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## Prolonged growth during the food-restricted dry season in a small African mammal

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1 **Running header:** Prolonged growth in striped mice

2

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24

25 Studying how different environmental parameters, such as resource availability and ambient  
26 temperature, affect growth rates aids to understand the evolution of different growth  
27 strategies. Low levels of food availability restrict growth, and high ambient temperature can  
28 constrain growth via trade-offs between body temperature maintenance and heat produced  
29 during digestion. We studied growth of African striped mice (*Rhabdomys pumilio*), a small  
30 mammal living in a seasonally arid habitat. Striped mice are born during spring with high  
31 food availability and low ambient temperature, and typically enter the food-restricted dry  
32 season before reaching adulthood. We predicted low food availability and high ambient  
33 temperature would negatively affect growth. We therefore expected an extended period of  
34 slow growth during the long dry season. We repeatedly measured body length of 369 free-  
35 living individuals, examined how ambient temperature and food availability influenced  
36 growth rate, and seasonal changes in growth rate. In addition, we investigated whether mice  
37 ( $N = 27$ ) born in summer (atypical breeding season) have slower growth rates than those born  
38 in spring. Growth rate increased with increasing food availability and decreased with  
39 increasing ambient temperature. Individuals born in summer grew slower than those born in  
40 spring. Sexes reached asymptotic body length at 258 days (females) and 285 days (males),  
41 which is an unusually long growth period compared with other small rodents. As most striped  
42 mice live for less than one year, this period encompasses the entire life for most individuals,  
43 but stops at old age, which could indicate senescence. Our results demonstrate a positive  
44 influence of food availability on growth, a relationship mediated by ambient temperature. We  
45 conclude that striped mice enter the food-restricted dry season before postnatal growth is  
46 terminated, and early exposure to harsh environmental conditions during the long dry season  
47 likely explains the prolonged growth period in striped mice.

48

49 Key words: Eco-physiology, pace-of-life, plasticity, postnatal growth, rodents, senescence

50

51

52 Growth, especially during early life, can have important consequences for  
53 reproduction and survival (Lindström 1999). Some species show competitive growth, where  
54 individuals increase their growth rate in response to increases in the growth rate of potential  
55 competitors (Huchard et al. 2016). Fast growth and good body condition can positively affect  
56 survival (Wauters et al. 1993; Festa-Bianchet et al. 1997); can lead to an earlier age of sexual  
57 maturity (Altmann and Alberts 2005); and influence fecundity (Mahlert et al. 2018),  
58 competitive ability (Schradin 2004; English et al. 2013) and fitness (Svendsen and White  
59 1997; Schradin and Lindholm 2011). Yet, fast growth also can have negative consequences  
60 (reviewed in Metcalfe and Monaghan, 2003), and has been linked to faster senescence (Kim  
61 et al. 2011; Geiger et al. 2012; Douhard et al. 2017). Growth rates represent a potential source  
62 of within-species variation in fitness, and thus studying factors that influence – either  
63 promote or limit - growth is fundamental to understanding the evolution of different growth  
64 strategies and life histories (Dmitriew 2011).

65 Environmental parameters, such as resource availability and ambient temperature, can  
66 affect growth rates (Voltura and Wunder 1998; Eifler and Slade 1999; Dmitriew 2011).  
67 Typically, high levels of food availability enhance growth (Nicieza and Metcalfe 1997;  
68 McAdam and Millar 1999; McAdam and Boutin 2003; Altmann and Alberts 2005), whereas  
69 food limitation restricts growth (Dmitriew 2011). Physiological processes may be limited by  
70 the ability to dissipate heat to maintain body temperature (i.e. heat dissipation limit  
71 hypothesis; Speakman and Król 2010a, b). Reduced food intake is a common consequence of  
72 heat stress (Renaudeau et al. 2012; Beale et al. 2018; Camp et al. 2018), and is thought to be  
73 driven by the interaction between the increase in metabolic heat production after food  
74 ingestion (diet-induced thermogenesis) and the need to balance heat dissipation to maintain

75 body temperature (Renaudeau et al. 2012). Somatic growth also produces heat, and thus, high  
76 ambient temperature can indirectly affect growth via an influence on heat dissipation, food  
77 intake and digestion. Thus, we predict trade-offs between body temperature maintenance,  
78 digestion, and growth.

79 Previous studies reported that the relationship between ambient temperature and  
80 growth depends on season, taxon, and habitat type occupied (Eifler and Slade 1999; Gardner  
81 et al. 2011). For example, adult size of fish decreases with increasing ambient temperature  
82 (Atkinson 1994; Barneche et al. 2019). Similarly, growth rates of meerkat (*Suricata*  
83 *suricatta*) pups are reduced at high ambient temperature, likely because of an increased cost  
84 of thermoregulation (Russell et al. 2002; van de Ven et al. 2020). In rodents, results are  
85 mixed; some species show an increase and others a decrease in body size (Gardner et al.  
86 2011). Because of the potential trade-off between body temperature maintenance and food  
87 intake at high ambient temperature, it is conceivable that high ambient temperature limits  
88 growth, for example during summers. Rarely has the effect of both ambient temperature and  
89 food availability on growth rates been studied simultaneously, particularly in animals  
90 inhabiting arid areas in the subtropics, where variation in ambient temperature and food  
91 availability is pronounced. Nonetheless, such studies would be important to promote an  
92 understanding of whether and how food availability and/or ambient temperature affect  
93 growth rate. Such information will become increasingly important given the progressively  
94 hotter and drier conditions predicted to occur as a consequence of climate change (Karl and  
95 Trenberth 2003; Seager et al. 2007) and the associated changes in selection for body size  
96 (Ozgul et al. 2009).

97 Here, we studied postnatal growth in African striped mice (*Rhabdomys pumilio*)  
98 living under a variety of environmental conditions. We focused on changes in body length as  
99 an indicator of skeletal growth. We did not consider body mass here because mass can

100 change seasonally without reflecting growth depending on fat stores and muscle mass, such  
101 that body mass does not always reflect skeletal size (Campbell and Dobson 1992). Body size  
102 is an important trait in striped mice because it confers an advantage in competitive  
103 interactions (Schradin 2004) and as such, also influences reproductive tactics adopted by both  
104 sexes (Schradin et al. 2009a; Hill et al. 2015). Large males are the most competitive  
105 individuals and follow a tactic that has a much higher reproductive success than smaller and  
106 less competitive males which follow alternative tactics (Schradin and Lindholm 2011).  
107 Heavier females are more likely to breed solitarily than communally (Hill et al. 2015),  
108 thereby avoiding reproductive competition with other females and female infanticide  
109 (Schradin et al. 2010a).

110         Striped mice are sensitive both to low and high temperatures, basking in the sun to  
111 warm up in winter and resting in the shade in summer (Schradin et al. 2007; Rimbach et al.  
112 2016; Zduniak et al. 2019). Dry seasons are energetically challenging periods for striped mice  
113 because of low food availability, and they show physiological signs of fasting, such as  
114 increased ketone body concentrations (Rimbach et al. 2017). When food resources decline  
115 and conditions become harsher, their health status deteriorates and non-survivors exhibit  
116 signs of permanent pathology (Schoepf et al. 2017). To reduce their daily energy expenditure,  
117 striped mice reduce their metabolism and activity during the dry season (Rimbach et al. 2017,  
118 2018b; a). Thus, since breeding season for striped mice is followed by a food restricted dry  
119 season, we expect them to have reduced growth rates but over a period of longer growth to  
120 reach a larger body size that enhances their competitive abilities in the following breeding  
121 season.

122         In temperate climates, mammals typically reproduce seasonally: young are born in  
123 spring and grow during summer when food availability is high, before they enter the food  
124 restricted winter (Bronson 1985, 2009). Similarly, striped mice have a short 3 – 4 month

125 spring breeding season but the following 5-month summer represents the food restricted dry  
126 season, likely limiting growth. Thus, to reach a greater body length, growth might continue  
127 slowly during the dry season and then accelerate again when rain falls and food again  
128 becomes abundant. Some years are characterized by high summer rainfall and a subsequent  
129 increase in food availability (although food availability during summer breeding is less than  
130 60% of that during the spring breeding season; see results), which allows for summer  
131 breeding. In this study, we repeatedly recorded body length of 369 striped mice with a known  
132 age (from 6 to 890 days old) to examine which environmental factors are associated with  
133 growth. Specifically, we tested three predictions. (i) Growth would be faster when food  
134 availability is high and ambient temperature low, compared with when food availability is  
135 low and ambient temperature high. (ii) Growth rate of striped mice would be slower in the  
136 dry season than in the moist season, when food is more abundant. Thus, we expected fast  
137 growth in the moist season after birth which would then decrease as food availability  
138 decreased and then accelerate again as food availability increased again after winter rains.  
139 (iii) Because of the higher ambient temperature and relatively lower food availability in  
140 summer compared with spring, we predicted that individuals born during an atypical summer  
141 breeding season to grow slower than individuals born during the typical spring breeding  
142 season.

143

144

## MATERIALS AND METHODS

145 *Study site and species.*—We collected data from November 2015 to January 2019 in Goegap  
146 Nature Reserve, Northern Cape Province, South Africa. The reserve lies within the semi-  
147 desert biome of the Succulent Karoo, characterized by cold and moist winters (June –  
148 August), in which most of the annual rain falls (average rainfall 2004 – 2018:  $155.2 \pm 76.6$   
149 mm; Supplementary Data SD1). Striped mice breed in spring, which typically lasts from

150 August to November and is characterized by high food abundance (Supplementary Data  
151 SD1). Food availability is lower in the hot and dry summers (December – May;  
152 Supplementary Data SD1; Schradin and Pillay 2005).

153 In the study area, striped mice are facultatively group-living. Groups typically consist  
154 of one breeding male, 2 – 4 breeding females and their philopatric offspring of both sexes  
155 (Schradin and Pillay 2004). Individuals of both sexes can become solitary if population  
156 density is low during the breeding season (Schradin et al. 2010a). Females can give birth to 2  
157 – 3 litters during the 3 – 4 month breeding season, with an average of 5 pups per litter  
158 (Schradin and Pillay 2005). Most individuals born during the breeding season remain in their  
159 natal group as non-breeders (i.e. philopatric) until the next breeding season. Striped mice can  
160 reach sexual maturity at around 6 weeks of age (Schradin and Pillay 2014; Schradin et al.  
161 2014a), but typically delay reproduction until the next spring (Schradin and Pillay 2004).  
162 Both sexes disperse, but female striped mice show a higher level of natal philopatry than  
163 males (Solmsen et al. 2011). Approximately 30% of young adult striped mice present at the  
164 start of the dry season survive until the next breeding season (Schradin and Pillay 2005), and  
165 survival rate is much lower in some years. We determined body mass ( $\pm 0.1$  g) using a  
166 portable electronic balance (Yamada HC-3, Yuet Hing Company, Kowloon, Hong Kong).  
167 We measured body length using a ruler from the tip of the nose to the anus to the nearest 0.1  
168 cm every 2 – 4 weeks. We collected body length measurements only in the morning to avoid  
169 a circadian influence on body size. Body length measurements were repeatable; the  
170 difference between body length measurements collected within 3 days for the same individual  
171 (190 body length measurements of 107 individuals) was  $0.53 \pm 1.66$  mm (range: -4 – 4 mm;  
172 Supplementary Data S2), and there was a strong correlation between the first and the second  
173 length measurement (Pearson's product-moment correlation:  $t = 94.58$ ,  $df = 188$ ,  $P < 0.0001$ ,  
174  $R^2 = 0.97$ ; Supplementary Data S2).



175           The study population has been monitored continuously since 2001 and striped mice  
176 within the field site are regularly trapped using Sherman-style live-traps (26 x 9 x 9 cm)  
177 baited with bran flakes, raisins, salt, and sunflower oil. For identification, we marked all mice  
178 permanently with ear tags (fish & small animal tags size 1, National Band and Tag Co.,  
179 Newport, KY, USA) at the first trapping event. We set traps in front of nest sites at dawn and  
180 in the afternoon, and checked them twice in the morning and once at dusk, 30 – 45 minutes  
181 after being set. For 3 consecutive days, we placed traps at the nest of several groups on a  
182 rotation schedule that allowed us to biweekly trap of each group throughout the year.

183           We carried out fieldwork under the necessary licenses. We collected all data following  
184 protocols approved by the Animal Ethics Screening Committee of the University of the  
185 Witwatersrand (AESC 2014/40/B), and followed the animal care guidelines of the American  
186 Society of Mammologists (Sikes et al. 2016)

187

188 *Growth curves.*—To determine growth curves of striped mice, we collected a minimum of  
189 five measurements of body length per individual. This resulted in a total of 2870 body length  
190 measurements of 280 individuals (1474 measurements of 149 females, 1396 measurements of  
191 131 males) with  $10.2 \pm 5.1$  measurements per individual; range was 5 – 40 measurements.  
192 Several different growth models, including Gompertz, logistic, von Bertalanffy, and  
193 Richards, have been used to describe mammalian growth, and earlier studies have assumed  
194 that sigmoid curves, like the Gompertz equation, adequately describe mammalian growth  
195 (Zullinger et al. 1984). However, subsequent studies have demonstrated species-specific  
196 variation in growth curves (Gaillard et al. 1997) and thus, using more flexible growth  
197 functions, such as the Richards equation (which allows for both sigmoidal and non-sigmoidal  
198 curves) should aid in accurately describing growth curves (Karkach 2006; Teleken et al.  
199 2017). Consequently, we used an approach without *a priori* assumptions of curve trajectories

200 and describe striped mouse growth curves using the R package “FlexParamCurve” (Oswald  
201 et al. 2012; Oswald 2015). This package includes functions to estimate parameters for 32  
202 different monotonic and non-monotonic curves and can model many sigmoidal forms (e.g.  
203 Richards, logistic, Gompertz, and von Bertalanffy).

204

205 *Growth rate.*—We calculated growth rate ( $\text{mm day}^{-1}$ ) as the change in body length (length 2  
206 – length 1/ days between measurements) of individuals over approximately one month  
207 (depending on the trapping intervals, average:  $27.3 \pm 12.2$  days). We chose the interval of one  
208 month to represent monitored monthly changes in food availability (see below). To examine  
209 which intrinsic and environmental factors influence growth rate, we used 1668 data points of  
210 growth rate from a total of 369 individuals (179 females and 190 males;  $4.5 \pm 3.5$  growth  
211 rates per individual, range: 1 to 24). We calculated birthdates from the body mass at first  
212 capture, using a population specific growth curve based on body mass (Schradin et al.  
213 2009b), only for individuals with a body mass  $< 30$  g at first capture ( $22.4 \pm 11.1$  days of age  
214 at first capture, range: 3 – 56 days;  $15.6 \pm 5.7$  g at first capture, range: 6.0 – 29.7 g). We  
215 excluded individuals whose birthdate we could not calculate reliably. No body length  
216 measurements were taken before 2015, thus some mice already were adults (older than 3  
217 months with a known birthdate) when we started collecting body length data. We included  
218 these older individuals because it enabled us to examine the growth rate of adult striped mice.  
219 Consequently, there was variation in age at the first body length measurement included in this  
220 study.

221

222 *Food availability.*—Striped mice feed on all parts (leaves, flowers and seeds) of annual and  
223 perianual plants (Schradin and Pillay 2006). Biweekly, we conducted plant surveys in the  
224 home ranges of eight different groups in the field site on eight monitoring plots (4 m<sup>2</sup> each).

225 Briefly, we recorded the number of palatable plant species in all plots and used the average  
226 number of plant species as a measure of food availability (as done previously, for example  
227 (Schradin et al. 2014b; Rimbach et al. 2018b)). Palatability of plants was known from  
228 behavioral observations (Schradin and Pillay 2006). For each mouse, we established average  
229 food availability during the period for which its growth rate was determined. We defined dry  
230 seasons as periods in which food availability was  $< 2.9$  species/ plots and moist seasons as  
231 periods in which food availability was  $\geq 2.9$  species/ plots (Supplementary Data S1), as  
232 physiological measures indicate fasting (decreased blood sugar and increased ketone levels)  
233 when food availability drops below 2.9.

234

235 *Ambient temperature.*—We recorded ambient temperature daily in the shade 10 cm above  
236 ground (where mice roam) using a digital thermometer (TFA Dostmann, Wertheim-  
237 Reicholzheim, Germany) that was installed permanently in the same location. For data  
238 analysis, we used the average daily minimum and maximum ambient temperature  
239 (Supplementary Data SD1).

240

241 *Data analyses.*

242 *Growth curves of striped mice.*—We used the R package “FlexParamCurve” (Oswald et al.  
243 2012; Oswald 2015), which includes functions to estimate parameters for 32 different  
244 monotonic and non-monotonic curves and to select the models that best fit the growth data.  
245 Male striped mice reach a larger body size relative to females, so we analyzed growth curves  
246 separately for each sex (Schradin and Pillay 2005). We grouped body length data by ID and  
247 used the functions ‘pn.mod.compare’ (compares all possible positive-negative Richards  
248 models) and ‘pn.modselect.step’ (backwards stepwise model selection) to select the most  
249 suitable model (Oswald 2015). Subsequently, we fitted a nonlinear least-squares model, and

250 plotted one curve per sex using the package “lattice” (Sarkar 2008). To examine body length  
251 as a function of age, we included data of 280 mice for which at least 5 measurements were  
252 available (a total of 2870 body length measurements;  $10.2 \pm 5.1$  measurements per  
253 individual). Growth curves could be fitted for 94.6% of females (141 of 149 individuals) and  
254 92.3% of males (121 of 131 individuals). We used one Mann-Whitney-U test to examine  
255 whether final body length differed by sex.

256

257 *Influence of intrinsic and environmental factors on growth rates.*—To analyze the influence  
258 of intrinsic and environmental factors on growth rates of striped mice, we used linear mixed  
259 models (LMMs) with Gaussian error structure and identity link using the R package ‘lme4’  
260 (Bates and Maechler 2010). As response variable we used the square root of the growth rates  
261 to reduce heteroscedasticity when fitting the models. We compared growth rates seasonally  
262 using 1668 data points of growth rate and included season (moist season 1, dry season 1,  
263 moist season 2 and dry season 2) as a fixed factor (Model 1). To investigate which  
264 environmental factor (food availability and/ or ambient temperature) influenced growth rates  
265 of striped mice, we also used 1668 growth rates, with food availability and ambient  
266 temperature treated as fixed factors (Model 2). For each mouse, we established average food  
267 availability and average ambient temperature for each measurement period (days between  
268 measurements:  $27.3 \pm 12.2$  days) for which its growth rate was determined. In both models,  
269 we also included age at initial length (as older mice grow slower; see results) and sex, and  
270 initial body length as a continuous variable to account for allometric effects. We included  
271 year and ID as random factors in both models because most mice were measured repeatedly.  
272 Using likelihood ratio tests, we tested for all two-way interactions by comparing a model  
273 which included the interaction with a model excluding the interaction and dropped non-  
274 significant interaction terms ( $P \geq 0.05$ ). We examined sex differences in initial body length,

275 and age at initial body length in the four seasons using Mann-Whitney-U tests. We split the  
276 data into four equally sized subsets represented by the quartiles of mean ambient temperature:  
277 (i) 9.88 to 18.4 °C; (ii) 18.4 to 21.5 °C; (iii) 21.5 to 23.9 °C; and (iv) 23.9–29.6 °C to  
278 illustrate how interactions between ambient temperature and food availability and ambient  
279 temperature and age at initial length influenced growth rates (Model 2).

280

281 *Growth rates of individuals born in summer vs spring.*—Some mice were born in the  
282 summers of 2016 (February – April) and 2018 (January – February) because of unusually  
283 high rainfall (in January 2016 and November 2017) and subsequently increased food  
284 availability (Supplementary Data SD1).

285 We used a LMM (Model 3) with Gaussian error structure and identity link using the R  
286 package ‘lme4’ (Bates and Maechler 2010) to examine whether growth rates differed  
287 between striped mice born in spring and summer. The response variable used was the square  
288 root of the growth rates to reduce heteroscedasticity when fitting the model. We included the  
289 season in which mice were born (spring vs summer), sex and age at initial length as fixed  
290 predictors, and we included initial body length as a continuous variable to account for  
291 allometric effects. We used individual ID and year as random factors. Using likelihood ratio  
292 tests, we tested for all two-way interactions by comparing a model including the interaction  
293 with a model excluding the interaction and dropped non-significant interaction terms ( $P \geq$   
294 0.05). We assessed differences in food availability and ambient temperature during summer  
295 and spring breeding seasons using Mann-Whitney-U test.

296 We tested all three LMMs for temporal autocorrelation of residuals using the  
297 ‘check\_autocorrelation’ function in the package “performance”. To account for the temporal  
298 autocorrelation between data points (i.e., non-random residual error), we included an  
299 autoregressive structure of order 1 (i.e., autocorrelation declines exponentially with time)

300 using the ('corAR1' function) in all three LMMs (Pinheiro and Bates 2000). For the  
301 validation of all three LMMs, we visually inspected Q – Q plots and scatterplots of residuals  
302 plotted against fitted values, to check for the assumptions of homogeneous and normally  
303 distributed residuals. In all models, we standardized (z-transformed) all numeric predictors  
304 for more accurate model fitting and to facilitate comparisons of model estimates (Schielzeth  
305 2010). We derived variance inflation factors (vifs) using the vif function of the “car” package  
306 (Fox and Weisberg 2011), which did not indicate collinearity (all vifs < 4; Zuur et al. 2009).  
307 We determined marginal and conditional  $R^2$  (Nakagawa and Schielzeth 2013) for all models  
308 with the function r.squaredGLMM from the “MuMIn” package (Bartoń 2013). Marginal  $R^2$   
309 ( $R^2_m$ ) represents the variance explained by the fixed effects and conditional  $R^2$  ( $R^2_c$ )  
310 represents the variance explained by the entire model (fixed and random effects).

311

312

## RESULTS

313 *Growth curves of striped mice.*—Growth of female and male mice were fit best by the  
314 Richards curve (Nelder, 1962; Fig. 1) described by this formula:

315

$$316 \quad y = A / ([1 + m \exp(-k(x - i))]^{1/m})$$

317

318 where  $A$  = asymptote,  $k$  = rate parameter,  $i$  = inflection point and  $m$  = shape parameter.

319 Growth parameters for female striped mice were  $A = 113.06$ ,  $k = 0.007$ ,  $i = -206.76$ ,  $m = -$   
320  $4.143$ , and for males were  $A = 120.86$ ,  $k = 0.008$ ,  $i = -184.10$ ,  $m = -4.144$ . Females reached  
321 asymptotic body length of 113.0 mm at (mean  $\pm$  SD)  $257.7 \pm 84.3$  days and males reached  
322 asymptotic body length of 120.8 mm at  $284.4 \pm 101.2$  days (Fig. 1). Only 13.4 % of females  
323 and 14.2 % of males survived until the age when the growth asymptote was reached; females  
324 disappeared at a mean age of  $193.0 \pm 151.9$  days and males at  $213.8 \pm 157.0$  days. Mean

325 body length after reaching the asymptotic body length was larger for males ( $123.7 \pm 2.7$  mm  
326 at  $367 \pm 170.4$  days) than for females ( $117.1 \pm 3.0$  mm at  $388 \pm 175.3$  days; Mann-Whitney-  
327 U test:  $U = 768$ ,  $P < 0.0001$ ).

328

329 *Influence of intrinsic and environmental factors on growth rates.*—Growth rate was higher in  
330 the moist season when mice were born (mean  $\pm$  SD;  $0.493 \pm 0.367$  mm day<sup>-1</sup>) compared with  
331 the following dry season (Dry 1:  $0.151 \pm 0.188$  mm day<sup>-1</sup>), the following moist season of  
332 their first reproduction (Moist 2:  $0.133 \pm 0.191$  mm day<sup>-1</sup>) and the subsequent dry season  
333 (Dry 2:  $0.124 \pm 0.174$  mm day<sup>-1</sup>; Table 1; Fig. 2). Growth rates did not differ between the  
334 other three seasons (moist season 2 and both dry seasons; Table 1; Fig. 2). The interaction  
335 between initial length and sex influenced growth rates, where males with a large initial length  
336 grew faster than females of the same initial length (Table 1).

337 Growth rate was influenced by the interactions between ambient temperature and food  
338 availability, ambient temperature and age at initial length, and sex and initial length (Model  
339 2). Growth rate increased with increasing food availability and was most pronounced at  $21.5$   
340  $- 23.9^\circ\text{C}$  (3<sup>rd</sup> quartile) and least pronounced at higher temperatures of  $23.9 - 29.6^\circ\text{C}$  (4<sup>th</sup>  
341 quartile; Fig. 3A). At low temperatures (quartiles 1 – 2), growth rate also increased with  
342 increasing food availability but at an intermediate level. Growth rate decreased with  
343 increasing age from low to medium high ambient temperature (quartiles 1 – 3), and growth  
344 rate did not change with age at  $23.9 - 29.6^\circ\text{C}$  (4<sup>th</sup> quartile), but remained stable at a low rate  
345 (Table 2; Fig. 3B). The interaction between initial body length and sex influenced growth  
346 rates, where males with a large initial length grew faster than females of the same initial  
347 length (Table 2).

348

349 *Growth rates of individuals born in summer vs spring.*—At the first body length  
350 measurement, striped mice were (mean  $\pm$  SD)  $36.4 \pm 16.4$  days old (range 6 – 77 days) and at  
351 the second measurement they were  $61.3 \pm 16.3$  days old (range 19 – 90 days). Mice born in  
352 spring (583 growth rates of 116 females and 142 males) had a faster growth rate ( $0.483 \pm$   
353  $0.35$  mm day<sup>-1</sup>) during the first three months after birth than individuals born in summer  
354 ( $0.337 \pm 0.29$  mm day<sup>-1</sup>; 60 growth rates of 17 females and 10 males; Table 3; Fig. 4A). Sex  
355 and the interaction between age at initial length and initial body length influenced growth  
356 rates (Table 3). Specifically, during the first month of life, growth rates were related inversely  
357 to initial body length (smaller animals grew more rapidly; Fig. 4B). During the second and  
358 third month, the relationship between initial length and growth rate was weaker (Fig. 4B).

359 Food availability was higher during spring breeding ( $4.4 \pm 1.3$  plant species/ plot)  
360 compared with summer breeding ( $2.5 \pm 0.4$  plant species/ plot; Mann-Whitney-U test:  $U =$   
361  $32643$ ,  $P < 0.0001$ ). Average ambient temperature did not differ between spring ( $18.8 \pm$   
362  $3.7^\circ\text{C}$ ) and summer breeding ( $22.2 \pm 1.2^\circ\text{C}$ ;  $U = 17328$ ,  $P = 0.90$ ).

363

364

## DISCUSSION

365 Striped mice can reach sexual maturity at an age of 45 days (Schradin and Pillay 2014). Here  
366 we demonstrated that they grow more than 5 times as long, for more than 250 days, which  
367 means they grow for most of their adult life. At our study site, some (less than 1%) striped  
368 mice live up to 3 years, but approximately 70% of mice disappear between the onset and the  
369 end of the dry season (Vuarin et al. 2019). Striped mice born in the atypical summer breeding  
370 season had slower growth rates, showing that harsh environmental conditions (low food and  
371 high ambient temperature) constrain growth of striped mice. Continued growth to attain a  
372 large body size can confer fitness benefits such as increased fecundity (Mahlert et al. 2018)  
373 and competitive ability (Schradin 2004; English et al. 2013). Thus, a prolonged growth period



374 is adaptive for striped mice whose postnatal growth starts under harsh environmental  
375 conditions. Finally, striped mice reached an asymptote in growth of body length, indicating  
376 that they show determinate growth, which is nearly ubiquitous in mammals and birds (Sebens  
377 1987; Karkach 2006). Nevertheless, the asymptote occurred late in adult life at an age of 9  
378 months. Most striped mice do not survive until the asymptote, including most individuals that  
379 survived the dry season and reproduced successfully during the spring breeding season when  
380 they were less than 9 months old. These results indicate a possible effect of senescence  
381 stopping growth in a few very old individuals.

382         To understand the growth strategy of striped mice one must look at the two distinct  
383 types of postnatal growth strategies that exist: determinate and indeterminate growth.  
384 Determinate growth is characterized by an initial phase of fast (often linear) growth which is  
385 followed by an asymptotic growth phase (Sebens 1987; West et al. 2001). Growth slows  
386 considerably or ceases after sexual maturity (Sebens 1987). Determinate growth is nearly  
387 ubiquitous in mammals and birds (Sebens 1987; Karkach 2006). Indeterminate growth is  
388 characterized by rapid growth in early age and continued growth, albeit at a slower pace, after  
389 reaching maturity (West et al. 2001). Indeterminate growth is nearly ubiquitous in  
390 invertebrates, fish, amphibians, and reptiles (Dutta 1994; Shine and Iverson 1995; Kozlowski  
391 1996; Charnov et al. 2001). While striped mice stop growing, and thus do not show  
392 indeterminate growth, they also do not cease growth soon after reaching sexual maturity, as  
393 most small mammals do.

394         Both male and female striped mice showed a linear and an asymptotic growth phase.  
395 Females reached the asymptotic body length at 258 days and males at 285 days, well after  
396 reaching sexual maturity, which they can reach at around 45 days of age. They can reproduce  
397 in the same breeding season in which they are born (Schradin et al. 2010b), but typically  
398 delay reproduction until the subsequent breeding season when they are 250 to 300 days old

399 (Schradin and Pillay 2004). Parents that do not delay reproduction produce offspring late in  
400 the breeding season that would be exposed to low food availability and high ambient  
401 temperature at an earlier age than offspring born earlier in the breeding season. Consequently,  
402 these offspring would have slower growth rates than early-born mice. Similarly, early-born  
403 roe deer (*Capreolus capreolus*), little brown bats (*Myotis lucifugus*), and common voles  
404 (*Microtus arvalis*), grow faster than late-born individuals (Reynolds 1999; Jacob 2003; Plard  
405 et al. 2015). Therefore, investment into growth and survival until the next breeding season  
406 might be more beneficial than investment into immediate reproduction.

407         Our study indicates that striped mice show determinate growth, that they have an  
408 extended growth period, and that most individuals grow during their entire life because they  
409 do not reach old age when growth terminates. The average age at disappearance was 200 days  
410 for both sexes, which likely is an overestimation because individuals that died very young  
411 (e.g. before weaning) were not included. Striped mice enter the second dry season at  
412 approximately 300 days of age and only 10 % lived beyond that point. Most mammals reach  
413 sexual maturity before they reach a growth asymptote (Ricklefs 2010). Many small rodents  
414 attain an asymptote in body length at a much younger age than striped mice and around the  
415 time of reaching sexual maturity. For example, Cabrera voles (*Microtus cabraerae*) reach an  
416 asymptote at 70 days (Fernández-Salvador et al. 2001), meadow voles (*Microtus*  
417 *pennsylvanicus*) at 30 – 50 days and simultaneously attaining sexual maturity (Campbell and  
418 Dobson 1992). Multimammate mice (*Mastomys natalensis* and *M. coucha*) reach an  
419 asymptote at 100 – 120 days (Jackson and van Aarde 2003). Female house mice (*Mus*  
420 *musculus*) reach a growth asymptote close to when they attain sexual maturity (Monteiro and  
421 Falconer 1966). Similarly to striped mice, hispid cotton rats (*Sigmodon hispidus*), garden  
422 dormice (*Eliomys quercinus*), and fossorial tuco tuco (*Ctenomys talarum*), attain sexual  
423 maturity before reaching a growth asymptote (Malizia and Busch 1991; Cameron and

424 Eshelman 1996; Schaub and Vaterlaus-Schlegel 2001; Stumpfel et al. 2017). In some species,  
425 such as common voles (*M. arvalis*), precocious fertile mating of non-weaned females occurs  
426 before reaching the growth asymptote (Tkadlec and Zejda 1995), but this early onset of  
427 reproduction is associated with an early reaching of the growth asymptote at an age of 1 to 2  
428 months (Jacob 2003). Thus, relative to many other rodents, striped mice show a prolonged  
429 period of growth, which might be associated with their specific environment and resulting life  
430 history.

431       Whereas our study species lives in a highly seasonal and arid environment with a  
432 short breeding season, its sister species *Rhabdomys dilectus* lives in a moist grassland  
433 environment with a long breeding season (Schradin 2005). Captive *R. dilectus* reach an  
434 asymptotic length of 107.8 mm at 112 days (Brooks 1982). Thus, *R. dilectus* reaches a shorter  
435 asymptotic length than *R. pumilio* (females: 113.0 mm; males: 120.8 mm) at a younger age  
436 (*R. pumilio*: females at 258 days, males at 285 days), at least in captivity. *R. dilectus* also  
437 does not show sex-specific differences in growth (Brooks 1982). The differences in growth  
438 curves might be related to socio-ecological differences between both species. *Rhabdomys*  
439 *pumilio* is group-living, has a 3 – 4 month (short) breeding season, juveniles have a low  
440 mortality, and most delay reproduction for one year (Schradin 2005). These traits indicate  
441 that for young adults, the short breeding season makes investment into growth and survival to  
442 the next breeding season more adaptive than immediate investment into reproduction.  
443 *Rhabdomys pumilio* also is territorial and body size is an important predictor of competitive  
444 interactions (Schradin 2004). Thus, a prolonged growth period can result in fitness benefits  
445 via access to mates and territories. In contrast, *R. dilectus* occurs in mesic grasslands, is  
446 solitary, occupies large territories, has a 7–month (long) breeding season, and juveniles have  
447 high mortality and reproduce in the breeding season in which they were born (Schradin  
448 2005). Consequently, *R. dilectus* likely would benefit from immediate investment into

449 reproduction rather than from a prolonged growth period as observed in *R. pumilio*. Thus, we  
450 hypothesize that environmentally driven differences in the trade-off between reproduction  
451 and growth explain the evolution of alternative growth strategies in the two *Rhabdomys* sister  
452 species.

453         Striped mice grew fastest in their first moist season (i.e., the season in which they were  
454 born). We did not find evidence of accelerated growth in the second moist season when food  
455 availability recovered. Therefore, striped mice show a typical growth curve for mammals  
456 with an initial period of rapid growth followed by a second period of less rapid growth. As  
457 predicted by allometric rules (West et al. 2001), growth rate decreased with increasing initial  
458 body length, a relationship that has previously been reported in birds (Ton and Martin 2016)  
459 and mammals (Sadowska et al. 2009; Larivée et al. 2010). Males with a large initial length  
460 grew faster than females of the same initial length, and males also grew to a larger final  
461 length than females, a pattern found in many species (Campbell and Dobson 1992; Lima et  
462 al. 1997). The 6% sexual size dimorphism in body length is the same as previously reported  
463 for body mass in striped mice (Schradin and Pillay 2005). The largest males are able to  
464 defend a group of communally breeding females and have a 10-times higher reproductive  
465 success than males of a medium size and 100-times greater reproductive success than small  
466 males, at least in years of high population density (Schradin and Lindholm 2011). In contrast,  
467 all adult females present at the onset of the breeding season produce litters (Schradin and  
468 Lindholm 2011). Thus, a stronger selective pressure on reaching a large body size in males  
469 than on females might explain the sexual dimorphism in body length.

470         A positive relationship between food availability and growth is intuitive and has been  
471 documented previously in many species (Nicieza and Metcalfe 1997; McAdam and Boutin  
472 2003; Auer et al. 2015). Our results demonstrate that the growth of striped mice is positively  
473 linked to food availability and that this relationship is mediated by ambient temperature. The

474 positive influence of food availability on growth rate was strongest at medium ambient  
475 temperature of 20°C. This relationship was weaker, although still positive, at lower and  
476 higher ambient temperatures. Similarly, high ambient temperature reduced growth rates of  
477 meerkat pups (Russell et al. 2002). These results might explain why striped mice rarely breed  
478 when it is very cold in winter even though food availability might be sufficient, and offer  
479 insights into why young females do not reproduce at the end of the breeding season, when  
480 offspring would suffer from slow growth because of high temperatures. That high  
481 temperatures and low food availability constrain growth of striped mice also is evident in the  
482 reduced growth rates of mice born in the atypical summer breeding season compared with  
483 individuals born in the typical spring breeding season. Growth rate decreased with increasing  
484 ambient temperature for individuals younger than 6.5 months, whereas growth rate of mice  
485 older than 6.5 months was not influenced by ambient temperature. The negative influence of  
486 ambient temperature on growth rate might indicate that the need to dissipate excess body heat  
487 created during growth constraints growth rate, especially at high ambient temperature  
488 (Speakman and Król 2010a; b). Heat stress also can result in reduced food intake (Renaudeau  
489 et al. 2012; Beale et al. 2018; Camp et al. 2018), and thereby negatively influence growth  
490 rate. These results demonstrate that the interplay of food availability and ambient temperature  
491 determines growth rate in this harsh semi-arid environment. A temperature-mediated growth  
492 of striped mice could explain why striped mice restrict breeding mainly to spring, when  
493 ambient temperature is close to the optimum for growth of their offspring, but switch  
494 investment into survival and slow growth when ambient temperature is too high in summer or  
495 too low in winter to produce offspring that could grow into competitive adults.

496 In conclusion, growth in striped mice was enhanced by high food availability but  
497 affected negatively by high ambient temperature, which might indicate that growth is  
498 constrained by the need to dissipate excess body heat, especially at high ambient temperature.

499 Striped mice enter the food-restricted dry season before postnatal growth is terminated. The  
500 following harsh environmental conditions with low food ability can explain why growth  
501 slows down considerably, while the proposed fitness benefits of reaching a competitive body  
502 size can explain why it does not terminate. This causes a prolonged growth period in striped  
503 mice, long past the age of sexual maturity.

504

505

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514

515 Supplementary Data

516 Supplementary Data SD1. Overview of environmental variables in the dry and moist seasons

517 Supplementary Data SD2. Repeated body length measurements of striped mice

518

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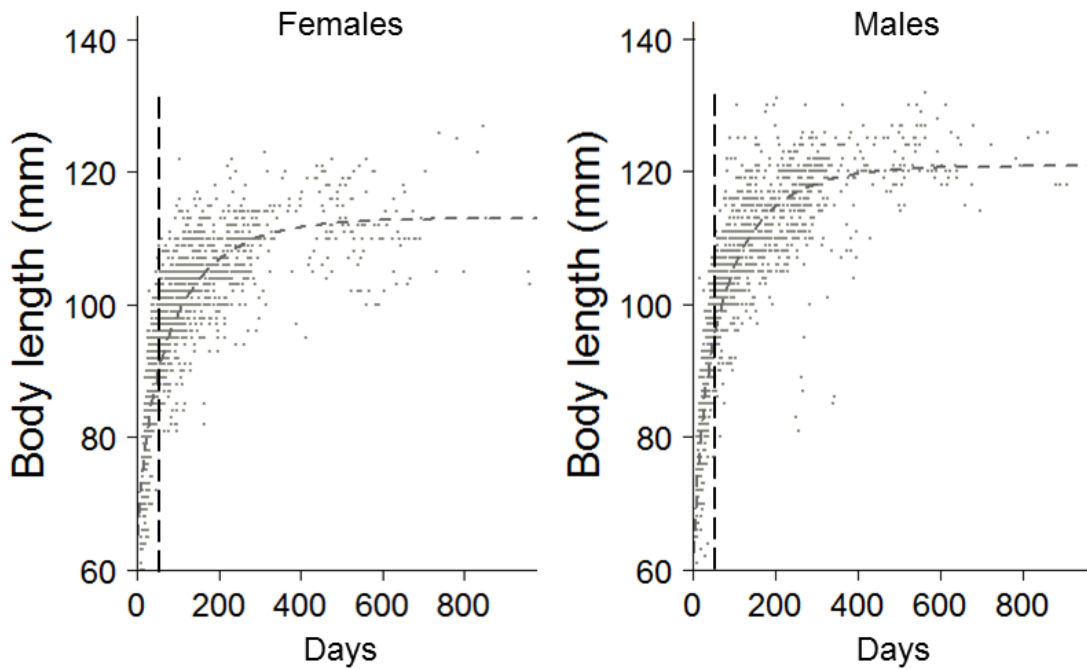
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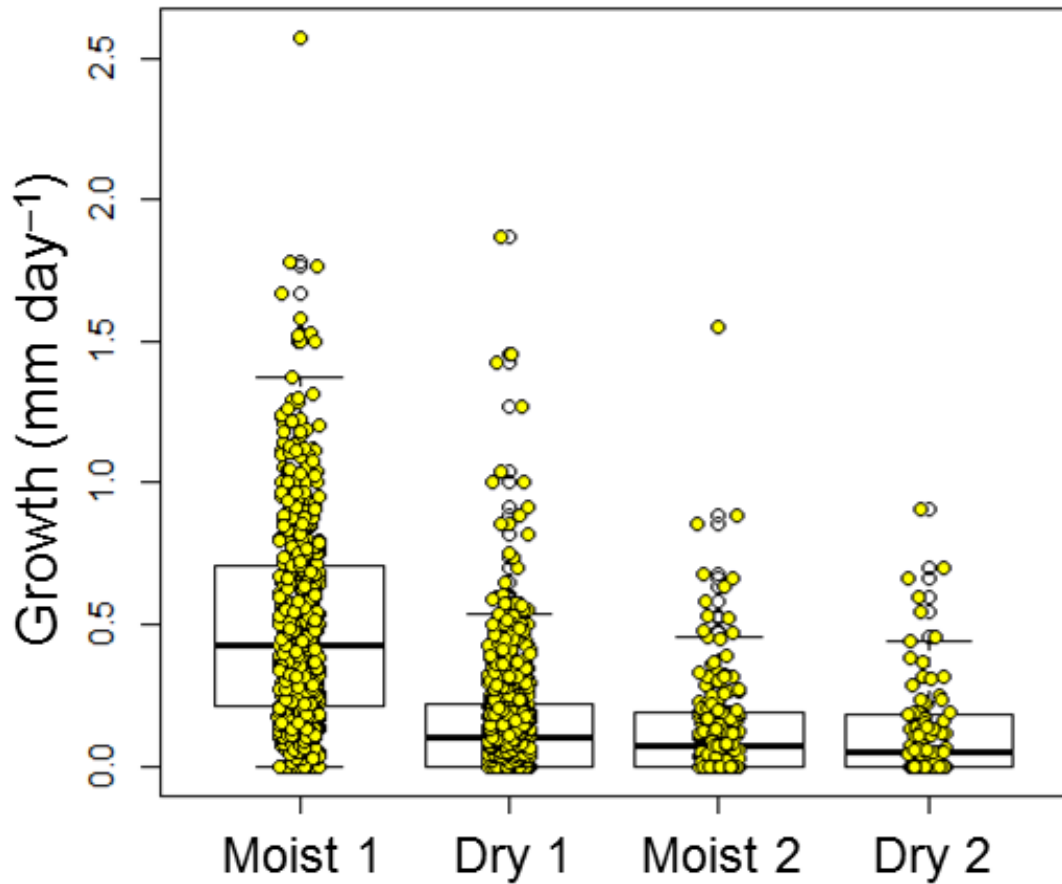
771 **Figure Legends**



772

773 **Fig. 1.**—Parametric curves fitted to growth data for female (left panel;  $N = 1474$   
774 measurements of 149 individuals) and male (right panel;  $N = 1396$  measurements of 131  
775 individuals) striped mice sampled between November 2015 and January 2019 in Goegap  
776 Nature Reserve, South Africa. The dotted curves represent the Richards curve fit to the data  
777 and the dashed vertical line indicates the earliest age of sexual maturity at 6 weeks.

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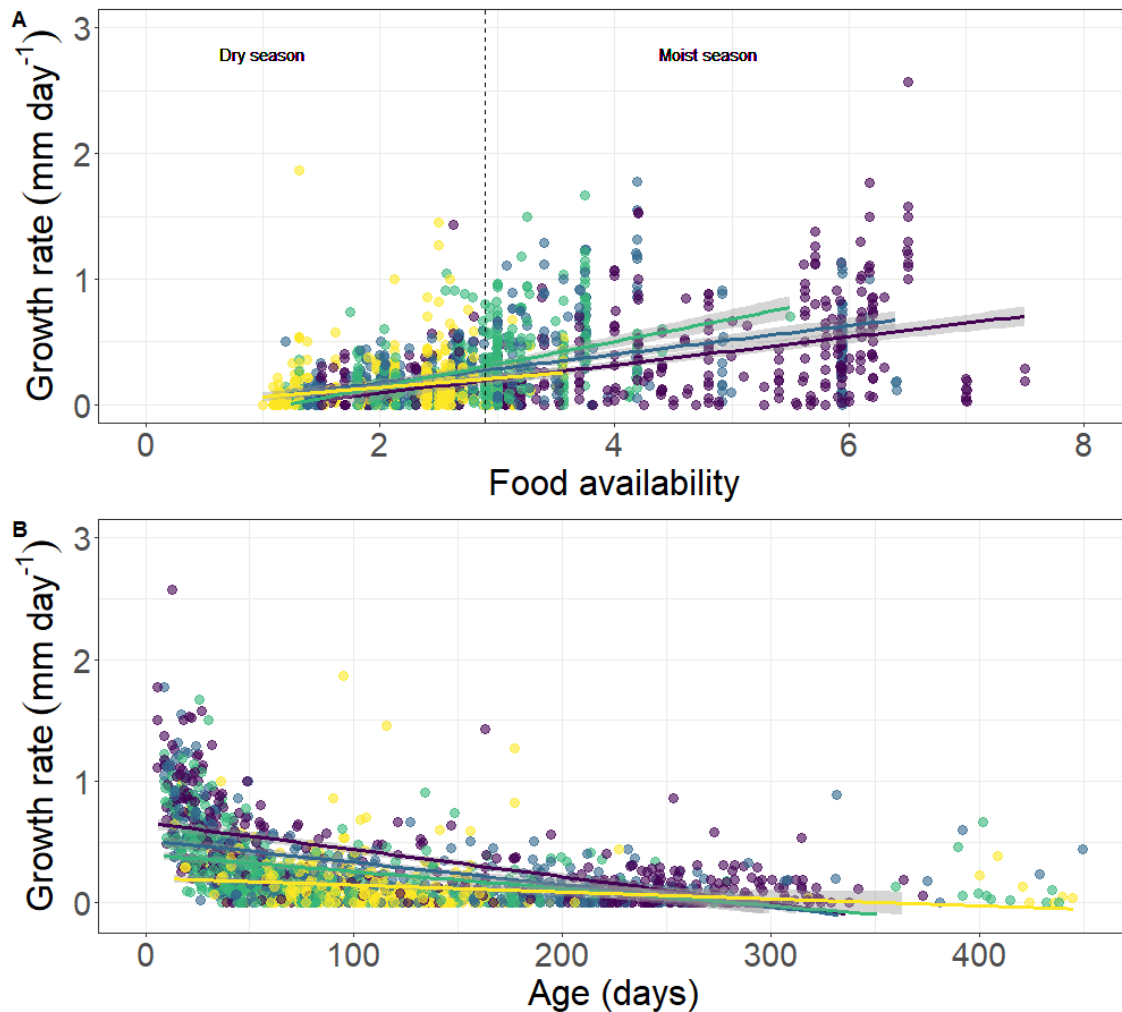
780 **Fig. 2.**—Growth rates of striped mice sampled between November 2015 and January 2019 in

781 Goegap Nature Reserve, South Africa during the moist season in which they were born

782 (Moist 1;  $N = 516$ ), the subsequent dry season (Dry 1;  $N = 862$ ), the second moist season

783 (Moist 2;  $N = 195$ ) and the subsequent dry season (Dry 2;  $N = 95$ ).

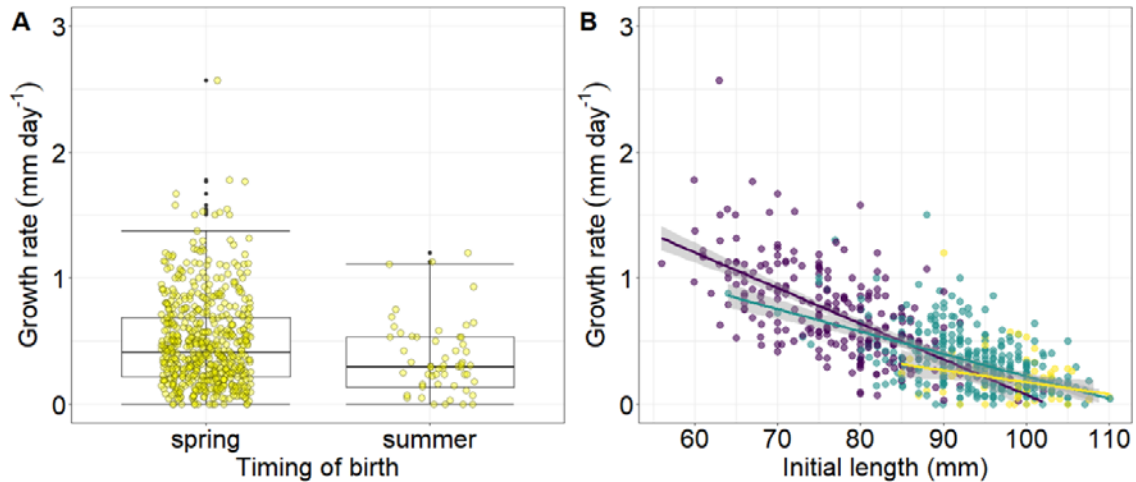
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786 **Fig. 3.**—(A) The interaction effect of food availability (plant species/ plot) and ambient  
 787 temperature on striped mouse growth rate sampled between November 2015 and January  
 788 2019 in Goegap Nature Reserve, South Africa (the vertical line at 2.9 for food availability  
 789 indicates the threshold for dry season vs moist season). (B) The interaction effect of ambient  
 790 temperature and age at initial body length on growth rate. For illustration, the data are split  
 791 into four subsets representing the quartiles of mean ambient temperature: (i) 9.88° – 18.4°C  
 792 (purple); (ii) 18.4° – 21.5 °C (blue); (iii) 21.5° – 23.9 °C (green); and (iv) 23.9° – 29.6°C  
 793 (yellow). Linear regression lines are shown and shaded areas indicate 95% CI.

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795

796 **Fig. 4.**—(A) Growth rates of striped mice sampled between November 2015 and January  
 797 2019 in Goegap Nature Reserve, South Africa born during spring ( $N = 583$  growth rates) and  
 798 summer ( $N = 60$  growth rates). Black lines indicate the median, boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartile,  
 799 whiskers minimum and maximum values of non-outlier data and yellow circles show raw  
 800 data. (B) The interaction effect of initial body length and age at initial body length on growth  
 801 rate. For illustration data are split into three subsets representing the first (purple dots),  
 802 second (green dots) and third (yellow dots) month after birth. Linear regression lines are  
 803 shown and shaded areas indicate 95% CI.

804 **Table 1.**—Results of the linear mixed model to test for an association between striped mouse  
805 (*Rhabdomys pumilio*) growth rate, study period (moist born, dry year 1, moist reproduction  
806 and dry year 2), sex, age at initial length and initial length ( $N = 1668$  growth rates) sampled  
807 between November 2015 and January 2019 in Goegap Nature Reserve, South Africa. Factors  
808 in bold type indicate significant predictors of growth rate.

Model 1	<i>Estimate</i>	<i>SE</i>	<i>t value</i>	<i>P</i>
$R^2_m = 0.56; R^2_c = 0.60$				
(Intercept)	2.428	0.078	30.787	0.0001
Moist (born) vs Dry season year 1	-0.094	0.015	-6.193	<b>0.0001</b>
Moist (born) vs Moist (reproduction)	-0.079	0.025	-3.146	<b>0.0017</b>
Moist (born) vs Dry season year 2	-0.101	0.038	-2.644	<b>0.0083</b>
Moist (reproduction) vs Dry season year 1	-0.015	0.019	-0.793	0.4276
Moist (reproduction) vs Dry season year 2	0.022	0.031	0.709	0.4783
Dry season year 1 vs Dry season year 2	0.006	0.033	0.195	0.8446
Sex <sup>a</sup>	-0.187	0.103	-1.813	0.0705
Age at initial length	0.000	0.000	4.535	<b>0.0000</b>
Initial length <sup>a</sup>	-0.020	0.000	-23.280	0.0000
Sex:age at initial length	0.000	0.000	0.528	0.5976
Sex:Initial length	0.002	0.001	2.610	<b>0.0091</b>

809 <sup>a</sup>Factors included in significant interaction terms cannot be interpreted as independent variables.

810

811 **Table 2.**—Results of the linear mixed model to test for an association between striped mouse  
812 (*Rhabdomys pumilio*) growth rate, average ambient temperature, food availability, sex, age at  
813 initial length and initial length ( $N = 1668$  growth rates) sampled between November 2015 and  
814 January 2019 in Goegap Nature Reserve, South Africa. Factors in bold type indicate  
815 significant predictors of growth rate.

Model 2	<i>Estimate</i>	<i>SE</i>	<i>t value</i>	<i>P</i>
$R^2_m = 0.58; R^2_c = 0.61$				
(Intercept)	0.352	0.010	34.249	0.0000
Food availability <sup>a</sup>	0.056	0.008	6.918	0.0000
Average ambient temperature <sup>a</sup>	-0.015	0.006	-2.282	0.0226
Sex <sup>a</sup>	0.114	0.012	8.780	0.0000
Age at initial length <sup>a</sup>	0.044	0.011	3.859	0.0001
Initial length <sup>a</sup>	-0.264	0.011	-23.363	0.0000
Food availability:ambient temperature	0.023	0.006	3.977	<b>0.0001</b>
ambient temperature:age at initial length	0.016	0.005	2.881	<b>0.0040</b>
Sex:age at initial length	0.001	0.015	0.080	0.9359
Sex:Initial length	0.045	0.014	3.157	<b>0.0016</b>

816 <sup>a</sup>Factors included in significant interaction terms cannot be interpreted as independent variables.

817 **Table 3.**—Results of the linear mixed model to test for an association between striped mouse  
818 (*Rhabdomys pumilio*) growth rate, timing of birth (spring vs summer), sex, age at initial  
819 length and initial length ( $N = 643$  growth rates) sampled between November 2015 and  
820 January 2019 in Goegap Nature Reserve, South Africa. Factors in bold type indicate  
821 significant predictors of growth rate.

Model 3	<i>Estimate</i>	<i>SE</i>	<i>t value</i>	<i>P</i>
$R^2_m = 0.57; R^2_c = 0.69$				
(Intercept)	2.501	0.109	22.866	0.0001
Timing of birth	-0.151	0.030	-4.965	<b>0.0001</b>
Age at initial length <sup>a</sup>	0.200	0.067	2.951	0.0034
Initial length <sup>a</sup>	-0.021	0.001	-17.547	0.0001
Sex	0.075	0.018	4.116	<b>0.0001</b>
Age at initial length:initial length	-0.001	0.0007	-2.715	<b>0.0069</b>

822 <sup>a</sup>Factors included in significant interaction terms cannot be interpreted as independent variables.