



# African striped mice have relatively smaller brains in the food deprived dry season than in the wet season

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## Abstract

The ability to alter the mass of energetically consumptive organs in response to seasonal variation in nutritional access has been demonstrated in several species from temperate climates, but less so from other climate zones. We predicted that adult striped mice (*Rhabdomys pumilio*) from the Succulent Karoo semi-desert in South Africa have lower organ masses during the hot summer dry season with low food availability ( $n=28$ ) when compared to the food-rich wet season ( $n=25$ ) as a possible adaptation to reduced energy expenditure. Food availability in the wet season was more than twice than that of the dry season. Body mass was positively correlated with most organ masses considered, except for the spleen. Mandible length, as a non-plastic measure of body size, was positively correlated with the mass of heart and stomach. Relative to body mass and to mandible length, kidneys and the small intestine were heavier in the wet season than during the dry season in both sexes. Liver masses were greater in females (but smaller in males) during the wet season, possibly due to increased female reproductive investment during this season. Both sexes had relatively heavier brains (by 9.6% on average) during the wet season than during the dry season, which is the first indication of the Dehnel phenomenon in a rodent, in a subtropical climate, and in the southern hemisphere. Future studies will have to test whether this change in brain size is reversible. Having relatively smaller brains during the dry season could be a mechanism to reduce energy consumption. In conclusion, our study indicates that striped mice may save energy during the food restricted dry season by reducing energetically expensive organ masses, including brain mass.

**Keywords** Dehnel phenomenon · Energy · Harshness · Food · Starving · Fasting

## Introduction

Adaptive phenotypic plasticity is a well-documented fitness-optimization strategy (Tieleman et al. 2002; Swallow et al. 2005; Naya et al. 2007), particularly in fluctuating environments (Piersma and Lindström 1997; Naya and Božinović

2006). Alterations in the phenotype are often reversible (phenotypic flexibility), allowing for acclimation to differences in prevailing food and water availability, or in ambient temperatures (Piersma and Drent 2003; Cortés et al. 2011). Adjustments in organ sizes (morphological flexibility) can be an adaptive response for organisms that need to trade-off between the energetic cost of tissue investment and the utility of those organs under varied environmental conditions (Pucek 1965; Chappell et al. 1999; Peña-Villalobos et al. 2013). While natural selection would eventually eliminate unnecessary energy investments in static environments, reversible changes make it possible for organisms to avoid unnecessary energy expenditure under changing conditions (Garland and Huey 1987). Seasonal plasticity in organ masses has been shown in birds (van Gils et al. 2005) and in small mammals from the temperate climate zone in winter versus summer (Pucek 1965; Zuercher et al. 1999; Nay et al. 2007), but little evidence of such plasticity exists from the

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subtropics, where differences between the dry and the wet season might make such plasticity adaptive.

Sex-dependent morphological flexibility is well documented, particularly in mammals (Hanwell and Peaker 1977; Naya et al. 2007, 2008b). Pregnant and lactating female mammals increase digestive tract, heart, kidney and liver sizes, and these adjustments are reversible (Hanwell and Peaker 1977). Morphologically flexible individuals can conserve energy in food-poor periods by ceasing breeding, and additionally by reducing the size of their reproductive organs (Bauchinger et al. 2007; Del Valle and López Mañanes 2011). Such changes increase their chances of survival until conditions become more favorable for reproduction, thus increasing their fitness (Chappell et al. 1999).

While reducing reproductive tissues in times of stress may conserve energy, there are additional organs that individuals may reduce when food becomes scarce. Digestive tissues, representing the “functional link” between food consumption and metabolically available energy, are particularly energetically costly to maintain (Piersma and Van Gils 2011; Jehl and Henry 2013). Thus, the digestive tract often shrinks when energy is limited (Schwaibold and Pillay 2003; Naya et al. 2008a; Maldonado et al. 2011). However, periods of constrained food availability are also often characterized by food of poorer quality, which needs a larger digestive system to extract energy (Cortés et al. 2011). In addition, animals might be forced to eat food with a higher content of toxins in seasons of low food availability, such that organs needed for the processing of toxins (e.g., liver, spleen) are enlarged (Liu and Wang 2007; Naya et al. 2007). It is therefore unclear how digestive systems respond to limited but poorer quality nutrition, particularly in free-ranging animals occupying seasonal environments.

Neural tissue is energetically costly. The brain uses a large amount of energy (Laughlin 2001) and, in honey bees (*Apis mellifera*), it is known to reduce in size in response to stress and deprivation as a means of maximizing energetic efficiency (Maleszka et al. 2009). Similarly, the mammalian brain can be sensitive to environmental fluctuations, as demonstrated by the Dehnel effect (Dehnel 1949; Hays and Lidicker 2000). First reported in shrews (*Sorex* spp.), the Dehnel effect describes a reduction in overall body and brain mass during winter, which can be interpreted as an adaptive strategy to reduce energy demands when food is limited (Dehnel 1949; Hays and Lidicker 2000). Long-term data collected over 50 years in shrews shows a strong effect of climate on skull size (as a correlate of brain size) (Taylor et al. 2022). The Dehnel effect received more attention recently (Lazaro et al. 2021). Using modern methods and repeated measures on the same individuals, it was shown that the braincase in shrews and in mustelids shrinks in autumn and winter, then increases again in spring (Dechmann et al. 2017), and that these shifts influence cognition (Lázaro et al. 2018).

African striped mice (*Rhabdomys pumilio*) inhabiting the subtropic Succulent Karoo semi-desert in South Africa face long, hot, dry seasons and short, fluctuating wet seasons. Given its ubiquity, visibility and proclivity for group living, the striped mouse has long been used as a model organism for studies of flexible behavioral and physiological responses to fluctuating environmental conditions, particularly those associated with the annual dry season and drought (Rymer et al. 2013, 2016). In the Succulent Karoo, striped mice breed in the austral spring (August to November), when food abundance is highest after rainfall in winter. The breeding season is concentrated to 3 months with females having 2–3 litters such that the difference in age between the first and last litter is approximately 2 months (Schradin and Pillay 2005a). They then have to survive the forthcoming summer dry season (December to April) characterized by very low food availability, to breed in the subsequent spring. Less than 5% of individuals survive for a second breeding season, so life expectancy in the wild is below 2 years. Body mass is not associated with the risk of disappearance during the dry season (Vuarin et al. 2019). Here, we compared the relative organ masses of striped mice between the wet and the dry seasons in the Succulent Karoo. As an adaptation to the food restricted dry season, we predicted that striped mice would have relatively smaller organ masses in the dry than in the wet season.

## Materials and methods

### Study period, study area and specimens

Specimens were 69 adult striped mice that were either removed and euthanized (overdose of di-ethyl ether followed by decapitation) during an experimental study to reduce population density (Schoepf and Schradin 2012) and to measure brain receptors (Schoepf et al. 2015), or died during trapping or anesthesia (comprising < 0.1% of approximately 62,000 animal trappings). The Animal Ethics Screening Committee (AESC) of the University of the Witwatersrand has considered and approved our request to use stored samples of striped mice carcasses to study seasonal variations in organs and tissues based on our ethical clearance for removing mice for brain sampling AESC 2007/38/04 and AESC 2007/40/01 during trapping. Specimens were collected over 8 years between March 2009 and September 2016 at the Succulent Karoo Research Station, Springbok, Northern Cape Province, South Africa. The body mass of all specimens was measured before they were dissected from anus to sternum and stored in 10% formaldehyde.

The mice were removed from formaldehyde, blotted dry with tissue paper and then pinned down flat dorsally onto a wax dissection board. The kidneys, spleen, adrenal glands,

liver, stomach, small intestine, cecum, large intestine, heart, lungs and brain were removed, cleared of fat (as necessary) and blotted dry with tissue paper, and then weighed using a Mettler AE163 scale with an accuracy of 0.001 g. We used the summed-up mass of both kidneys and adrenal glands per individual, respectively. The stomach, small intestine, cecum and large intestine were pinned and opened longitudinally using a scalpel, and then rinsed in Ringer's solution and blotted dry to obtain empty mass measurements. To get a measure for non-plastic body size independent of body mass, we measured the length of the left mandible (e.g., Klingenberg and Navarro 2012) following the description in Skinner and Chimimba (2005)

### Sample size

Organ masses and individual body masses from  $N = 69$  adult African striped mice were available (20 females and 18 males collected during the dry season; 9 females and 22 males during the wet season). However, mandible length, which we used as a proxy of body size, could only be obtained for  $n = 53$  individuals, because the heads were not available from some individuals for which the brain had been used for other studies (Schoepf and Schradin 2014). This reduced the sample size for the main analysis (see Table 1) to 13 females and 15 males collected during the dry season and to 8 females and 17 males collected during the wet season. The main results would have been the same with the full sample size of  $N = 69$  without mandible length as a covariate. Furthermore, for one male sampled during the dry season, the masses of the adrenal glands could not be obtained, thus reducing the sample size to  $n = 52$  individuals for this specific analysis (see Table 1b).

### No general differences in organ masses in relation with different causes of death

The animals from our sample were either found dead in their traps or were euthanized by using ether, see above. This information on the cause of death was available for 46 out of the 53 individuals used for later analysis. That is, 11 animals (23.9%) were known to be found dead in the trap and 35 animals (76.1%) were known to be euthanized by ether. Prior to our analysis of seasonal variation in organ masses, we tested for a possible influences of the cause of death, as one may hypothesize potentially lower organ masses in animals deceased within the traps due to effects of dehydration. Using a Mann–Whitney  $U$  test, we found no significant differences between animals who died either in the traps or were euthanized by ether regarding all organ masses considered in our study (all  $P > 0.10$ ).

### Quantification of food availability

Food availability in the habitat was determined using a bimonthly assessment of eight  $2 \text{ m} \times 2 \text{ m}$  plots using the Braun-Blanquet Method, which averaged the number of different edible plant species observed to calculate food availability (Werger 1974; Schradin and Pillay 2006).

### Statistical analyses

All statistical analyses were done by linear mixed-effects models (LMM) using the *nlme* package (Pinheiro et al. 2022) of the software R, version 4.3 (R Core Team 2023). We included 'year' as a random intercept factor to account for potential among-year ( $n = 8$ ) variation.

We analyzed the effects of sex and season (factors with 2 levels) on organ masses (response variables) by multifactorial LMMs. To check whether seasonal differences were sex-specific, we included the 2-way interaction between these factors. All models included the individual body mass and mandible length (covariates) to account for possible body mass or body size-dependent differences in organ masses (Lazic et al. 2020). We also considered the 2-way interactions between body mass or mandible length and season to check whether the slope of the potential allometric association between the different organ masses and the individual body mass or body size were season-specific. When non-significant, interaction terms were stepwise removed from the models before these were re-calculated (Engqvist 2005). Using the *plot\_model* function of the R package *sjplot* (Lüdtke 2022), we plotted predicted values of organ masses dependent on sex and season, which were based on the model estimates of multifactorial LMMs, thus correcting for the possible effects of the covariates body mass and mandible length (Lazic et al. 20,220). Post hoc comparisons carried out after significant interactions (sex  $\times$  season) were also done by LMMs.

$P$ -values were calculated by 10,000 Monte-Carlo permutations using the package *pgirmess* (Giraudeau 2022). Such non-parametric permutation tests do not require normal distribution of model residuals (Good 2005). However, by plotting fitted values versus the residuals we verified for all full models that variances were homogenous (Faraway 2006), as unequal variances in permutation testing can lead to inflated type I error rates (Huang et al. 2006). For the analysis of the masses of the adrenal glands and the spleen, homogeneity of variances was obtained after  $\log[x]$  transformation of the response variables.

Standardized estimates ( $\beta$ ) based on the analysis of scaled data (covariates and response variables) are given in Table 1. For assessing the proportion of variance explained by body mass within the multifactorial LMMs, we calculated partial, marginal  $R^2$  (after Nakagawa et al.

**Table 1** Effects of different predictor variables on organ masses

Organ mass	<i>N</i>	Predictor	Estimates [ <i>CI</i> <sub>95%</sub> ]	<i>P</i>
(a) Kidneys (total)	53	Body mass	0.662 [0.466, 0.858]	<b>&lt;0.001</b>
		Mandible length	0.103 [-0.092, 0.297]	0.314
		Sex (male)	-0.351 [-0.773, 0.069]	0.075
		Season (wet season)	0.489 [0.083, 0.896]	<b>0.020</b>
		Body mass × Season	0.090 [-0.335, 0.514]	0.669
		Mandible length × Season	-0.134 [-0.530, 0.261]	0.491
		Sex × Season	-0.618 [-1.464, 0.229]	0.140
(b) Adrenal glands (total) <sup>1,2</sup>	52	Body mass	0.625 [0.404, 0.846]	<b>&lt;0.001</b>
		Mandible length	0.095 [-0.124, 0.313]	0.423
		Sex (male)	-0.165 [-0.615, 0.284]	0.430
		Season (wet season)	0.349 [-0.096, 0.793]	0.130
		Body mass × Season	-0.134 [-0.629, 0.361]	0.583
		Mandible length × Season	0.097 [-0.360, 0.554]	0.667
		Sex × Season	-0.049 [-1.034, 0.935]	0.918
(c) Liver	53	Body mass	0.577 [0.374, 0.780]	<b>&lt;0.001</b>
		Mandible length	-0.068 [-0.260, 0.124]	0.485
		Sex (male)	0.049 [-0.488, 0.587]	0.853
		Season (wet season)	0.751 [0.096, 1.406]	<b>0.028</b>
		Body mass × Season	0.157 [-0.265, 0.579]	0.451
		Mandible length × Season	0.136 [-0.530, 0.258]	0.482
		Sex × Season	-1.299 [-2.128, -0.407]	<b>0.003</b>
(d) Spleen <sup>1</sup>	53	Body mass	0.182 [-0.081, 0.446]	0.162
		Mandible length	0.151 [-0.111, 0.414]	0.244
		Sex (male)	0.588 [-0.049, 1.226]	0.063
		Season (wet season)	-0.028 [-0.596, 0.552]	0.974
		Body mass × Season	-0.378 [-0.845, 0.369]	0.428
		Mandible length × Season	-0.083 [-0.676, 0.508]	0.775
		Sex × Season	0.198 [-1.046, 1.442]	0.748
(e) Heart	53	Body mass	0.688 [0.491, 0.886]	<b>&lt;0.001</b>
		Mandible length	0.238 [0.042, 0.435]	<b>0.020</b>
		Sex (male)	-0.010 [-0.448, 0.428]	0.964
		Season (wet season)	-0.074 [-0.490, 0.341]	0.726
		Body mass × Season	0.258 [-0.151, 0.667]	0.202
		Mandible length × Season	-0.274 [-0.655, 0.107]	0.146
		Sex × Season	-0.735 [-1.563, 0.092]	0.073
(f) Stomach (empty)	53	Body mass	0.654 [0.443, 0.865]	<b>&lt;0.001</b>
		Mandible length	0.263 [0.055, 0.471]	<b>0.015</b>
		Sex (male)	-0.035 [-0.460, 0.391]	0.872
		Season (wet season)	0.047 [-0.375, 0.469]	0.829
		Body mass × Season	0.162 [-0.300, 0.628]	0.478
		Mandible length × Season	-0.180 [-0.611, 0.251]	0.398
		Sex × Season	-0.320 [-1.244, 0.603]	0.483
(g) Caecum (empty)	53	Body mass	0.565 [0.335, 0.795]	<b>&lt;0.001</b>
		Mandible length	0.165 [-0.063, 0.394]	0.167
		Sex (male)	-0.270 [-0.814, 0.273]	0.311
		Season (wet season)	0.499 [-0.048, 0.946]	0.092
		Body mass × Season	0.148 [-0.370, 0.666]	0.563
		Mandible length × Season	-0.326 [-0.827, 0.175]	0.188
		Sex × Season	-0.389 [-1.444, 0.667]	0.456

**Table 1** (continued)

Organ mass	<i>N</i>	Predictor	Estimates [ <i>CI</i> <sub>95%</sub> ]	<i>P</i>
(h) Small intestine (empty)	53	Body mass	0.288 [0.253, 0.722]	<b>&lt;0.001</b>
		Mandible length	0.024 [−0.208, 0.256]	0.841
		Sex (male)	−0.548 [−1.022, −0.074]	<b>0.024</b>
		Season (wet season)	0.488 [0.018, 0.958]	<b>0.044</b>
		Body mass × Season	0.021 [−0.488, 0.530]	0.934
		Mandible length × Season	−0.062 [−0.536, 0.412]	0.791
		Sex × Season	−0.798 [−1.814, 0.218]	0.112
(i) Large intestine (empty)	53	Body mass	0.370 [0.110, 0.629]	<b>0.005</b>
		Mandible length	0.230 [−0.027, 0.487]	0.077
		Sex (male)	−0.193 [−0.740, 0.353]	0.482
		Season (wet season)	0.285 [−0.247, 0.818]	0.296
		Body mass × Season	0.347 [−0.228, 0.923]	0.222
		Mandible length × Season	−0.205 [−0.567, 0.517]	0.926
		Sex × Season	−0.132 [−1.287, 1.022]	0.816
(j) Brain	53	Body mass	0.333 [0.082, 0.585]	<b>0.009</b>
		Mandible length	0.012 [−0.237, 0.262]	0.922
		Sex (male)	−0.030 [−0.591, 0.532]	0.913
		Season (wet season)	0.552 [0.021, 1.083]	<b>0.042</b>
		Body mass × Season	−0.271 [−0.812, 0.270]	0.311
		Mandible length × Season	0.229 [−0.280, 0.730]	0.368
		Sex × Season	0.844 [−0.237, 1.926]	0.114
(k) Lung	53	Body mass	0.657 [0.447, 0.867]	<b>&lt;0.001</b>
		Mandible length	0.170 [−0.037, 0.378]	0.108
		Sex (male)	0.101 [−0.324, 0.535]	0.634
		Season (wet season)	0.209 [−0.212, 0.209]	0.325
		Body mass × Season	0.098 [−0.349, 0.545]	0.657
		Mandible length × Season	−0.338 [−0.754, 0.078]	0.100
		Sex × Season	0.607 [−1.499, 0.286]	0.169

Data collected from *N*=53 adult African striped mice sampled over 8 years. Analysis by multifactorial LMMs including year as a random factor. Standardized estimates with 95% confidence intervals are given. *P*-values were calculated by 10,000 Monte Carlo permutations, highlighted in bold when statistically significant

<sup>1</sup>Log[*x*] transformation for statistical analysis to obtain variance homogeneity

<sup>2</sup>The sample size for adrenal gland masses was smaller as the data from one individual could not be obtained

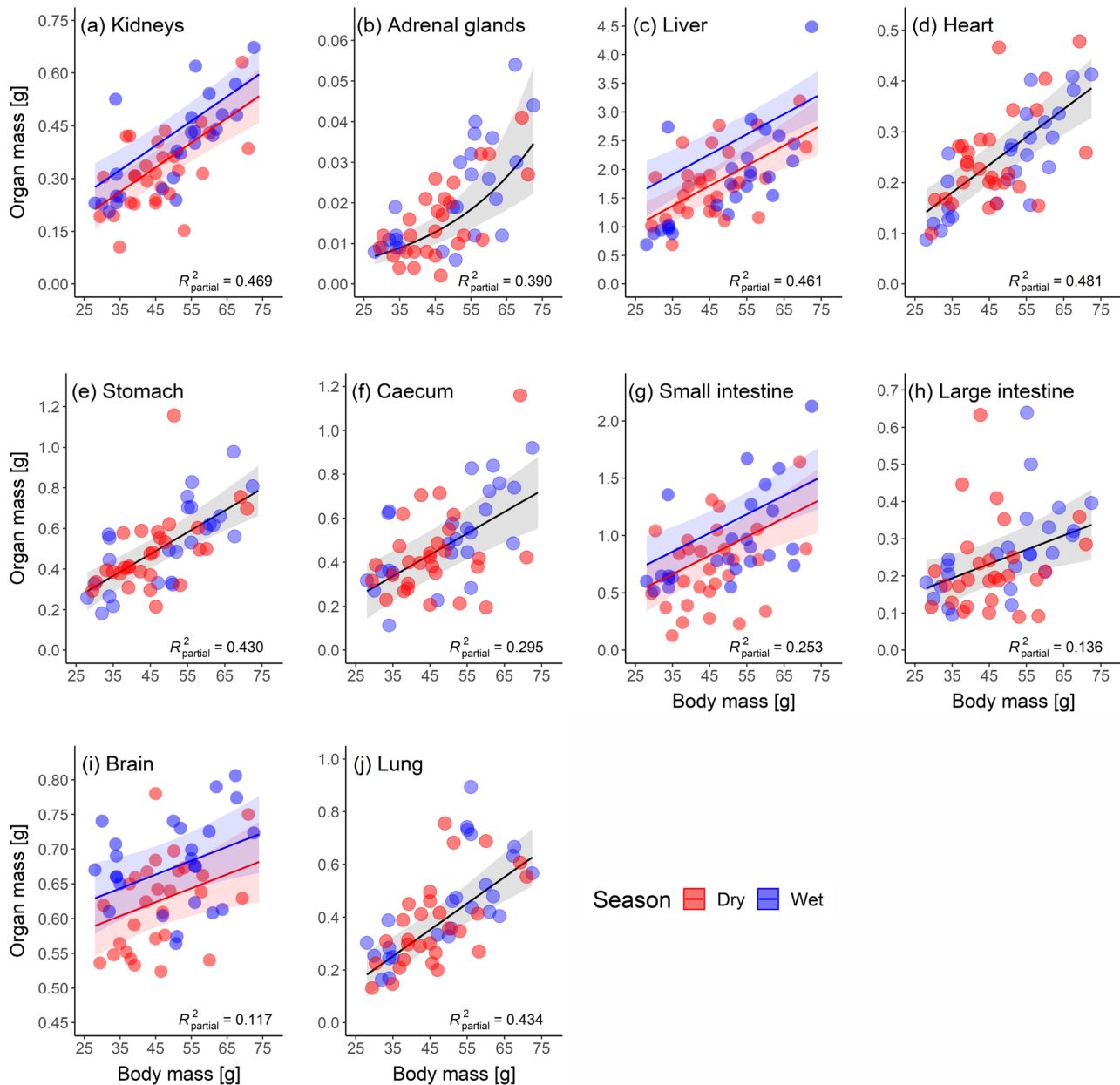
2017) using the R package *r2glmm* (Jaeger 2017) (see Figs. 1, 2). We also calculated variance inflation factors (VIF) for all full models including the interaction terms ‘bodymass × season’, ‘mandible length × season’ and ‘sex × season’ (see Table 1). VIF were always < 3.1, thus indicating that there were no notable (multi)collinearities between the different model predictors (Faraway 2006). In particular, mandible length and body mass were not significantly correlated (LMM:  $\beta = -0.025$ ,  $CI_{95\%} = [-0.306, 0.257]$ ,  $P = 0.86$ ), suggesting that larger individuals were not necessarily the heavier ones.

## Results

### Seasonal differences in food availability, body mass and mandible length

Food availability was significantly higher in the wet season [5.1 food plants per 4 m<sup>2</sup> on average;  $CI_{95\%} = (4.4, 5.9)$ ] than during the dry season [2.3 food plants per 4 m<sup>2</sup> on average;  $CI_{95\%} = (2.0, 2.6)$ ]; LMM:  $P < 0.001$ ].

For body mass, we found a significant interaction between sex and season (LMM:  $P = 0.039$ ). Post hoc



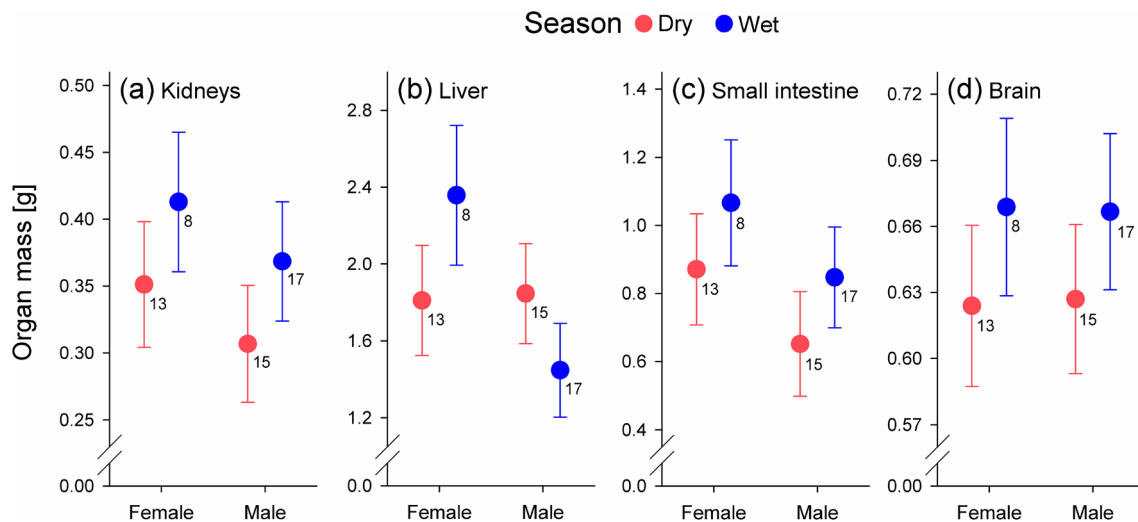
**Fig. 1** Correlations between individual body masses of adult African striped mice and the masses of different organs. All correlations shown were statistically significant (see Table 1 for  $P$ -values, and partial marginal  $R^2$  in the figures). Regression lines (two if seasonal differences were significant; otherwise, one for both seasons combined) are based on parameter estimates obtained from multifactorial LMMs

comparisons showed that females in our sample [mean wet season = 51.6 g,  $CI_{95\%}$  = (41.4 g, 61.7 g); mean dry season = 39.4 g,  $CI_{95\%}$  = (34.4 g, 44.4 g)] were significantly heavier during the wet season compared to the dry season (LMM:  $P = 0.016$ ), while male body mass (mean wet season = 47.1 g,  $CI_{95\%}$  = (41.0 g, 53.3 g); mean dry season = 49.0 g,  $CI_{95\%}$  = (43.2 g, 54.9 g)] did not differ significantly between seasons (LMM:  $P = 0.69$ ).

as given in Table 1; see also this table for sample sizes. Shadings around the regression lines depict 95% confidence bands. For (b), the response variable was  $\log[x]$  transformed for analysis, and thus this regression line is based on back-transformed parameters. Note that the scaling of the y-axis for (i) does not start with a zero

The mandible length did not differ significantly between dry and wet season (LMM:  $P = 0.95$ ) or between females and males ( $P = 0.82$ ), and the interaction between sex and season was also not significant ( $P = 0.94$ ). On average, the mandible length was 15.5 mm [ $CI_{95\%}$  = (15.1 mm, 15.9 mm)] during the wet season and 15.6 mm [ $CI_{95\%}$  = (15.2 mm, 16.0 mm)] during the dry season.





**Fig. 2** Predicted masses with 95% confidence intervals of (a) kidneys, (b) liver, (c) small intestine and (d) brain of adult African striped mice, dependent on season and sex, based on the results of multi-

factorial LMMs (details in Table 1a, c, g, i). Sample sizes are given inside the graphs; results of post hoc comparisons for (b) after the significant interaction 'sex  $\times$  season' are given in the text

### Associations between body mass, mandible length and organ masses

The individual body mass was significantly and positively correlated with the masses of most organs considered (except for the spleen), with partial (marginal)  $R^2$  values between 0.111 and 0.481 (details in Fig. 1; statistics in Table 1). For all organs considered, the interactions between body mass and season were non-significant (Table 1), indicating that the significant associations between body mass and the different organ masses was sufficiently assessed by the same regression slope.

Mandible length was significantly and positively associated with the masses of heart and stomach (Fig. A in Suppl. Materials; statistics in Table 1). We did not find any significant interactions between mandible length and season (Table 1).

### Effects of season and sex on organ masses

The following results were obtained when correcting for the above described body mass-related and mandible size-related allometries of organ masses (Table 1; Fig. 1, A in Suppl. Materials).

Kidney masses (Table 1a; Fig. 2a), the masses of the small intestine (Table 1h; Fig. 2c) as well as the masses of the brain (Table 1j; Fig. 2d) were significantly greater during the wet season than during the dry season. On average, the mean kidney masses differed between seasons by 22.5% (0.072 g), and the mean masses of the small intestine differed between seasons by 40.4% (0.275 g). The mean brain mass was 9.6% (0.059 g) heavier during the wet season.

We found sex-specific seasonal differences with respect to the masses of the liver (Table 1d). In females, the liver mass was on average 61.6% (0.986 g) greater during the wet season compared to the dry season, which was supported by a statistical tendency (LMM:  $P=0.054$ ; Fig. 2b). In contrast, in males, the mean liver mass was significantly lower during the wet than during the dry season, by 31.0% (0.450 g) (LMM:  $P=0.041$ ; Fig. 2b).

### Discussion

We found significant seasonal differences in relative masses of most visceral organs and the brain of striped mice in association with changes in food availability. Most organs were smaller in the food restricted dry season, possibly to reduce energy expenditure. These seasonal organ differences were significant when taking into account individual variation in body mass and body size (the latter was assessed by the animals' mandible length; Klingenberg and Navarro 2012). The most interesting morphological change was the significantly smaller (lighter) brains in the dry season with low food abundance.

Several organ masses were significantly greater in the wet season compared to the dry season, including those of the digestive system. This is in agreement with the observation that periods of increased food availability trigger breeding in striped mice (Schradin and Pillay 2005b). The spleen, the stomach, the caecum and the lungs showed no seasonal pattern. The small intestine were generally larger in females, maybe indicating their energetic needs during breeding. Only females had larger livers in the wet breeding

season, which could be due to the liver's important role in metabolism and milk production (Hanwell and Peaker 1977). Importantly, the relative liver mass was similar between the sexes in the dry season. This could be linked to the toxicity of *Zygophyllum retrofractum*, a perennial succulent plant, which is the main food source for striped mice in the dry season (Schradin, unpubl. data). It is known to be mildly poisonous when consumed in large quantities, which might necessitate proliferation of liver tissue in the dry season to combat its increased consumption (Schoepf et al. 2017). Our study indicates that striped mice optimize their energetic efficiency by breeding when sustenance is sufficient to allow investment in high organ mass.

The relatively smaller brain sizes in the dry season could be due to shrinking of this energetically expensive tissue (Dehnel phenomenon) or it could be a starvation response. In laboratory mice, brain volume decreases during fasting by approx. 10% (Frintrop et al. 2019), and we also observed brains being approximately 10% less heavy in the dry season. However, only females were heavier during the wet season, probably due to pregnancy, but not males, and there was no significant difference in body size (as assessed by mandible length) between seasons. Thus, there was no indication that fasting lead to overall smaller mice. This makes it unlikely that the smaller brains in the dry season were due to fasting.

Neural tissue is energetically very expensive and the central nervous system consumes a significant amount of energy (Laughlin 2001). The seasonal differences in brain mass of striped mice are consistent with the Dehnel phenomenon, which describes how food and water stress are associated with a reduced investment in neural tissue, resulting in a smaller brain (Dehnel 1949). The reduction in brain size is assumed to be reversible, though this was only assumed and not proven in the original study (Dehnel 1949). Similarly, our study found that brain size was lower in the dry season, but could not prove that this was due to brains decreasing in size. For this, one would need to measure brain size in living individuals before, during, and after the dry season. In shrews and in mustelids, the braincase shrinks in autumn/winter and then increases again in spring, and it is assumed that the same is true for the brain itself (Dechmann et al. 2017). While the Dehnel phenomenon has been shown to occur in the Northern hemisphere in Eulipotyphla (shrews and moles, Nováková et al. 2022; Taylor et al. 2022) and in mustelids (Dechmann et al. 2017), to our knowledge ours is the first study finding indication for its occurrence in a rodent, in a subtropical climate, and in the southern hemisphere.

Striped mice are born in spring and many reach adulthood in the same season, then they have to survive the subsequent dry season as adults before breeding in the next spring; few survive into the next dry season (Rimbach

et al. 2016). This makes it possible that brain sizes are not only relatively smaller in the dry season, but also decrease from spring to summer, to increase again in the following spring. To test whether brain mass of striped mice changes flexibly (i.e., the changes are reversible), we would need to measure brain mass of the same individuals repeatedly, which was not possible in our current study. Measuring the size of the braincase via computed tomography (CT) scans would be a future solution (Dechmann et al. 2017). Whatever the mechanism, the relatively smaller brain in the dry season indicates that striped mice invest relatively less energy into brain function during this season. Interestingly, cognitive performance in striped mice also changes seasonally, especially in males, which have worse spatial memory in the dry compared to the wet season (Maille et al. 2015).

## Conclusion

Striped mice live in a seasonal habitat, in which individuals need to survive a harsh food restricted dry season (Schradin et al. 2023) before breeding in the subsequent wet season. We found support for lower organ masses including lower brain mass in the period of low food availability as a potential mechanism to save energy. This adds to our knowledge of behavioral (Rimbach et al. 2016) and physiological (Rimbach et al. 2017) flexibility in striped mice as adaptations to fluctuating environmental conditions. More studies are needed to determine whether our findings of seasonal differences in striped mice brain mass does reflect individual-level flexibility, as predicted by the Dehnel phenomenon.

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**Author contributions** JM, NP and CS contributed to the study conception and design. Material preparation and data collection were performed by JM and LM. Statistical analysis was done by HGR. The manuscript was written by JM, HGR and CS. All authors read and approved the final manuscript.

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**Data availability** The raw data are available as electronic supplement.



## Declarations

**Conflict of interest** The authors have no conflict of interest to declare.

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