Reading, Christopher J.; Jofré, Gabriela M. 2021. **Declining common toad body size correlated with climate warming.**

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28   **Running head**: Declining toad body size and climate warming

29   ABSTRACT

30   Accumulating evidence shows that the body size of organisms in many taxa is declining in

31   response to global warming. We investigated the potential effect of rising temperatures on the

32   body size of a common toad (*Bufo bufo* L.) population in southern England between 1983 and

33   2020. The body length (SVL-mm) and body mass (g) of 15,550 males and 4,004 females

34   arriving at their breeding pond for the first time were recorded. Toad body condition was

35   estimated using a Scaled Body Mass index (SMI).

36   Over the study period, the mean annual temperature increased by approximately 1.3°C

37   whilst the mean SVL and SMI of both sexes declined. Multiple regression analysis showed that

38   female and male SMI were negatively correlated with increases in mean summer temperatures,

39   with females also minimally impacted by mean winter rainfall. Mean body size (SVL) was

40   positively correlated with toad abundance, over the period between emerging as toadlets and

41   arriving at the pond to breed for the first time. Common toads exhibit phenotypic plasticity in

42   response to warming environmental conditions, resulting in a reduction in SMI and subsequent

43   reductions in SVL and overall egg production which occurred over a 10-year period.

44

45   **Key words**:   amphibians, climate change, *Bufo bufo*, rainfall, summer temperatures, toad

46   abundance, toad body condition, toad SVL, winter temperatures.

47

48   INTRODUCTION

49   It is widely accepted that global temperatures have increased since the 19th century (Ring *et al*.

50   2012) and that these are continuing by 0.15-0.2°C per decade (Hansen *et al*. 2010). Numerous

51   studies have shown that the body size of aquatic and terrestrial fauna has declined and that

52   these changes were correlated to increases in water and terrestrial temperatures (Caruso *et al*

53   2015; Gardner *et al*. 2011; Sheridan & Bickford 2011; Van Buskirk *et al* 2010) and food

54   availability (Yom-Tov & Geffen 2011). In some North Sea fish species their reduced body size

55 over a 50-year period (Audzijonyte *et al* 2013) has made them less susceptible to oxygen

56 deprivation, resulting from warming water temperatures, than larger fish (Baudron *et al* 2014).

57 Conversely, in a long-term study of common lizards *Lacerta vivipara*, living at altitude in

58 France, female body size increased in relation to rising temperatures and more offspring were

59 produced (Chamaillé-Jammes *et al* 2006). Rising temperatures have also resulted in higher

60 metabolic rates (Gillooly *et al* 2001; Dillon *et al* 2010; Sheridan & Bickford 2011), accelerated

61 life cycles and decreased adult survival rates threatening the survival of many animal

62 populations (Bestion *et al* 2015).

63   Bergmann's Rule (Bergmann 1847) has frequently been cited to explain variation in

64 body size in relation to environmental temperature and along gradients of latitude. However,

65 this rule was essentially derived from studies of endotherms whilst the evidence for compliance

66 by ectotherms (including amphibians) is inconsistent and contradictory (Ashton 2002). For

67 amphibians at least six possible hypotheses (Olalla-Tárraga & Rodríguez 2007), including

68 water availability, food availability and thermal stress (Sheridan et al. 2017; Cvetković *et al*.

69 2009; Green & Middleton 2013) have been postulated to explain observed body size

70 discrepancies with respect to environmental temperature, suggesting that Bergmann's rule is

71 too simplistic because the complex interactions between the different factors impacted by

72 climatic temperature change, each affected in a particular way and dependent on locality, are

73 not adequately considered or understood, requiring further investigation (Boult & Evans 2021).

74   During a study of common toads *Bufo bufo* L. in southern England, between 1983 and

75 2020, all captured females and males arriving at a pond to breed for the first time were

76 measured and it became apparent that their body size had declined over the 38 year period but

77 had not done so at a consistent rate with most of the decline occurring over a relatively short

78 ten year period. This decline initially appeared to be correlated to changing climatic variables

79 (temperature and rainfall), although the mechanism about how they were affecting toad growth

80   rate was unclear. They may also have been associated with declines in invertebrate prey

81   availability resulting from changes in climate (Robinet & Roques 2010; Harris et al. 2019;

82   Halsch *et al*. 2021). In the study reported here we investigated the relationships between toad

83   abundance and a changing climate, on toad growth rate and changes in toad body size (SVL)

84   based on the assumptions that a) growth was dependent on body condition (Peig & Green

85   2009), b) that age at sexual maturity did not change during the course of the study (Reading

86   1988) and c) that an estimated 'abundance index' reflected the overall number of sexually

87   immature toads in the surrounding habitat (Reading & Clarke 1995), allowing us to postulate

88   possible mechanisms for how this occurs.

89

90   MATERIALS AND METHODS

91   STUDY SITE

92   A common toad, *B. bufo,* population breeding in a flooded clay pit (approximately 0.34 ha)

93   situated to the north of the Purbeck Hills in south Dorset, UK (50°38'N, 2°07'W) was studied

94   annually between 1979 and 2020. Until 2005 the pond was surrounded by dense rhododendron

95   (*Rhododendron ponticum* L.) wood, the habitat changing into mixed deciduous woodland as

96   the distance from the pond increased and subsequently into pasture. During the winter of

97   2005/2006 all the vegetation immediately surrounding the pond was cleared, resulting in

98   largely open rough grassland with some limited low scrub cover (regenerating rhododendron

99   *R. ponticum* L., gorse *Ulex europaeus* L. and heather *Calluna vulgaris* L.). The mixed

100   deciduous woodland beyond the cleared area remained largely unchanged.

101

102   DATA COLLECTION AND ANALYSIS

103   Daily temperature data were obtained from the Swanage Tourist Information Centre and UK

104   Meteorological Office, situated approximately seven miles south-east of the toad study pond.

105   The mean temperature of two annual periods were determined (summer: 1st April to 31st

106   October; winter: 1st November to 31st March). In addition, the mean temperatures experienced

107   by toads between metamorphosis and returning to breed for the first time were estimated. For

108   females and males this included 5-year and 4-year means of summer temperatures respectively,

109   allowing for the age of attaining sexual maturity in each sex (Reading 1991) with the mean of

110   the first summer, following metamorphosis, including temperatures between 1st June and 31st

111   October (metamorphosis occurring at around the end of May each year) and the mean

112   temperature for the winter immediately prior to breeding (1st November to the start of

113   spawning).

114   Between 1979 and 2020 the daily number of common toads, *B. bufo*, arriving to breed

115   each year at the study pond was recorded. The pond was visited daily from the end of January

116   to determine when the toads started to arrive at the pond until two days after the last toads were

117   seen after spawning had finished. Two searches were made each day by walking around the

118   pond perimeter on stepping stones placed within it. Toads were searched for visually and by

119   touch. All detected toads were captured and subsequently measured (snout-vent length (SVL)

120   mm: millimetre ruler), weighed (g: Salter model 12 spring balance) and marked either by toe-

121   clipping to denote the year of capture or, between 1993-2014, using PIT (Passive Integrated

122   Transponder: Trovan ID 100) tags to identify individuals. All the toads from the two searches

123   were released at their respective capture locations within the pond after processing. The

124   duration of each search varied, being dependent on the number of toads found, but typically

125   took about one hour for the first search each day and less for the second. Although the study

126   was started in 1979 only toads captured between 1983-2020 were used in the current study to

127   ensure, as far as possible, that first time breeders could be distinguished from those that had

128   arrived at the pond to breed in previous years.

129   The estimation of body condition based on the allometric relationship between body

130   length (SVL) and body mass has been validated for use in anurans (Băncilă *et al*., 2010;

131   MacCracken & Stebbings, 2012). We used a Scaled Mass Index: SMI (Pieg & Green 2009,

132   2010):

$$\text{SMI: } \widehat{M}_i = M_i \left(L_0/L_i \right)^{b_{SMA}} \text{ where } b_{SMA} = b_{OLS} / r.$$

134    $\widehat{M}_i$ = predicted body mass of individual i when the SVL was standardised to L_0; M_i and L_i =

135   body mass and SVL of individual i; L_0 = mean SVL of all first time breeding toads (females;

136   78.0mm; males: 65.0mm) captured between 1983 and 2020; b_{SMA} = scaling exponent estimated

137   from the standardised major axis (SMA) regression of Log$M$ on Log$L$; b_{OLS} = regression

138   coefficient of Log$M$ on Log$L$; r = Pearson's correlation coefficient.

139   Estimates of a toad 'abundance index' were based on the total number of toads (females

140   plus males) that were caught annually at the breeding pond and were therefore present in the

141   surrounding environment in at least these numbers prior to breeding for the first time. The

142   estimated age of sexual maturity was five and four years for females and males respectively

143   (Reading & Clarke 1995). A mean annual abundance index of toads in the surrounding habitat

144   was based on the annual capture data of either four (females) or three (males) years preceding

145   their first attempt to breed, as arrival at the breeding pond occurs immediately following

146   emergence from hibernation and before growth for that year starts. The mean size of first time

147   breeding females and males each year was then plotted against a mean annual abundance index.

148   Correlations between variables were determined using regression analysis (linear,

149   polynomial, and multiple) to generate predicted models with a *p*-value of 0.05 as the threshold

150   for significance. In multiple regression analyses the response variable was SMI and the

151   predictor variables were summer temperature, winter temperature, summer rainfall and winter

152   rainfall. All the assumptions of the regression analyses were met. Standardised regression

153   residuals were tested for normality and the presence of outliers (Anderson-Darling test) and

154   homoscedasticity (Levene's test). Multicollinearity between correlated variables was corrected

155   for by standardising the continuous variables (subtracting the mean and dividing by the

156   standard deviation). Where appropriate mean SVL values were compared using Student's *t*-

157   test. All analyses and data standardisation were completed using Minitab 18.1 software

158   (Minitab 18).

159

160   DATA AVAILABILITY

161   The data used in this research are available from the corresponding author following a

162   reasonable request.

163   RESULTS

164   ENVIRONMENTAL TEMPERATURE AND RAINFALL

165   Between 1980 and 2020 the mean annual temperature rose significantly (*P*<0.001) by

166   approximately 1.3°C (Fig. 1a). Over the same period there was also a significant positive, but

167   relatively weaker, correlation between the mean summer temperature and following mean

168   winter temperature (MeanWinterT: = - 1.862 + 0.6525 MeanSummerT: *P*=0.008, r^2 = 17.09%,

169   *n* = 41).

170   Over the same time period there was no significant trend in the total annual rainfall

171   (Fig,1b: Total rainfall = - 1824 + 1.330 Year, r^2 = 2.03%, *P*=0.374, *n* = 41). Similarly, for the

172   five years (♀) and four years (♂) immediately prior to breeding for the first time there were no

173   significant trends, over time, in the mean summer rainfall (♀: Mean rainfall = 35.6 + 0.1756

174   Year, r^2 = 0.51%, *P*=0.675, *n* = 37; ♂: Mean rainfall = 468.0 − 0.0425 Year, r^2 = 0.02%,

175   *P*=0.938, *n* = 38) or winter rainfall (♂: Mean rainfall = -1687 + 1.046 Year, r^2 = 7.44%,

176   *P*=0.097, *n* = 38). There was, however, a significant increase in the mean winter rainfall, over

177   the same period, relating to females (Mean rainfall = -1790 + 1.099 Year, r^2 = 13.77%,

178   P=0.022, n = 38).
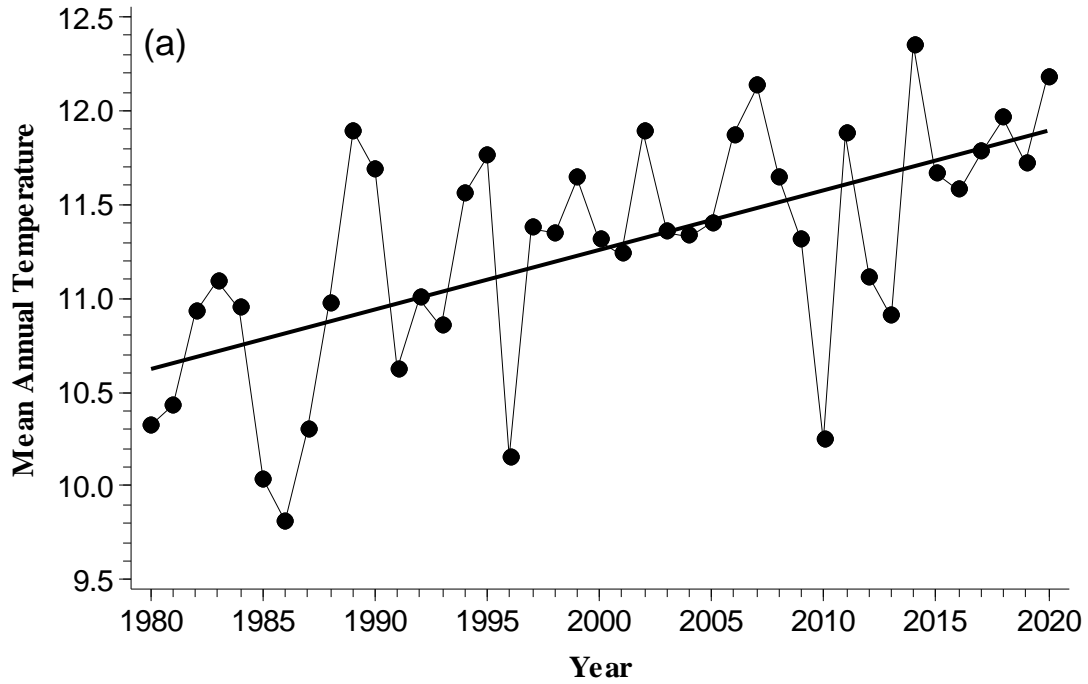
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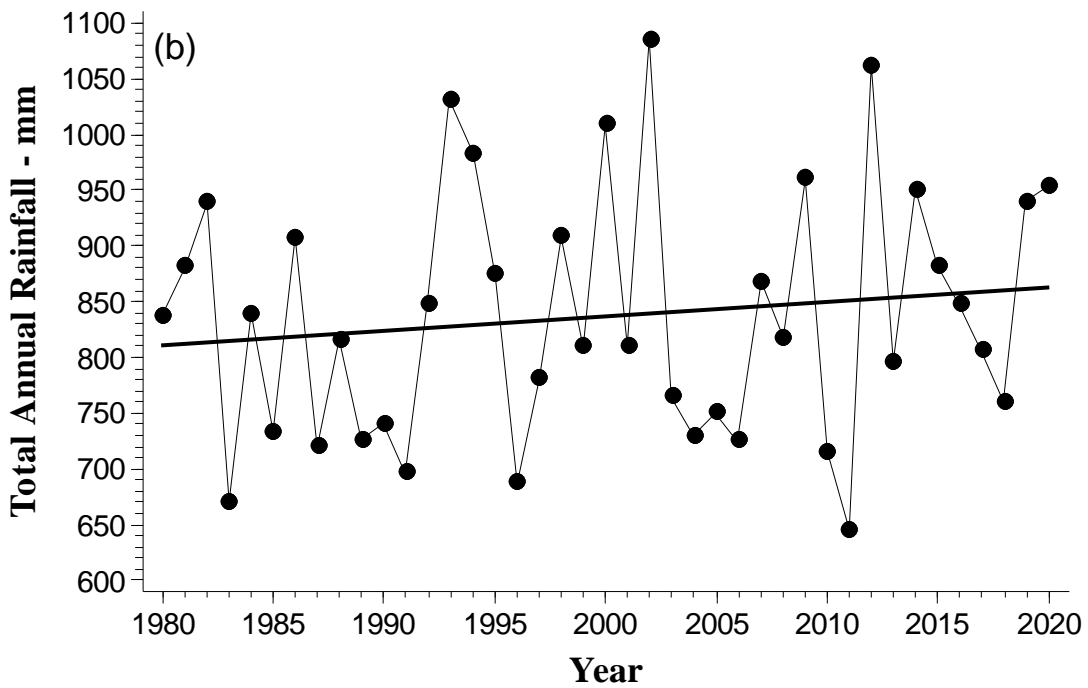
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181 **Figure 1.** (a) Annual mean temperature °C (1980-2020) and (b) total annual rainfall for

182 Swanage, UK.

183 Mean Annual Temperature = - 52.56 + 0.03191 Year; $r^2 = 36.57\%$, $P<0.001$, $n = 41$.

184 Total Annual Rainfall = -1824 + 1.33 Year; $r^2 = 2.03\%$, $P=0.374$, $n = 41$.

185

186 TOAD SVL VS ABUNDANCE

187 The total number of male and female toads arriving at the pond to breed each year was used as

188 a measure of relative toad abundance. Overall breeding toad abundance declined significantly

189 ($P<0.001$) between 1983 and 2020 (Fig. 2a). There were also significant positive correlations

190 between the mean SVL of breeding female and male toads and mean estimates of overall toad

191 abundance during the five (females) and four (males) years culminating in arriving at the

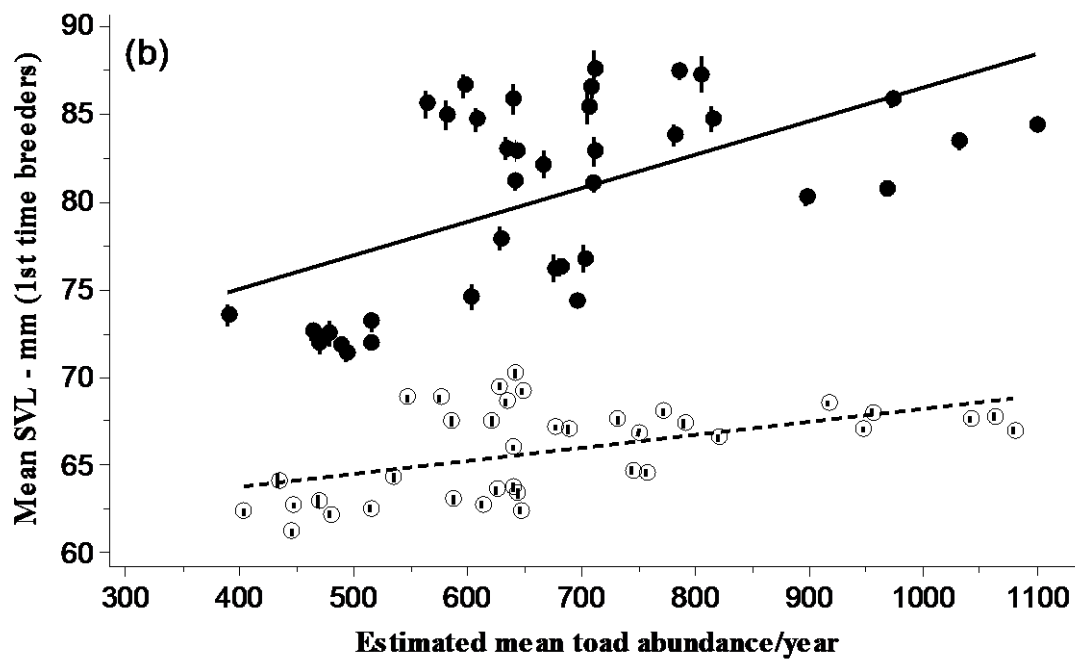192 breeding pond for the first time (Fig. 2b).
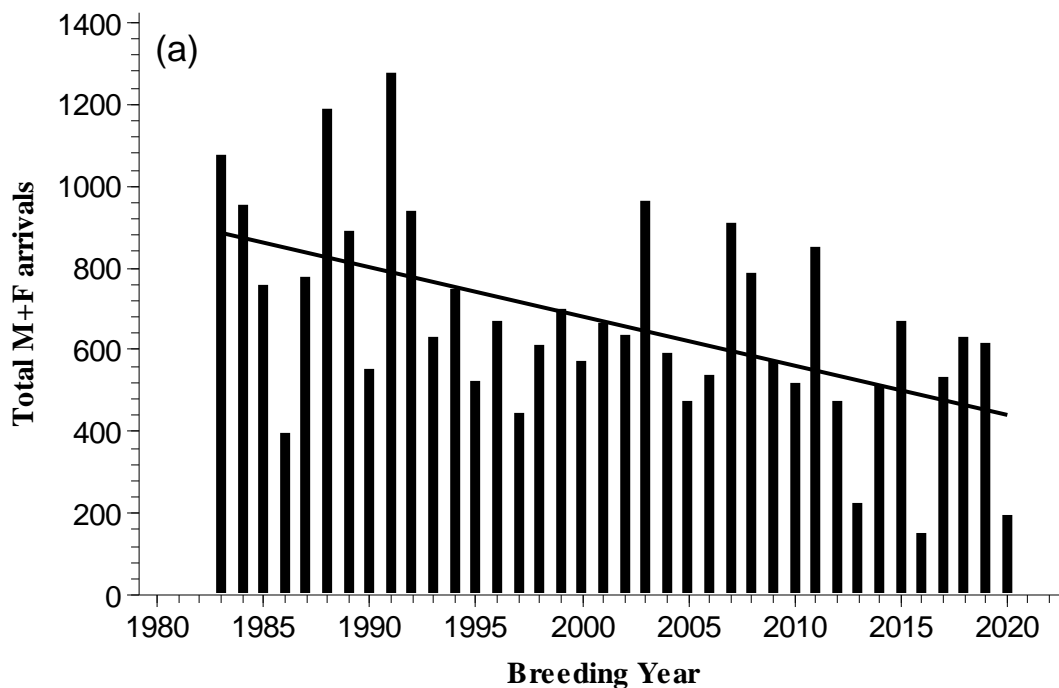
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Figure 2. (a) Total number of toads (females + males) arriving annually (1983-2020) to the breeding pond: Total M+F: Breeding=24728 - 12.02 Breeding Year; $r^2 = 29.05\%$; $P < 0.001$, $n = 38$. (b) Correlation between the mean SVL ($\pm$SE) of 1st time breeding female ($\bullet$) and male ($\bigcirc$) toads and estimated mean annual toad abundance index during the growth period between metamorphosis (toadlets) and arriving to breed for the first time.

Mean ♀ SVL = 67.33 + 0.01921 Mean toad abundance: $r^2 = 32.6\%$; $P < 0.001$, $n = 37$.

Mean ♂ SVL = 60.84 + 0.007413 Mean toad abundance: $r^2 = 26.2\%$; $P = 0.001$, $n = 38$.

207

208   CHANGES IN SVL AND SMI OVER TIME

209   Between 1983 and 2020 a total of 4,004 first time breeding females and 15,550 first time

210   breeding males were captured with the number of each sex varying annually (♀: 46-253; ♂:

211   96-712). The overall mean SVL and SMI of both female and male toads declined between 1983

212   and 2020 (Fig. 3). However, the decline in SVL was not uniform over time (Table 1), remaining

213   relatively constant between 1983-1999 (period 1: ♀: $\bar{x}$ = 84.5mm, range: 65-108mm; ♂: $\bar{x}$ =

214   69.1mm, range:52-85mm), declining between approximately 2000-2010 (period 2: ♀: $\bar{x}$ =

215   77.7mm, range: 60-110mm; ♂: $\bar{x}$ = 65.9mm, range:48-87mm) and then remaining relatively

216   stable between 2011-2020 (period 3: ♀: $\bar{x}$ = 71.9mm, range: 55-95mm; ♂: $\bar{x}$ = 62.6mm,

217   range:49-78mm). The decline in the mean SVL values for both females (14.9%) and males

218   (9.4%) between the first and third periods were significantly different (♀: *t*=50.84, *df*=2542,

219   *P*<0.001; ♂: *t*=69.78, *df*=7398, *P*<0.001). The SMI showed a more consistent decline between

220   1983 and 2009 before levelling off between 2010 and 2020. The decline in the mean SMI

221   values for both females (30.2%) and males (19.4%) between the first (♀: $\bar{x}$ = 81.80, range:

222   70.3-108.1; ♂: $\bar{x}$ = 37.40, range: 34.5-45.2) and third periods (♀: $\bar{x}$ = 57.10, range: 54.8-62.7;

223   ♂: $\bar{x}$ = 30.13, range: 28.2-32.3) were significantly different (♀: *t*=40.47, df=2148, *P*<0.001; ♂:

224   *t*=64.04, *df*=6687, *P*<0.001).

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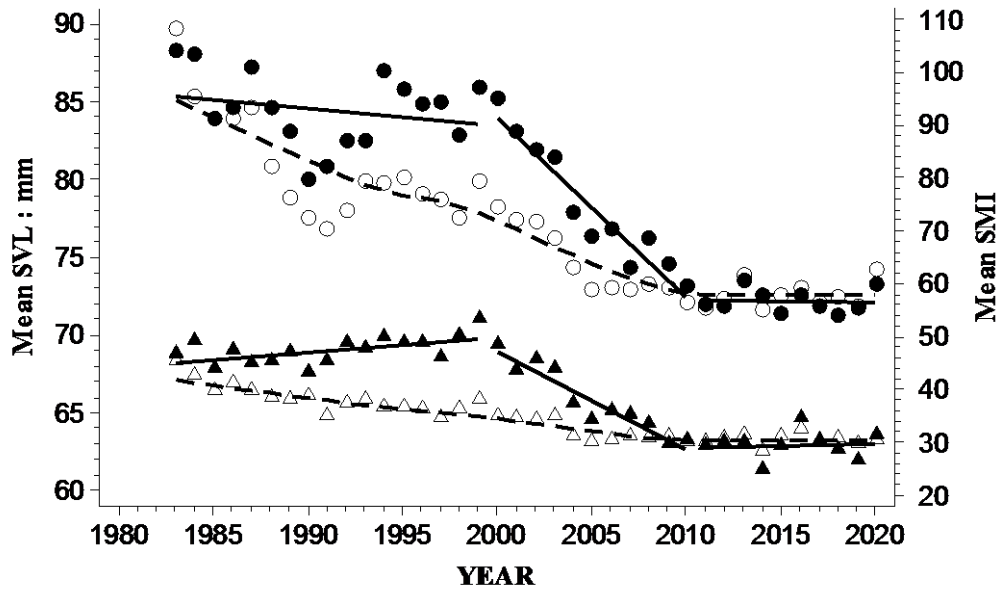
Figure 3.   Change in mean female (●) and male (▲) SVL and mean body condition (SMI: female: ○; male: △) between 1983 and 2020. Linear regression equations for female and male SVL against year are shown in Table 1. Each SMI fitted line is a Lowess Smoother (Degree of smoothing = 0.5; number of steps = 2).

A polynomial regression analysis of SMI against SVL revealed a significant quadratic correlation between these two variables (Fig. 4) and showed that the lowest SMI, for both sexes, was in the smallest individuals and highest in the largest individuals. The analysis also revealed a highly significant relationship between female and male SMI over time (1st ♂ SMI = 12.78 + 0.3061 1st ♀ SMI; $r^2 = 93.39\%$, $P<0.001$, $n = 38$) with both sexes having the highest SMI during the 1980's and the lowest between 2010 and 2020.

236

Table 1.   Linear regression analysis of female and male SVL against Year (Yr), Overall and for each Period. Significant P-values (<0.05) shown in bold.

Sex	Years	Linear Regression equation	r^2	p	n

12

♀ SVL

Overall	1983-2020	SVL = 1020.0 - 0.4697 Yr	81.05%	**<0.001**	38
Period 1	1983-1999	SVL = 303.4 - 0.1099 Yr	5.40%	0.369	17
Period 2	2000-2010	SVL = 2385.0 - 1.150 Yr	90.72%	**<0.001**	11
Period 3	2011-2020	SVL = 95.6 - 0.01165 Yr	0.21%	0.900	10

♂ SVL

Overall	1983-2020	SVL = 506.0 - 0.2196 Yr	71.79%	**<0.001**	38
Period 1	1983-1999	SVL = 121.1 + 0.0955 Yr	31.34%	**0.019**	17
Period 2	2000-2010	SVL = 1319 - 0.6251 Yr	90.30%	**<0.001**	11
Period 3	2011-2020	SVL = 22.30 + 0.0201 Yr	0.46%	0.852	10

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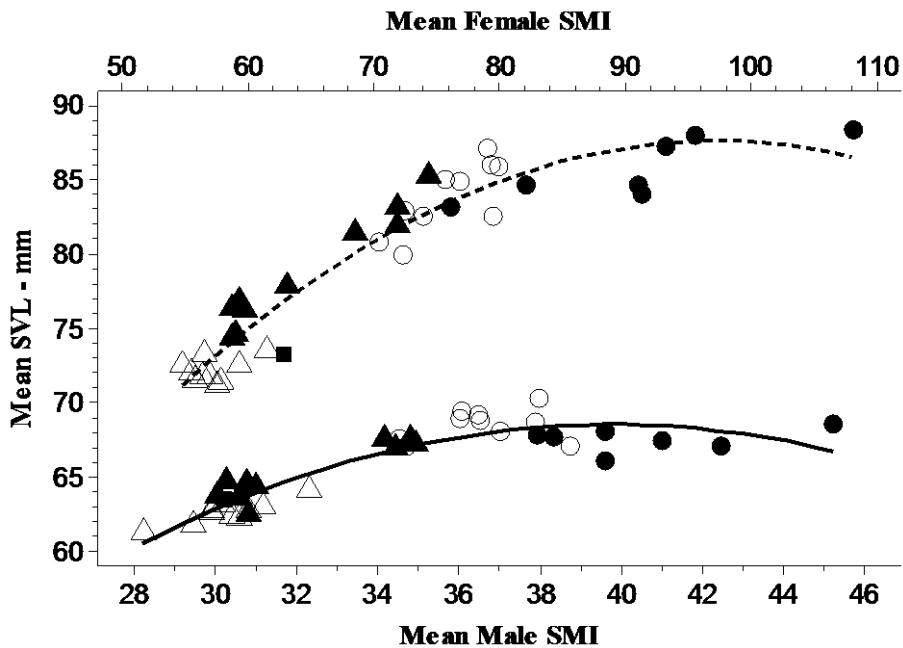
241 **Figure 4.** The relationship between mean SVL and mean SMI in first time breeding

242 female (---) and male (▬) toads from 1983-2020 (1980's: ●; 1990's: ○; 2000's: ▲; 2010's:

243 △; 2020's: ■).

244   ♀ SVL = 1.149 + 1.779 ♀ SMI - 0.009153 ♀ SMI^2; r^2 = 91.85%, $P<0.001$, n = 38.

245   ♂ SVL= -25.17 + 4.711 ♂ SMI - 0.05922 ♂ SMI^2; r^2 = 84.30%, $P<0.001$, n = 38.

246

247   RELATING SVL AND SMI TO ENVIRONMENTAL TEMPERATURE AND RAINFALL

248   Female and male mean SVL (1983-2020) were negatively correlated ($P<0.001$) with the mean

249   summer temperatures experienced by the toads between the year of their metamorphosis and

250   their first year of breeding (Table 2). In both sexes this was mainly due to highly significant

251   ($P<0.001$) negative correlations with the mean summer temperatures between 2000 and 2010.

252   There were also significant negative ($P<0.001$) correlations between the SMI of both sexes and

253   the mean annual temperatures over the study period (Fig. 5a).

254

255   Table 2.   Linear regression analysis of female and male SVL against annual mean

256   summer temperatures (SummerT) between the year of metamorphosis and the

257   year of breeding for the first time, Overall and for each Period. Significant P-

258   values (<0.05) shown in bold.

Sex	Years	Linear Regression equation	r^2	P	n
♀ SVL					
Overall	1983-2020	SVL = 239.8 - 11.25 SummerT	55.61%	**<0.001**	37
Period 1	1983-1999	SVL = 130.1 - 3.268 SummerT	9.97%	0.217	17
Period 2	2000-2010	SVL = 315.3 - 16.240 SummerT	80.83%	**<0.001**	11
Period 3	2011-2020	SVL = 95.21 - 1.600 SummerT	19.89%	0.229	9
♂ SVL					
Overall	1983-2020	SVL = 125.7 - 4.179 SummerT	41.85%	**<0.001**	38
Period 1	1983-1999	SVL = 48.67 + 1.450 SummerT	20.90%	0.065	17

Period 2	2000-2010	SVL = 169.7 - 7.088 SummerT	73.13%	**0.001**	11
Period 3	2011-2020	SVL = 56.37 - 0.005 SummerT	1.21%	0.762	10

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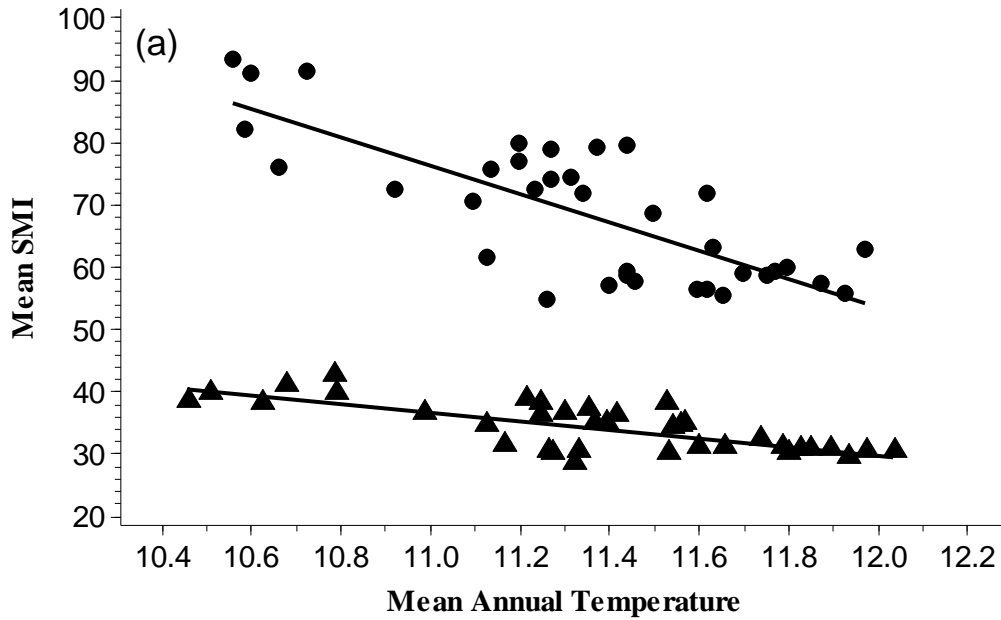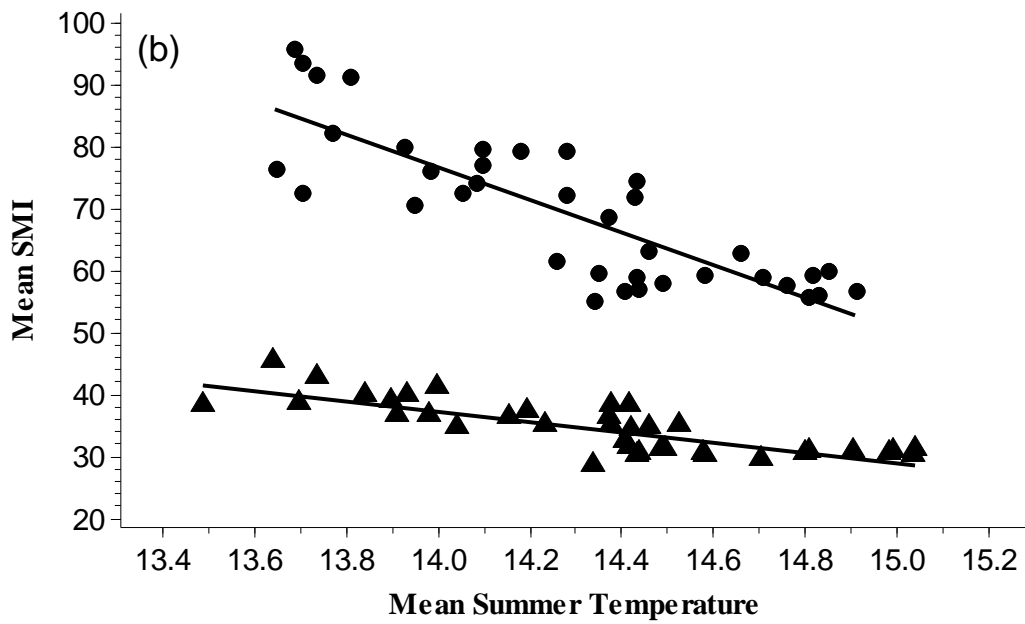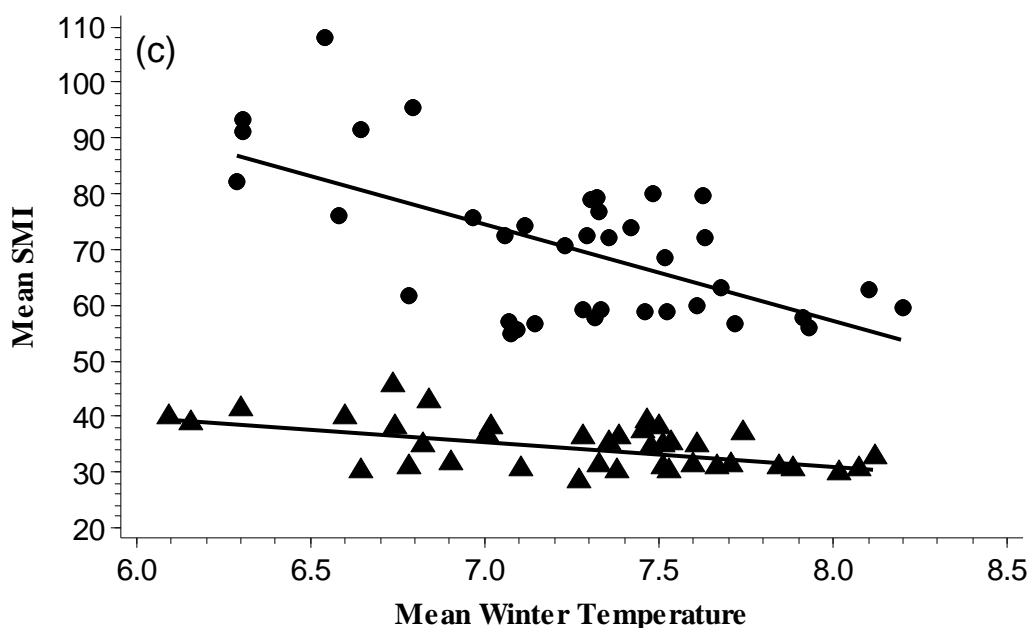
Figure 5.   The relationship between mean female (●) and male (▲) SMI and

(a) Annual mean temperatures °C (females: 5 years; males: 4 years prior to breeding).

♀ SMI = 326.1 - 22.70 Mean Annual Temperature; r^2 = 59.98%, *P*<0.001, *n* = 36.

♂ SMI = 112.3 - 6.886 Mean Annual Temperature; r^2 = 55.10%, *P*<0.001, *n* = 37.

(b) Mean summer temperatures °C (females: 5 years; males: 4 years prior to breeding).

♀ SMI = 444.2 - 26.26 Mean Summer Temperature; r^2 = 68.91%, *P*<0.001, *n* = 37.

♂ SMI = 154.5 - 8.377 Mean Summer Temperature; r^2 = 65.28%, *P*<0.001, *n* = 38.

(c) Mean winter temperatures °C (females: 5 years; males: 4 years prior to breeding).

♀ SMI = 196.2 - 17.37 Mean Winter Temperature; r^2 = 38.23%, *P*<0.001, *n* = 38.

♂ SMI = 66.63 - 4.451 Mean Winter Temperature; r^2 = 29.33%, *P*<0.001, *n* = 38.

272

A multiple regression analysis of mean annual SMI against mean summer temperatures, winter

temperatures and winter rainfall was completed. Male SMI was significantly negatively

correlated with mean summer temperatures (Fig. 5b) whilst female SMI was negatively

276   correlated to a combination of mean summer temperatures and mean winter rainfall (Mean ♀

277   SMI = 461.1 - 25.44 Mean summer T - 0.0695 Mean winter Rainfall; $r^2 = 72.59\%$, $P<0.001$, n

278   = 37) with the largest contribution to the relationship resulting from mean summer temperatures

279   ($r^2 = 68.91\%$, Fig. 5b). Given the strength of the correlation between SMI and mean summer

280   temperatures, mean winter temperatures were removed in the reduced model. There were,

281   however, significant negative correlations ($P<0.001$) between mean winter temperatures and

282   female and male SMI (Fig. 5c).

283

284   DISCUSSION

285   The first assumption made during this study was that the increase in individual toad body length

286   (SVL), was dependent on their ability to acquire sufficient energy (prey) and that this would

287   present as changes in body condition (SMI). Climatic factors potentially impacting on the

288   observed changes in SMI were therefore investigated, though their impact on prey availability

289   and/or toad behaviour outside the breeding season could not be determined.

290   The second assumption was that female and male toads attained sexual maturity at five

291   and four years respectively. These ages were based on studies of common toad

292   skeletochronology from Wales (Gittins *et al*. 1982), the Netherlands (Hemelaar 1983) and on

293   age estimates between 1981 and 1985 (Reading 1988) in addition to known aged toads (1984-

294   1990: marked as emergent metamorphs) at the study pond (Reading 1991). These studies

295   reported data from before 1999, when the steep decline in toad SVL started at the study pond,

296   and so toads captured after 1999 may have matured at a younger age. However, even if the

297   toads were smaller because they were younger, rather than due to a reduced growth rate

298   resulting from a decline in energy intake (Jorgensen 1986), it would not explain the observed

299   decline in toad body condition as SMI estimation is standardised and independent of SVL (Pieg

300   & Green 2009, 2010).

301   A more prosaic explanation is that SMI and SVL declines were linked, particularly

302   between 2000 and 2010, and were due to reduced energy intake causing a reduced growth rate,

303   a view supported by their strong negative correlation with increasing mean summer

304   temperatures. As ectotherms, toad metabolic rate is higher during warm summers than cool

305   summers (Dillon *et al* 2010, Sheridan & Bickford 2011) and this, in tandem with a potential

306   decline in prey availability during warm summers, may explain a reduced growth rate as shown

307   by a declining SVL. Toad growth rates may also slow, or cease, during periods of aestivation

308   as found in *Bufo calamita* (Sinsch *et al*. 2007) though not reported for *B. bufo*. Reduced anuran

309   gut performance has been found in some bufonids during periods of aestivation (Secor 2005)

310   and may also result in reduced growth rates.

311   The third assumption was that the toad abundance index estimation was a realistic

312   reflection of the actual abundance of immature toads in the environment. It was clearly an

313   underestimate of actual numbers as we were unable to estimate annual metamorph numbers or

314   subsequent mortality rates for each subsequent immature annual cohort category. However, we

315   believe that the annual estimated indices provide a reliable indication of toad abundance that

316   could be used when investigating the potential effects of overall toad abundance (competition

317   for food), between metamorphosis and attainment of sexual maturity for females and males, on

318   the subsequent observed changes in the SVL of first time breeders. Although the significant

319   positive relationships between toad abundance and the mean SVL of first time breeding females

320   and males were the reverse of that reported for the Natterjack toad (Denton & Beebee 1993)

321   they do reinforce our assertion that increasing climatic temperature, rather than competition for

322   food, is the principal cause of the observed decline in toad SVL.

323   The observed difference in the patterns of decline between the sexes may be explained

324   by physiological differences. During the summer immediately prior to breeding for the first

325   time females divert energy into oocyte maturation rather than somatic growth (Jorgensen

326   1986). In addition, a wet winter immediately prior to breeding for the first time, may indicate

327   relatively warm winter hibernation temperatures and have a negative impact on female body

328   condition as stored energy reserves will be utilized at a faster rate (Reading 2007) than during

329   a dry cold winter. In males, sperm production is less energy expensive than egg production

330   (Hayward and Gillooly 2011) and energy intake during the summer preceding sexual maturity

331   is not diverted into gamete production, though increased utilization of stored energy reserves

332   during warm winters is still likely to occur. It may also be the result of intermittent growth

333   resumption, by sexually immature toads, during mild periods of the winter when stored energy

334   reserves are utilised, but feeding is unlikely, as found in *B. calamita* (Sinsch *et al*. 2007).

335   The apparent levelling off, and stabilisation, of both SVL and SMI, in both sexes, after

336   2010 is a further indication of the link between energy intake and growth suggesting that before

337   1999, and despite apparently higher toad abundance potentially increasing competition for

338   food, their energy intake was, nevertheless, able to sustain a higher rate of somatic growth

339   resulting in larger body sizes, with higher metabolic demands, than after 2000.

340   Although the availability of energy (invertebrate prey) for toads was not studied around

341   the breeding pond during the summer months (April-October) the observed decline in toad SMI

342   suggests that it became less available after 1999, an observation supported by recent studies of

343   the link between declining invertebrate abundance and climatic warming (Robinet & Roques

344   2010; Harris et al. 2019; Halsch *et al*. 2021) with an 83% decline in beetle abundance and 39%

345   decline in the number of beetle taxa between the mid 1970's and 2015-2017 (Harris et al. 2019).

346   An additional possibility is that the 19-30% (male;female) reduction in SMI after 2010,

347   compared to before 1999, may signal future declines in SVL, as happened after 1999, or that

348   toads may become locally extinct if insufficient energy is available to support growth and

349   reproduction.

350   The link between summer temperatures and toad SVL, in the current study, is similar

351   to that found for the Natterjack toad (*B. calamita*) from the fossil record in Spain during the

352   early to late Pleistocene though winter rainfall was also found to be an important additional

353   factor (Martinez-Monzón *et al*. 2018). However, the precise length of time over which these

354   changes occurred cannot be determined from the fossil record but can occur over a very short

355   period of time, as found in some other terrestrial vertebrates (Yom-Tov & Geffen 2011).

356   Our study of *B. bufo*, along with that of *B. calamita* suggests that changes in SVL of

357   these two closely related northern hemisphere bufonids are the result of a high degree of

358   'phenotypic plasticity', rather than a 'micro-evolutionary adaptation' (Gienapp *et al*. 2008; Van

359   Buskirk *et al*. 2010; Ohlberger 2013) to a changing climate (Yom-Tov & Geffen 2011;

360   Ohlberger 2013; Parmesan 2006) and that this is relatively common where the impacts of

361   climate change on vertebrates have been studied (mammals and iguanas: Yom-Tov & Geffen

362   2011; Gienapp *et al*. 2008; birds: Van Buskirk *et al*. 2010; Gardner *et al* 2011; Sheridan &

363   Bickford 2011; North Sea fish: Audzijonyte *et al*. 2013; Baudron *et al*. 2014; salamanders:

364   Caruso *et al*. 2015).

365   A further potential impact of a warming climate concerns female fecundity. During the

366   toad breeding seasons of 1981-1982 a significant positive relationship was found between

367   common toad SVL and the number of eggs produced by females (Reading 1986). Assuming

368   that this relationship remains valid then the reduction in female SVL since 1999 may have

369   resulted in a reduction in female fecundity thereby potentially impacting on the population

370   dynamics of the common toad at the study pond. This negative impact of a warming climate is

371   the reverse of that found in the common lizard (*Lacerta vivipara*) where females benefitted

372   from climate warming by growing larger and producing more young (Chamaillé-Jammes *et al*.

373   2006).

374   The current study has demonstrated that, in *B. bufo*, a warming climate is correlated

375   with a decline in body condition (SMI) in both sexes resulting in a decline in SVL, that was

376   not the result of increased toad abundance, and that this may have resulted in a decline in

377   fecundity. These effects can occur over a relatively short period of time (10 years) compared

378   to that found in the fossil record for *B. calamita* (Martinez-Monzón *et al*. 2018). The ability of

379   common toads to adapt to changing climatic conditions should be seen as an example of

380   'phenotypic plasticity' rather than 'evolutionary adaptation' though it is possible that this could

381   develop over time with an analysis of their genetics required to verify this.

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