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Invasive toads adopt marked capital breeding when introduced to a cooler, more seasonal environment

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Amphibians from cold and seasonal environments show marked capital breeding and sustained resource allocation to growth when compared with conspecifics from warmer, less seasonal environments. Capital breeding fuels reproduction by using only stored energy, and larger sizes and masses confer higher fecundity, starvation resistance and heat and water retention. Invasive populations act as experiments to explore how resources are allocated in novel environments. We investigated resource allocation of the southern African toad *Sclerophrys gutturalis* in a native source population (Durban) and in an invasive population recently (< 20 years) established in a cooler, more seasonal climate (Cape Town). After dissection, lean structural mass (bones and muscles), gonadal mass, liver mass and body fat percentage were measured in 161 native and invasive animals sampled at the beginning and the end of the breeding season. As expected, female gonadal mass decreased throughout the breeding season only in the invaded range. Thus, invasive female toads adopt a more marked capital breeding strategy than native conspecifics. Conversely, males from both populations appear to be income breeders. Also, male and female toads from the invaded range allocate more resources to growth than their native counterparts. Such a novel allocation strategy might be a response to the low temperatures, reduced rainfall and heightened seasonality encountered by the invasive population.

ADDITIONAL KEYWORDS: adaptive response – amphibians – clutch size – ectotherm – energy storage – environmental novelty – life-history traits – resource allocation strategy – *Sclerophrys gutturalis*.

INTRODUCTION

Different levels of acquired resources are directed to storage, growth, maintenance and reproduction throughout the life of an individual (Drent & Daan, 1980; Jönsson, 1997). Any extra allocation to one of these processes (e.g. storage) should be counterbalanced by a lower allocation to another process (e.g. growth; Dmitriew, 2011; Ejsmond *et al*, 2015). Given that life-history traits associated with these processes can be considered as adaptive investments of energy and resources (Stearns, 1977), organisms should present the combination of traits that determines their highest possible fitness in a specific environment (Stearns, 1989). The evolution of distinct allocation strategies in response to different environmental circumstances of temperature or seasonality is thus expected (Stearns, 1989; Varpe, 2017). The study of such strategies across contrasting environments can be challenging, especially in species with indeterminate growth, such as amphibians and fish, characterized by high variability in reproductive investment and age or size at maturity (Kozłowski *et al.*, 2004). The challenge is exacerbated when the allocation to storage, growth, maintenance and reproduction confers fitness benefits that are realized across different life-history stages or generations, such as in amphibians (Ejsmond *et al.*, 2015; Hudson *et al.*, 2015).

Allocation of resources to energy storage represents a temporary investment that maximizes lifetime fitness by buffering environmental fluctuations (Shine & Brown, 2008; Fischer *et al.*, 2011). In anuran amphibians, energy reserves are mainly stored as lipids in fat bodies, although liver and somatic tissue can also allocate energy in the form of lipids and glycogen (Bonnet *et al.*, 1998; Jönsson *et al.*, 2009; Chen *et al.*, 2011). Stored energy can be remobilized to growth or maintenance to withstand unfavourable

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*Corresponding author. E-mail: gvimercati@outlook.com environmental conditions, such as winter starvation. Sustained energy storage is thus expected in species or populations living in more seasonal environments. For instance, populations of anurans living at high elevation, high latitude or desiccating environments have heavier storage organs than populations from less seasonal environments (Jönsson *et al.*, 2009; Brown, *et al.*, 2011; Chen *et al.*, 2013). Similar patterns were detected in caecilians (Measey & Gower, 2005) and fish (McBride *et al.*, 2015), whereas in snakes (Gregory, 2006) and copepods (Sainmont *et al.*, 2014) manipulative and theoretical studies have emphasized the advantage of being heavier and storing more energy at high elevations.

Stored resources can also be used to fuel energy-intensive reproductive activities, such as female egg production (Jørgensen, 1992) and male calling behaviour (Bevier, 1997; de Andrade *et al.*, 2017). Storage of resources to fuel these activities well before the onset of the breeding season has been termed capital breeding (Bonnet *et al.*, 1998). This strategy is particularly useful to boost reproduction in early spring, i.e. immediately after a period of low energy acquisition, to maximize reproductive success (Verhulst & Nilsson, 2008) or to have sufficient energy reserves to perform demanding activities, such as gametogenesis (Tejedo, 1992; Warne *et al.*, 2012) or courtship behaviours (Abrahams, 1993). Commencing reproductive activities earlier in the season is adaptive in seasonal environments where offspring reproductive prospects diminish rapidly (e.g. over summer; Ejsmond *et al.*, 2015). Given that pure capital breeders rely only on stored energy to fuel reproduction, their reproductive investment should drastically decrease towards the end of the breeding season, i.e. as soon as energy reserves are depleted (Ejsmond *et al.*, 2015). Conversely, a mixed strategy that uses endogenous resources for reproduction in early spring (capital breeding) and uses exogenous resources for reproduction (income breeding; Bonnet *et al.*, 1998) later in the season should maximize fitness in less seasonal environments (Ejsmond *et al.*, 2015).

Resources allocated to growth and maintenance represent a long-term investment in reproductive potential and survival (Peters, 1986; Ejsmond *et al.*, 2015). Such resources are generally directed to structural tissues, such as bones, muscles, circulatory and nervous systems, from which remobilization of the stored resources is costly (Dmitriew, 2011; Giacomini & Shuter, 2013). Sustained allocation of resources to growth allows species with indeterminate growth to attain a larger body size and heavier mass, which might increase future reproductive output (Peters, 1986; Kozłowski *et al.*, 2004; Ejsmond *et al.*, 2015). Larger size and increased mass might also enhance survival in ectotherms inhabiting cold environments, although both adaptive and non-adaptive hypotheses have been suggested to explain a positive correlation between body size and elevation/latitude (Van Voorhies, 1996; Partridge & Coyne, 1997; Blackburn *et al.*, 1999; Chown & Klok, 2003). The advantage of larger animals in the cold can be explained by their superior resistance to starvation in seasonal and unpredictable environments (Cushman *et al.*, 1993) and their improved retention of body heat owing to a lower surface-to-volume ratio (Olalla-Tárraga *et al.*, 2006; Rubalcaba *et al.*, 2019). An analogous mechanism, involving increased water retention by larger and heavier amphibians that inhabit desiccating environments, has been advocated to explain negative geographical clines between amphibian body size and water availability (Olalla-Tárraga & Rodríguez, 2007; Gouveia & Correia, 2016; Amado *et al.*, 2019; Pincheira-Donoso *et al.*, 2019).

Sustained allocation of resources to storage and growth can be obtained at the expense of reproduction (Stearns, 1977). A shift in allocation may be adaptive in seasonal environments, where the advantages of longer lifetime survival and bigger body size should outweigh the disadvantages of lower reproductive investment (Dmitriew, 2011). Species or populations may also respond to this lower investment by increasing the survival of their offspring through the differential resources allocated to reproduction or through parental care (Shine, 1978; Nussbaum, 1987). For instance, female frogs living at high elevations mature at an older age, reach a larger body size and produce fewer but larger eggs than their counterparts from low elevations (Berven, 1982; Morrison & Hero, 2003; Liao *et al.*, 2016). Clutch size (number of eggs) is also inversely correlated with egg size in numerous amphibian anurans (Cummins, 1986; Liao *et al.*, 2014; Liedtke *et al.*, 2014). Given that larger and heavier eggs contain a larger amount of yolk than smaller eggs (Komoroski *et al.*, 1998), frogs from colder and more seasonal environments might trade fecundity for higher survival of offspring (Morrison & Hero, 2003; Liao *et al.*, 2016).

Optimal resource allocation should direct resources to growth and maintenance, energy storage and reproduction according to specific environmental circumstances in order to maximize individual fitness. Comparison of species or populations that share a common evolutionary history but inhabit different environments might thus identify contrasting allocation strategies and produce insights into divergent evolution of life-history traits (Berven, 1982). Invasive populations, especially those established in environments that differ significantly from those of the historical or native range, represent a valuable source of information to test eco-evolutionary hypotheses (Hierro *et al.*, 2005; Van Kleunen *et al.*, 2010). When the establishment of such populations is recent and the source of their founder individuals known, it is possible to explore whether novel environmental conditions represent a challenge or an opportunity to the phenotype of the species, before adaptations reduce eventual mismatches (Brown *et al.*, 2011; Hendry *et al.*, 2011). It can be hypothesized that when a species is introduced into a novel environment, a new resource allocation strategy should be adopted to maximize fitness (i.e. the evolution of increased competitive ability; Blossey & Notzold, 1995).

Here, we ask whether and how the allocation strategy of an anuran amphibian changes after its recent introduction to a cooler, more seasonal environment. The study species is the guttural toad, *Sclerophrys gutturalis* (Power, 1927) (Anura: Bufonidae), which naturally inhabits summer rainfall areas of central and southern Africa. Guttural toads were introduced at the end of the 1990s to Cape Town (De Villiers, 2006), which is characterized by winter rainfall climate. Through genetic analyses, the founders of the invasive population are known to come from north-eastern South Africa (Telford *et al.*, In press). Thus, the guttural toad has been moved to a climate that is not only cooler but also characterized by a different rainfall pattern from that of the native range (Fig. 1). We sampled guttural toads from the Cape Town invasive population and a native population from Durban, KwaZulu-Natal. This native population inhabits a peri-urban habitat similar to that of the invasive population and is close to its original gene source (Telford *et al.*, In press). This allowed a comparison of two populations from areas that differ in latitude and climate but not in habitat or genetic identity. Recent studies investigating the same two populations showed that, despite the very recent establishment (< 20 years; Measey *et al.*, 2017), invasive toads have responded adaptively to the novel environment by: (1) shortening the length of the breeding season (Fig. 1; Vimercati, 2017; Vimercati *et al.*, 2018); and (2) reducing sensitivity and exposure to the colder and drier environmental conditions of the invaded range (Vimercati *et al.*, 2018).

Resource allocation to energy storage and reproduction is a temporary investment that should vary across the breeding season in response to reproductive activity and seasonality. Thus, we collected invasive and native toads from both sexes at two sites, during specific sampling periods: the beginning and the end of their breeding season. In accordance with previous empirical and theoretical studies conducted on ectotherms with indeterminate growth, such as anurans and fish, we hypothesize that guttural toads adopt a more marked capital breeding strategy when introduced to a cooler, more seasonal environment. We also hypothesize that invasive toads allocate more resources to growth and energy storage than do conspecifics from the native range in order to withstand the novel environmental conditions of temperature and rainfall. According to our hypotheses, we expect a seasonal variation in the mass of the fat bodies and liver in both populations, with energy reserves that are depleted in early spring to boost reproduction and replenished later in the season to withstand winter starvation.

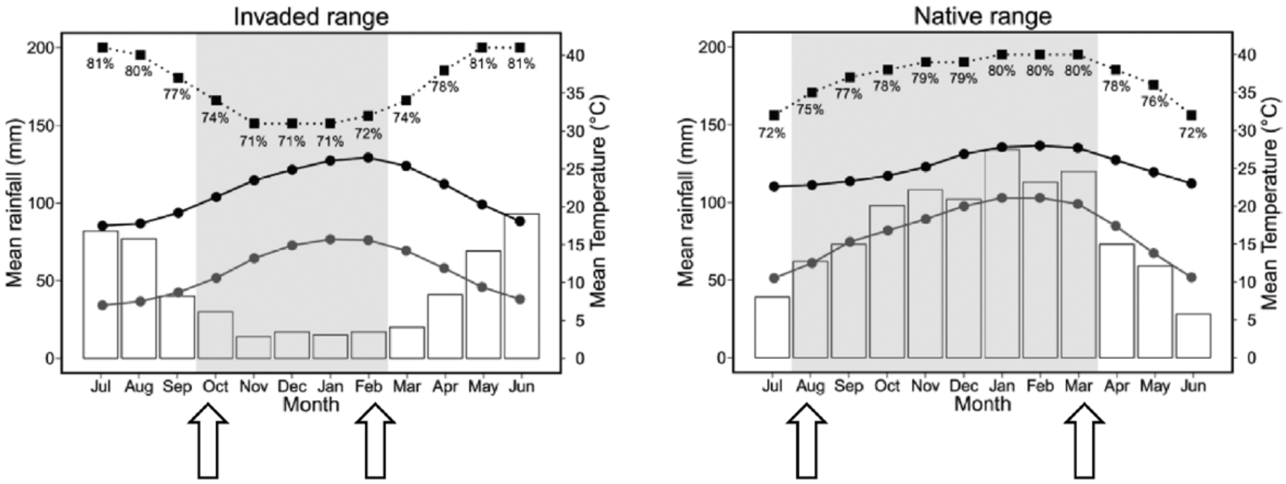

Figure 1. Mean monthly rainfall (bars), maximal temperature (black dots and line), minimal temperature (grey dots and line) and relative humidity (black squares and dotted line) at the locations of Cape Town (invaded range) and Durban (native range) where guttural toads (*Sclerophrys gutturalis*) were sampled. For each location, the open arrows represent the sampling periods and the shaded area represents the breeding season of the guttural toad. This season represents the period during which males form breeding choruses, and it has been delimited according to our experience in the field (2011–2018). Climate data were sourced from the World Meteorological Organization, http://public.wmo.int/

Also, we expect a more marked seasonal decline of reproductive investment in invasive toads when compared with their native conspecifics in both sexes, which indicates a sustained capital breeding strategy in the cooler, more seasonal environment. Such a lower investment in reproduction might be compensated for by larger and heavier eggs in invasive female toads. Lastly, we expect heavier body mass and structural mass (bones and muscles), independently from the season, and heavier fat bodies and liver at the end of the breeding season, in invasive toads compared with native ones.

MATERIAL AND METHODS

STUDY SPECIES

The guttural toad, *S. gutturalis*, is a large African bufonid naturally distributed across central and southern Africa (du Preez *et al.*, 2004). The species is tolerant of different elevations (from sea level to ~1800 m a.s.l.) and latitudes (from 8° N to 32°S). It inhabits a range of vegetation types in the savanna, grassland and thicket biomes (du Preez *et al.*, 2004) and, owing to synanthropic behaviour, it is common in peri-urban areas. The species is extra-limital in the Western Cape, where an invasive population was established in Cape Town at the end of the 1990s (De Villiers, 2006; Measey *et al.*, 2017). It was probably introduced as eggs or tadpoles with a consignment of aquatic plants (De Villiers, 2006) from the Durban area in north-eastern South Africa (Telford *et al.*, In press).

STUDY LOCALITIES AND CLIMATE

We selected one native and one invasive population for this study. The native population inhabits a peri-urban area of Durban, South Africa (75 m a.s.l., 29°47′S, 31°01′E), where the breeding periodicity (from August to March) mostly mirrors precipitation patterns (Fig. 1). The climate is classified as humid-subtropical by the Köppen–Geiger climate classification (Peel *et al.*, 2007), being characterized by hot, humid summers and relatively mild, dry winters (mean July minimal temperature, 10.5 °C; Fig. 1). The South African invasive population inhabits a peri-urban area of Cape Town (Constantia, 87 m a.s.l., 34°00′53″S, 18°25′50″E), where the species breeds from October to February (Fig. 1). The climate is classified as mediterranean by the Köppen–Geiger climate classification (Peel *et al.*, 2007), being characterized by hot, dry summers and relatively mild, wet winters (mean July minimal temperature, 7 °C; Fig. 1).

DATA COLLECTION

Adult toads were collected in Durban (native population) and Cape Town (invasive population) at the beginning (in 2015) and at the end (in 2016) of the breeding season (Fig. 1). At each sampling site, individuals were captured opportunistically by hand after sunset within an area of ~10 km^2. Each toad was euthanized immediately after capture by immersion in a 1 g L^{-1} solution of tricaine methane sulfonate (MS222) for 20 min. The carcasses were then frozen in labelled plastic bags until dissection. Ethical clearance was obtained from Stellenbosch University Animal Ethics Committee (protocol no. U-ACUD14-00112); collections in the native area (Durban) occurred under permit from Ezemvelo KwaZulu-Natal Wildlife (permit no. OP553/2015), whereas collections in the invaded area of Cape Town occurred under a permit from CapeNature (permit no. 0056-471 AAA041-00088).

In the laboratory, after defrosting each specimen at ambient temperature, individuals were weighed (± 0.001 g; FA 304 T balance, Avery Berkel) and their snout–vent length (SVL, i.e. the straight-line distance from the posterior cloacal margin to the snout tip) was measured using digital callipers (± 0.01 mm). Fat bodies, liver, gonads and stomach were weighed (± 0.001 g; FA 304 T balance, Avery Berkel) after dissection of each organ; tissues were patted dry with a paper towel before weighing. In gravid females, clutch size (number of eggs) was estimated by counting the number of eggs contained in a small sample (1 g) of the clutch. The mean egg size for each clutch was also estimated by averaging the diameter of 20 eggs measured using digital callipers (± 0.01 mm), whereas mean egg mass was obtained by dividing the gonadal mass by the clutch size. Given that the mass of ingested prey items may determine supplementary variability in body mass measurements, we obtained the stomach-free mass (hereafter, body mass) for each individual following Courant *et al.* (2017). The percentage of body mass composed of fat reserves (hereafter, body fat %) was obtained from the ratio between the mass of fat bodies and body mass (Brown *et al.*, 2011). Lastly, individuals were fully eviscerated and weighed to obtain lean structural mass.

DATA ANALYSIS

Preliminary analyses showed that body mass, lean structural mass, liver mass and gonadal mass were positively correlated with SVL in both male and female guttural toads. Somatic organs are known to scale allometrically with body size (Gould, 1966; Peig & Green, 2009), and the allometry may also differ between sexes in the case of sex-specific morphogenesis (Peig & Green, 2010). Thus, we calculated a scaled mass

Table 1. Results of two-way ANOVAs on the effects of population and sampling period and their interaction on lean structural body (SMI_{lean}), SMI, liver (SMI_{liver}), body fat (body fat %), and gonad residuals, separately for each sex

Variable	Sex	Population (Cape Town vs. Durban)	Sampling period (beginning vs. end)	Sampling period × population
SMI_{lean}	Females	$F_{1,76} = 10.57$ $\boldsymbol{P = 0.0017}$	$F_{1,76} = 6.53$ $\boldsymbol{P = 0.0126}$	$F_{1,76} = 0.55$ $P = 0.462$
	Males	$F_{1,77} = 11.99$ $\boldsymbol{P = 0.0009}$	$F_{1,77} = 0.02$ $P = 0.901$	$F_{1,77} = 0.21$ $P = 0.652$
SMI	Females	$F_{1,76} = 2.82$ $P = 0.097$	$F_{1,76} = 1.89$ $P = 0.173$	$F_{1,76} = 0.73$ $P = 0.395$
	Males	$F_{1,77} = 10.71$ $\boldsymbol{P = 0.0016}$	$F_{1,77} = 3.27$ $P = 0.075$	$F_{1,77} = 0.52$ $P = 0.474$
SMI_{liver}	Females	$F_{1,76} = 0.47$ $P = 0.496$	$F_{1,76} = 7.87$ $\boldsymbol{P = 0.0064}$	$F_{1,76} = 0.00$ $P = 0.982$
	Males	$F_{1,77} = 9.89$ $\boldsymbol{P = 0.0024}$	$F_{1,77} = 10.90$ $\boldsymbol{P = 0.0015}$	$F_{1,77} = 3.72$ $P = 0.0573$
Body fat %	Females	$F_{1,76} = 0.99$ $P = 0.323$	$F_{1,76} = 44.76$ $\boldsymbol{P < 0.0001}$	$F_{1,76} = 1.16$ $P = 0.286$
	Males	$F_{1,77} = 19.75$ $\boldsymbol{P < 0.0001}$	$F_{1,77} = 13.16$ $\boldsymbol{P = 0.0005}$	$F_{1,77} = 6.88$ $\boldsymbol{P = 0.0105}$
Gonad residuals	Females	$F_{1,76} = 7.03$ $\boldsymbol{P = 0.0098}$	$F_{1,76} = 7.74$ $\boldsymbol{P = 0.0068}$	$F_{1,76} = 2.69$ $P = 0.1049$
	Males	$F_{1,77} = 1.31$ $P = 0.256$	$F_{1,77} = 0.13$ $P = 0.719$	$F_{1,77} = 0.34$ $P = 0.561$

Abbreviation: SMI_{lean} = Scaled mass index for lean structural mass; SMI = Scaled mass index for body mass; SMI_{liver} = Scaled mass index for liver mass
Significant differences ($P < 0.05$) are highlighted in bold.

index for body mass, lean structural mass and liver mass separately for each sex, following the equation proposed by Peig & Green (2009):

$$M = M_i \times \left(\frac{L_0}{L_i}\right)^{b_{\mathrm{SMA}}} \quad (1)$$

where M_i and L_i represent, respectively, organ mass and body length (SVL) of the individual i, and L_0 represents an arbitrary value (i.e. average SVL across the two populations). We calculated L_0 from the SVL of all individuals collected in the two populations separately for each sex (females: $L_0 = 85.6$ mm, $N = 80$; males: $L_0 = 74.1$, $N = 81$). The exponent b_{SMA} represents the slope of the standardized major axis (SMA) regression on ln-transformed mass and length and was calculated with the *lmodel2* package in R (Legendre, 2014) using data from the two populations separately for each mass and sex (Supporting Information, Table S1; $N = 161$). The corrected mass obtained by applying equation (1) for body mass, lean structural mass and liver mass is defined here as SMI, $\mathrm{SMI}_{\mathrm{lean}}$ and $\mathrm{SMI}_{\mathrm{liver}}$, respectively. In order to correct for the effect of body size on reproductive investment, we calculated the residuals from regression of gonadal mass on SVL separately for each sex, following Chen *et al.* (2013).

The SMI indicates the general body condition of an individual (Peig & Green, 2009), whereas $\mathrm{SMI}_{\mathrm{lean}}$ is a measure of structural mass, i.e. the amount of resources allocated across the whole lifespan to structural tissues that do not include the reserves (Dmitriew, 2011; Giacomini & Shuter, 2013). Conversely, $\mathrm{SMI}_{\mathrm{liver}}$ and body fat % indicate current energy reserves (i.e. storage) that may be invested in future reproduction/growth, and gonad residuals represent the current reproductive investment, i.e. the amount of resources allocated to reproduction (Varpe, 2017).

The SMI, $\mathrm{SMI}_{\mathrm{lean}}$, $\mathrm{SMI}_{\mathrm{liver}}$, body fat % and gonad residuals were analysed using a two-way ANOVA to explore the effect of population, sampling period and their interaction, separately for females and males; Tukey's post hoc tests were used to explore pairwise differences between populations and sampling periods. To assess additional differences in reproductive investment between the two populations, ANCOVAs were performed, with clutch size, egg size and egg mass as response variables and body size (SVL) as a covariate. Before each analysis, data were tested for assumptions of normality and homoscedasticity using Shapiro's and Levene's tests, respectively. When the assumptions were violated (i.e. body fat %) we used the *bestNormalize* package in R to choose the most appropriate transformation of the data. In order to investigate how resources are allocated differentially among structural mass, storage organs and gonads, we used the *FactoMineR* package in R (Lê *et al.*, 2008) to perform a principal components analysis (PCA) using $\mathrm{SMI}_{\mathrm{lean}}$, $\mathrm{SMI}_{\mathrm{liver}}$, body fat % and gonad residuals (Naya *et al.*, 2010). Given that the pattern of covariation may change across the breeding season and differ between males and females, we ran the PCA separately for each sampling period and sex.

All analyses and visualizations were performed in R v.3.5.3 (R Development Core Team, 2018) by using the *ggplot2* package (Wickham, 2016) and the *factoextra* package (Kassambara & Mundt, 2016).

RESULTS

REPRODUCTION

As expected, invasive females had a more marked seasonal decline of reproductive investment when compared with native females; gonads were significantly lighter at the end of the breeding season only in the invasive population, whereas no significant seasonal difference in terms of gonadal mass was detected in the native population (Table 1; Fig. 2A). Gravid females from the invaded range ($N = 33$) also had smaller ($F_{1,57} = 7.54$, $P = 0.0081$) and lighter eggs ($F_{1,57} = 6.79$, $P = 0.0117$) than their native counterparts ($N = 26$), whereas a noticeable, but not significant, trend towards less numerous eggs in the invasive population was observed ($F_{1,57} = 3.20$, $P = 0.079$). In gravid females, body size was positively correlated with clutch size ($F_{1,57} = 20.81$, $P < 0.0001$), egg size ($F_{1,57} = 7.82$, $P = 0.0077$) and egg mass ($F_{1,57} = 7.70$, $P = 0.0074$).

The PCA showed that females allocating more resources to reproduction (i.e. having heavier gonads) in early spring were significantly lighter in terms of fat bodies, liver mass and lean body mass (Table 2; Fig. 3A), and the same pattern was noted in both populations (data not shown). This indicates that resources allocated to energy storage in winter were significantly deployed to fuel reproduction in the next season (capital breeding). Such an allocation strategy seems temporary, given that female reproductive investment was uncorrelated with other organs at the end of the breeding season (Table 2; Fig. 3B). Conversely, male reproductive investment did not differ between sampling periods or populations (Table 1; Fig. 2B) and seemed to be uncorrelated with energy storage (Table 2; Fig. 3C, D).

ENERGY STORAGE

Contrary to our expectations, energy storage expressed as body fat % and $\mathrm{SMI}_{\mathrm{liver}}$ did not differ for females between the two populations at the end of the breeding season (Table 1; Fig. 2C, E). Instead, invasive male toads had lighter storage organs than their native counterparts (Table 1; Fig. 2D, F).

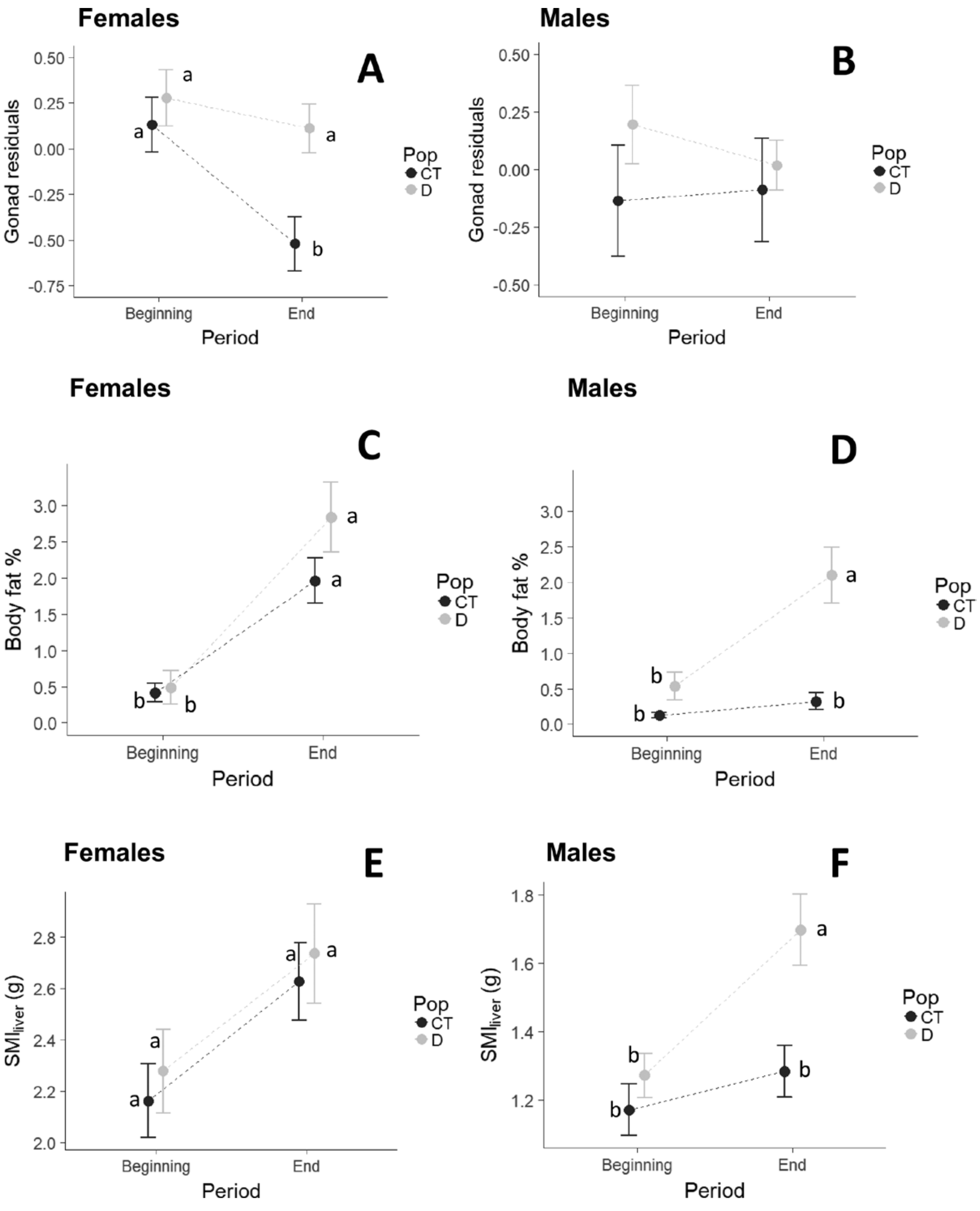

Figure 2. Means values (± SE) of gonad residuals, percentage of body fat (body fat %) and scaled mass index for liver mass (SMI_{liver}) obtained from guttural toads (*Sclerophrys gutturalis*) sampled in Cape Town (CT) and Durban (D). Data are presented separately for each sex and sampling period. Means sharing a letter are not significantly different ($P > 0.05$) according to Tukey's post hoc pairwise comparisons. When no differences between sex or sampling period were detected through two-way ANOVAs, post hoc comparisons were not conducted.

Table 2. Results of principal components analyses conducted on the scaled mass index for lean structural body mass (SMI_{lean}), body fat (body fat %), scaled mass index for liver mass (SMI_{liver}) and gonads (gonad residuals), separately for each sex and sampling period

Sex	Mass	Beginning		End	
		Dim1	Dim2	Dim1	Dim2
Female	Lean body	0.614	**0.590**	**0.741**	–0.197
	Body fat	**0.705**	–0.494	**0.767**	0.153
	Liver	0.677	0.464	**0.859**	0.264
	Gonads	**–0.729**	0.450	–0.209	**0.947**
Males	Lean body	**0.634**	0.229	0.328	**0.762**
	Body fat	–0.071	**0.940**	**0.741**	–0.555
	Liver	**0.745**	0.194	**0.913**	–0.166
	Gonads	**0.634**	0.229	0.328	**0.762**

Correlation values obtained between each mass and the first two dimensions (Dim1, Dim2) of each principal components analysis are reported. Results in bold indicate masses that contribute significantly to the first two dimensions.

In accordance with our expectations, the energy allocated to storage increased significantly from the beginning to the end of the breeding season in both sexes and populations (Table 1; Fig. 2C–F). The PCAs conducted on data from both males and females showed that the positive correlation between the fat bodies and the liver was particularly high at the end of the breeding season (Table 2; Fig. 3B, D).

GROWTH

In accordance with our predictions, both females and males from the cooler, more seasonal environment of the invaded range had significantly heavier structural masses (expressed as SMI_{lean}) than those from the native range (Table 1; Fig. 4A, B).

Females showed slightly but significantly heavier structural masses at the end of the breeding season in both populations, suggesting that some energy might also be allocated secondarily to somatic tissues, such as muscles, in addition to storage (Table 1; Fig. 4A). This was confirmed by the PCA conducted on females sampled at the end of the breeding season; females having heavier fat bodies and livers (dimension 1) were also significantly heavier in terms of structural mass (Table 2; Fig. 3B). Conversely, a negative correlation between gonad mass and structural mass was detected in females, especially in early spring (Table 2; Fig. 3A). Principal components analysis conducted on data from male toads showed that individuals with heavier structural mass also had heavier gonads throughout the entire breeding season. Thus, allocation trade-offs between reproduction and growth differed between the sexes (Table 2; Fig. 3C, D).

Only male toads from the invasive population showed a scaled mass index significantly heavier than that of their native conspecifics (Table 1; Fig. 4C, D).

DISCUSSION

We show that invasive female guttural toads introduced to a cooler, more seasonal environment adopt a more marked capital breeding strategy than native females. This difference may be induced by the low temperature, reduced water availability and heightened seasonality encountered by the invasive population. Conversely, male reproductive investment does not show any seasonal variation and appears to be uncorrelated with energy storage in both sampling periods. We also show that invasive toads allocate more resources to growth than do native conspecifics. This shift in allocation is consistent between sexes and might be an adaptive response to the novel conditions of temperature and seasonality of the invaded area.

Female toads from the invaded range show a marked decrease of reproductive investment from the beginning to the end of the breeding season, whereas no seasonal difference is detected in the native population (Fig. 2A). Given that environmental seasonality is stronger in the invaded area than in the native one (Fig. 1), our results are in accordance with theoretical studies, which predict a more marked seasonal reduction in reproductive investment in more seasonal environments (Ejsmond *et al.*. 2010, 2015). We suggest that changes of gonadal mass over the breeding season, rather than the mass itself, can be used to quantify the degree of capital breeding in each population. The breeding period in the invaded range is characterized by more limited water availability than is the native subtropical environment (Fig. 1), and this could reduce the abundance of the arthropod prey of the toads in the invaded range. Such a lower availability of food resources should negatively affect reproductive investment in invasive female toads, especially at the end of the breeding season, i.e. when

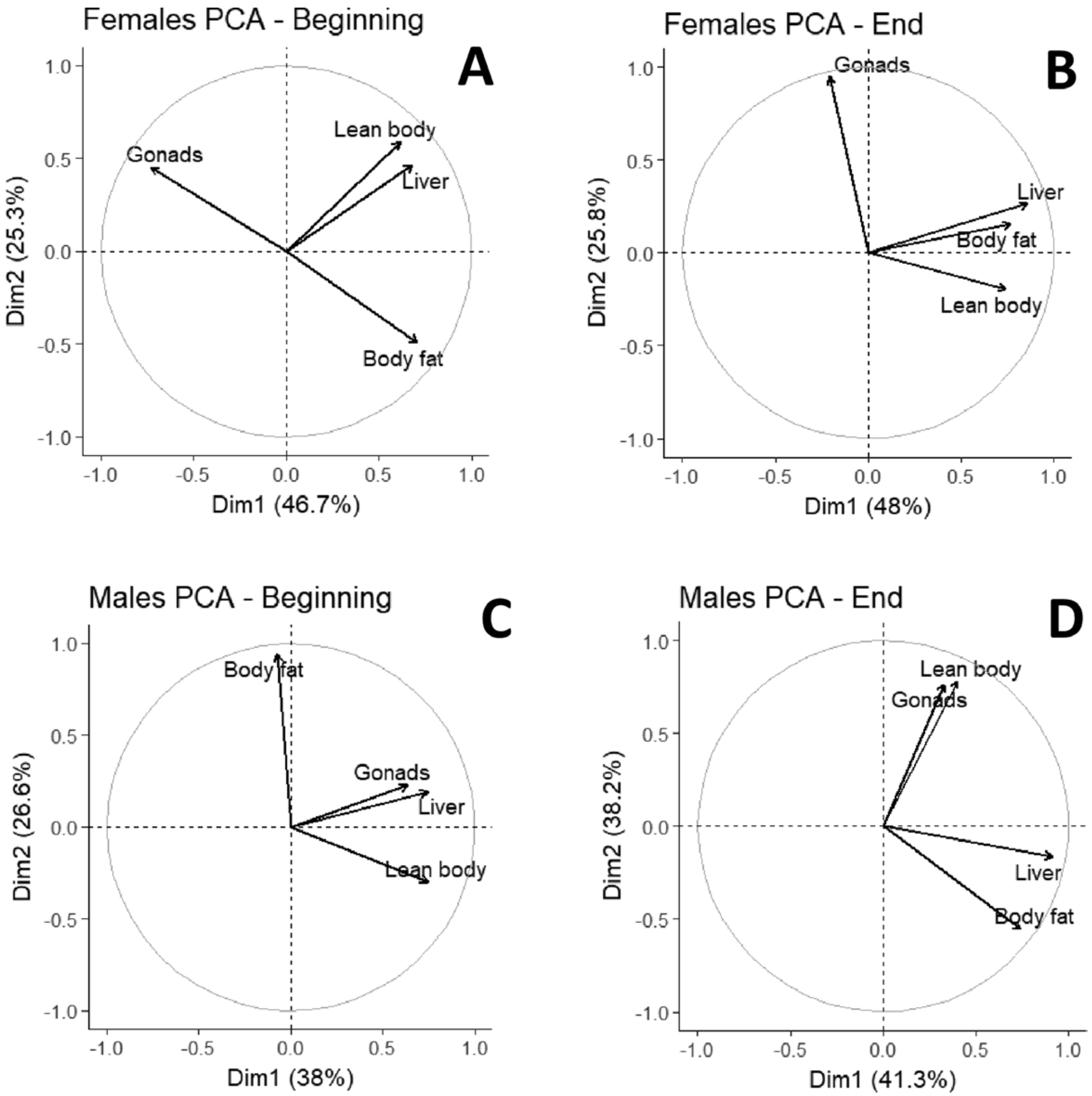

Figure 3. Graphical representations of principal components analyses conducted on lean structural mass, storage organs and gonads, separately for each sex and sampling period. The total amount of variance explained by the two first dimensions (Dim1 and Dim2) is reported in the axes.

exogenous resources (income breeding) are favoured over endogenous resources (capital breeding) to fuel reproduction (Ejsmond *et al.*, 2015; Varpe, 2017). Conversely, abundant or temporally stable food resources during the breeding season in the subtropical native range could sustain reproduction further than in invasive conspecifics by using an exogenous resource. Our study fully confirms these predictions (Fig. 2A). Furthermore, previous authors have shown that in the invaded range, arthropod abundance associated with endemic plants is significantly higher in the cold, wetter autumn (March–May) and winter (June–August) than in summer (Coetzee, 1989; Roets *et al.*, 2006).

The results thus indicate that invasive female toads have moved towards a more marked capital breeding strategy than their native counterparts. However, we suggest caution in considering native female toads as

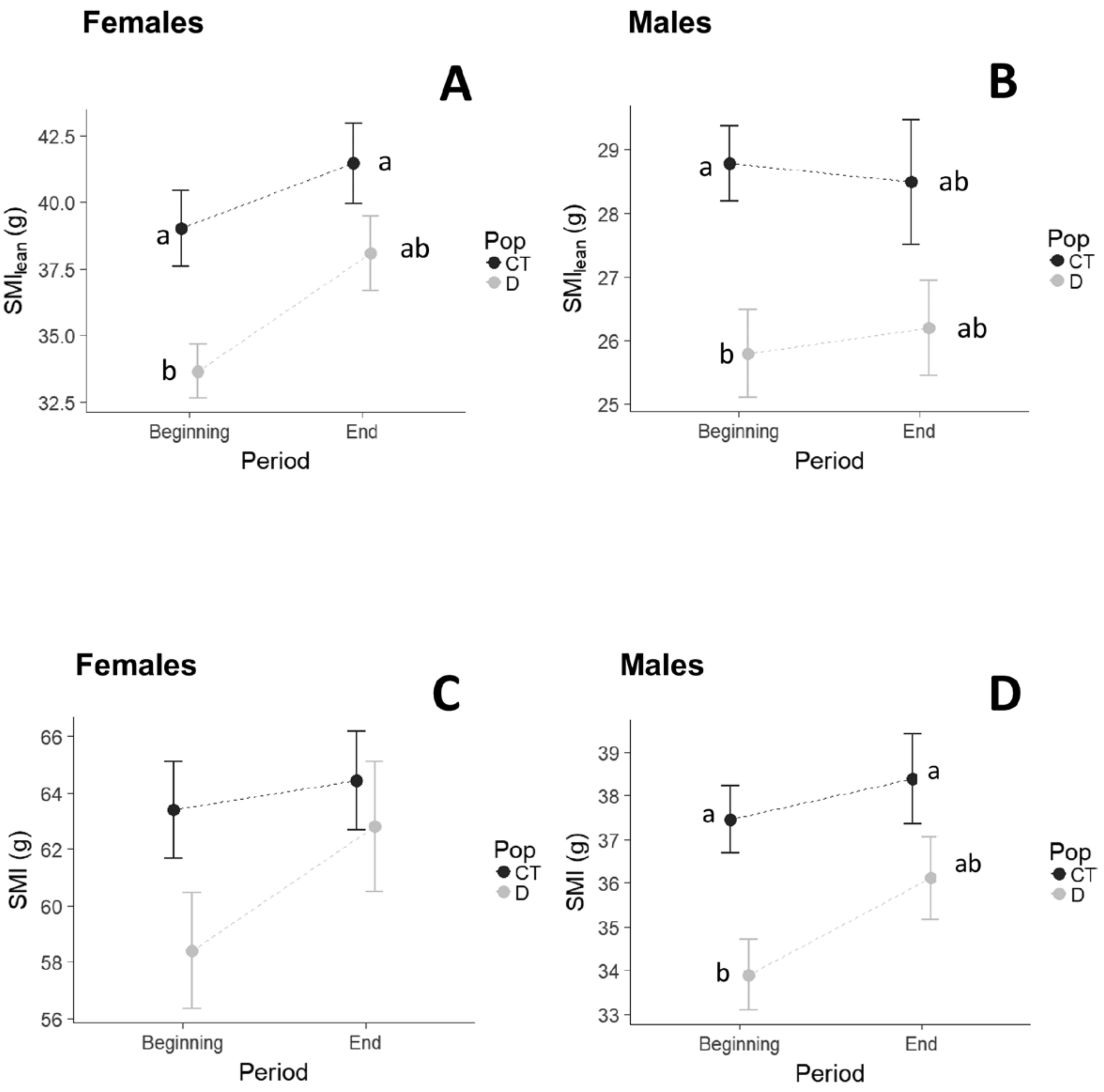

Figure 4. Mean values (± SE) of scaled mass index for lean structural mass (SMI_{lean}) and scaled mass index for body mass (SMI) obtained from guttural toads (*Sclerophrys gutturalis*) sampled in the invaded range (Cape Town, CT) and in the native range (Durban, D). Data are presented separately for each sex and sampling period. Means sharing a letter are not significantly different ($P > 0.05$) according to Tukey's post hoc pairwise comparisons. When no differences between sex or sampling period were detected through two-way ANOVAs, post hoc comparisons were not conducted.

pure income breeders. Instead, their strategy should be considered as intermediate along a capital–income breeding continuum (Bonnet *et al.*, 1998; Warne *et al.*, 2012). In both sexes and populations, guttural toads allocate significantly more resources to energy storage at the end of the breeding season, i.e. before winter inactivity (Fig. 2C–F). During this period of the year, all the structures available to achieve storage capacity should be deployed; therefore, it is not surprising that a very high positive correlation between fat bodies and liver was detected in both sexes (Table 2; Fig. 3B, D). However, stored energy is used differentially in females and males later in the year, with females depleting reserves to boost gametogenesis in early spring (capital breeding; Table 2; Fig. 3A) and males not showing a significant trade-off between energy storage and reproductive investment (Table 2; Fig. 3C). Females should allocate more resources to reproductive investment than males (for more details, see Supporting Information, Table S1) to fuel vitellogenic growth in their ovaries (Jørgensen, 1992; Houston *et al.*, 2007; Soulsbury, 2019). Therefore, we suggest that females adopt a typical capital breeding strategy before the breeding season in both populations.

Additionally, native female toads appear able to switch to income breeding later in the season to fuel reproduction, whereas invasive toads seem constrained by the novel environment to reduce their reproductive output drastically (Fig. 2A). Females from both populations also replenish approximately the same amount of stored energy before winter starvation (Fig. 2C, E), although invasive females must accomplish this task during a much shorter period (Fig. 1). We speculate that in the invaded range, the shorter breeding season induces female toads to direct resources to energy storage more quickly than do native conspecifics, consequently constraining their reproduction. In other words, invasive female toads may be considered as pure capital breeders, whereas native female toads should rather be classified as mixed capital–income breeders (Ejsmond *et al.*, 2015). Testing this hypothesis in the field, for instance by the use of stable isotopes (Warner *et al.*, 2008; Van Dyke *et al.*, 2012), might help to quantify the relative contribution of exogenous and endogenous resources to storage and reproduction.

The lower reproductive output of invasive female toads is not counterbalanced by compensatory trade-offs towards larger and heavier eggs (Morrison & Hero, 2003; Liao *et al.*, 2016). Instead, toads from the invasive population have smaller and lighter eggs than toads from the native population. The lack of any compensatory response in invasive toads is intriguing and could be explained by the very recent introduction of the species. The guttural toad was introduced to Cape Town < 20 years ago (De Villiers, 2006). This could have been insufficient time for local adaptation to occur in the invasive population, if differences in egg size and clutch size between populations inhabiting contrasting environments are genetically determined (Berven, 1982). However, a suboptimal phenotype in the invaded range can still not explain the smaller and lighter eggs we observed in invasive toads when compared with the eggs of native conspecifics. Given that invasive female toads at the end of the breeding season have the smallest and lightest eggs among all females across periods and populations (data not shown), we speculate that in the invaded range, the lower allocation of resources to reproduction is reinforced by lower resource acquisition from the environment. Lack of income breeding in the invaded range might thus decrease not only gonadal mass but also egg mass and egg size in gravid females.

Contrary to our expectations, reproductive investment in males does not vary throughout the breeding season in either population (Fig. 2B) and seems to be uncorrelated with energy storage (Fig. 3C, D). This might suggest that unlike females, invasive and native male toads adopt an income breeding strategy both at the beginning and the end of the breeding season. The capital–income breeding dichotomy applies equally to male reproduction, but compared with females there are different constraints, both physical and physiological, that affect the adoption of each strategy (Soulsbury, 2019). In amphibians, capital breeding is often detected in males from populations or species characterized by explosive breeding or lekking, such as the common frog *Rana temporaria* (Ryser, 1989). Conversely, in populations or species where the breeding season spans several months and males spend only a fraction of their time in lekking and the rest in foraging, such as in the European tree frog *Hyla arborea*, income breeding should be favoured (Soulsbury, 2019). Given that the breeding season of the guttural toad in both invaded and native ranges spans between 5 and 8 months, it seems reasonable to assume that male guttural toads are income breeders. However, we suggest that further studies on guttural toads should not only measure the seasonal variation of gonadal mass and body mass, but should also quantify energy expenditure in behavioural activities, such as calling or combat (Soulsbury, 2019). Given that the intensity and frequency of these activities cannot be quantified simply by measuring the mass of the testes, our conclusions concerning the interaction between energy storage and reproduction in males of the guttural toads are tentative.

Invasive toads possess not only heavier structural masses and heavier body masses than their native conspecifics (for more details, see Supporting Information, Table S1), but this difference remains significant after correcting for body size through SMI_{lean} and SMI (Table 1; Fig. 4A, B, D; Supporting Information, Table S1). This indicates that more resources are allocated to growth in the invasive population, possibly to cope with the colder and drier environment of Cape Town. For allometric reasons, volume grows faster than surface area; therefore, larger body sizes and heavier body masses are expected to retain body heat and moisture better in conditions of low temperature and water availability. Therefore, the occurrence of heavier structural masses and body masses in invasive toads might represent an additional adaptive response to the invaded environment. Previous studies found that invasive toads noticeably outperformed native conspecifics in terms of locomotive endurance, when both groups were dehydrated experimentally (Vimercati *et al.*, 2018). Whether the heavier structural mass (i.e. bones and muscles) possessed by invasive guttural toads confers higher locomotor performance in conditions of low water availability is currently unknown.

The guttural toad has already undergone rapid (< 20 years) adaptive physiological responses that reduce its sensitivity and exposure to the conditions of lower temperature and reduced water availability in Cape Town (Vimercati *et al.*, 2018). Sustained allocation of resources to growth in the invasive population might also confer greater resistance to starvation during longer winters (Cushman *et al.*, 1993) and prolong individual lifespan. A longer lifespan, which increases the lifetime number of reproductive events (Cichoń, 1997, 2001), might counterbalance the shorter breeding season (and thus the lower annual reproductive investment) in the invaded range.

Invasive species might allocate more resources to growth in environments where their predators or pathogens are absent (Blossey & Notzold, 1995), and this could possibly be the case for the invasive guttural toad. Release from natural enemies that are present in the native range might allow reallocating defence resources to somatic and reproductive tissues to accelerate growth, promote higher biomass and increase reproductive investment, although such trade-offs are more commonly observed in invasive plants (Blossey & Notzold, 1995). Guttural toads from Cape Town were found to have lower parasite loads than conspecifics from Durban (Kruger, 2017). Establishing whether this lower parasite load promotes heavier body mass (i.e. higher body condition index) and heavier structural masses in the invaded range could inspire future research on the interplay between resource allocation trade-offs and enemy release in invasive animals.

In conclusion, we show that invasive guttural toads from Cape Town adopt a different resource allocation strategy when compared with their native conspecifics from Durban. In the invasive population, a more marked capital breeding is adopted by females, whereas proportionally more resources are invested in growth by both sexes. Such allocation strategies might be a rapid (< 20 years) adaptive response to the challenging conditions of temperature, water availability and seasonality encountered by the invasive population. Both local genetic adaptation and environmentally induced phenotypic plasticity may promote an adaptive response, which increases fitness of the invaders in the novel environment during a short period of time (Hendry *et al.*, 2011). Thus, controlled translocation or common-garden experiments will certainly help in the future to distinguish between genetic changes and adaptive phenotypic plasticity in the allocation strategy of the guttural toad. More generally, more field and experimental studies should be conducted across different taxonomic groups to explore whether and how optimal allocation strategies might vary across populations that are introduced and become invasive in novel environments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Mean values (± SE) of snout–vent length (SVL), body mass, scaled mass index for body mass (SMI), lean structural mass, scaled mass index for lean structural mass (SMI_{lean}), liver mass, scaled mass index for liver mass (SMI_{liver}), percentage of body mass composed of fat reserves (body fat %) gonadal mass and gonad residuals obtained from guttural toads (*Sclerophrys gutturalis*) sampled in Cape Town and Durban. Data are presented separately for each sex, population and sampling period.