al., 2022), a hypothesis which would need to be tested (e.g. using skeletochronology; Bastien & Leclair, 1992; Sinsch, 2015).

4.2 | Reproductive correlates of smaller size in coastal toads

In coastal amplexant pairs, we failed to find any relationships between male and female body size. In contrast, we found a marginally non-significant positive relationship between male and female body size in inland amplexant pairs. Such result may suggest that

smaller body size in coastal individual may alter processes linked to size-related mate selection and/or assortative mating (Crespi, 1989; Shine et al., 2001). Yet, we suggest this result to be taken with caution as assortative mating remains a topic of debates in amphibians (Green, 2019) and because such pattern was not previously found in inland populations of the same study species (Renoirt et al., 2022).

We found that coastal females produced both smaller clutches and smaller eggs. This result could be attributed to allometric-dependent reproductive investment (Ito, 1997; Marshall et al., 2000; Moran & McAlister, 2009). That is, because coastal females are smaller, they produce fewer and smaller eggs, a result found by Marangoni et al. (2008) in two coastal anurans. Yet, we found that the slope of the relationship between female size and fecundity differed between coastal and inland individuals. Such result demonstrates that coastal females produced proportionally smaller clutch than their inland counterparts, and further suggest that size-relative energetic investment in reproduction was lower in coastal females. This result is further supported by complementary indices of energetic investment in reproduction. For instance, egg density was higher in coastal females, suggesting that the amount of vitelline membrane deposited by the oviduct around the eggs (i.e. egg jelly composed of glycoproteins; Bonnell & Chandler, 1996; Yurewicz et al., 1975) was lower. Such lower investment in egg jellies (further suggested by the lower body condition for coastal females) may bear strong consequences for embryonic development, as vitelline membrane has been shown to enhance egg fertilization and to protect developing embryos from pathogens (Altig & McDiarmid, 2007). Taken together, these results suggest that energetic investment during vitellogenesis and vitelline membrane production by the oviduct were proportionally lower in coastal females.

Importantly, the lower reproductive energetic investment of coastal females not only affected fecundity and egg protection but also egg size. That is, coastal females produced smaller eggs. Yet, perhaps more importantly, we found a positive correlation between egg size and clutch size in coastal females but not in inland females. Such result is interesting insofar as, usually, fecundity negatively trades-off with egg size (Lasne et al., 2018; Smith & Fretwell, 1974). This pattern also contrasts with what would have been expected from the fractional egg hypothesis (Ford & Seigel, 2010; Nussbaum, 1981; Ricklefs, 1968), which posits that species with large clutch sizes and small eggs (typical of Bufonid toads; Wells, 2007) would add additional offspring and not change offspring size should extra energy become available (Nussbaum, 1981; Ricklefs, 1968). We found that increased clutch size is concomitant with increased egg size in coastal females solely, suggesting that higher energy available to reproduction positively influenced both parameters simultaneously. In strong contrast, inland females followed the prediction of the fractional egg hypothesis, with egg size being independent from increasing clutch size.

Similarly to the effect on body size discussed above, we believe that the underlying proximate mechanisms involve the spatial gradient of salinity between coastal and inland sites (Angiolini

et al., 2013; Canfora et al., 2014; Lorrain-Soligon, Robin, et al., 2022; Santoro et al., 2006); and the associated energetic costs linked to osmoregulation (Goolish & Burton, 1989; Gutiérrez et al., 2011). The deviation from an allometric-dependent reproductive investment strongly suggests the existence of additional energetic costs in reproductive females from coastal sites. Other alternative hypotheses (e.g. involving predation pressure, competition, resource availability or dehydration) are unlikely to explain this pattern, and would have induced similar size-dependent reproductive investment between locations (see Marangoni et al., 2008). Importantly, these additional energetic costs affected all components of reproduction (fecundity, egg size and egg protection) suggesting strong potential consequences for future embryonic and larval development and survival (Giménez & Anger, 2001; Moran & McAlister, 2009; Olson, 2019; Xu et al., 2019).

Interestingly, if coastal brackish water bodies are suboptimal for embryonic and larval development (Albecker & McCoy, 2017; Hopkins et al., 2013, 2014; Lukens & Wilcoxon, 2020; Tornabene, Breuner, et al., 2021), one would have expected coastal females to produce larger and more protected eggs in order to improve survival of their offspring under such detrimental environmental conditions (a similar pattern as what has been found in halophile species exposed to low salinity environments, e.g. Giménez & Anger, 2001). We suggest that the additional energetic costs linked to osmoregulation in coastal sites may induce a selfish maternal effect (Marshall et al., 2008; Schwarzkopf & Andrews, 2012), with females allocating proportionally less energy to their offspring in order to favour their own homeostasis. This hypothesis needs to be tested by formally measuring osmotic costs (and osmolality) in coastal and inland females. Alternatively, females may be able to adjust their reproductive effort (fecundity and egg size) according to the environment in which their offspring will develop, to improve their offspring performance and survival in order to maximize their own lifetime reproductive success (Fox et al., 1997; Kudo & Nakahira, 2005; Marshall et al., 2008; Marshall & Uller, 2007; Schwarzkopf & Andrews, 2012). In our context, this hypothesis can be supported by three different explanations. First, coastal females may produce fewer and smaller eggs because they reproduce in brackish ponds where competition, predation and pathogens pressures are lower (Clulow et al., 2018; Gutiérrez, 2014; Hintz & Relyea, 2019; Yohannes et al., 2009). Second, coastal females may produce fewer and smaller eggs because they reproduce in brackish water, which they may consider as a poor-quality environment for their offspring given the detrimental effects of salinity on embryonic and larval development (Albecker & McCoy, 2017; Lukens & Wilcoxon, 2020; Tornabene, Breuner, et al., 2021; Tornabene, Hossack, et al., 2021). Finally, it is also possible that because of our experimental design for which we maintained amplexant pairs in freshwater, coastal females may have produced fewer and smaller eggs because they may consider freshwater as a poor-quality environment (see Fox et al., 1997; Marshall et al., 2008) if they are locally adapted to live and reproduce in saltier environments. Whether females can

modify reproductive allocation so rapidly (e.g. during short captivity) deserves to be investigated. Future studies are required to test whether the patterns we found are a result of a selfish strategy improving future survival of females or a manipulative strategy adjusting reproductive effort to local (brackish) developmental conditions of their offspring.

5 | CONCLUSIONS

Coastal toads are characterized by smaller body size and size-specific reproductive output compared to inland individuals. These patterns may be related to the marked spatial gradient of salinity found in coastal areas and the subsequent additional costs of osmoregulation in saltier habitats. Assessing whether females adjust their reproductive effort to favour their own fitness or that of their offspring in such suboptimal environments remains to be tested. Whatever the underlying mechanisms, the differences we found between inland and coastal populations remain intriguing as growth and reproduction of coastal individuals appears limited in these habitats. To better understand the fitness consequences of living along the coast, it remains essential to decipher whether salt exposure, as well as other environmental contrasts between coastal and inland habitats, can induce local adaptation and to test if coastal adults, embryos and larvae display an increased tolerance to salt exposure than their inland counterparts.

AUTHOR CONTRIBUTIONS

Léa Lorrain-Soligon, Frédéric Robin and François Brischoux have conceptualized the study. Léa Lorrain-Soligon, Luca Périssé and Marko Jankovic participated to data collection. Léa Lorrain-Soligon and François Brischoux analysed the data and wrote the initial draft. All authors have reviewed and edited the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.nk98sf7z8> (Lorrain-Soligon et al., 2023).

ETHICS STATEMENT

This work was approved by the French authorities under permits DREAL/2020D/8041 (animals capture) and APAFIS #33592-2021102610033982 (animals husbandry).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Summary of individual and clutch characteristics in coastal [N=30] and inland [N=20] locations, either during the breeding season or outside the breeding season.

Appendix S2: Variations in body mass (Δ mass, computed as the difference in mass between time at capture and after laying, as a proportion of mass at capture [%]), between locations (coastal [N=30] and inland [N=20]) and sexes, for individuals captured during breeding season.

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