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The cost of breeding for male common toads.

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ABSTRACT

The potential impact of pairing on male survivorship and future breeding success, in common toads, was investigated between 1993 and 2014. A total of 8,132 males arriving at a breeding pond in southern England were measured, weighed, individually marked and their breeding history recorded. The body condition (BC) of all males was estimated using a) residuals from an ordinary least squares regression analysis of $\log_{10}$ body mass against $\log_{10}$ body SVL (OLS) and b) a scaled mass index (SMI), standardised for SVL. Each year each male was allocated to one of four categorical groups: Paired/Unpaired, and whether or not it returned to breed the following year: Return/No Return.

The BC of both paired and unpaired males that subsequently returned was significantly higher than that of those that failed to return. Male pairing success was highest in the youngest males and lowest in the oldest. The overall cost for male common toads that successfully paired was a significantly decreased BC and survival rate. First time breeding males had a 21.2% chance of surviving and returning to breed the following year, increasing to 28.3-37.0% for those returning for up to five consecutive years.

ADDITIONAL KEYWORDS: amplexus - body condition - breeding frequency - breeding success - *Bufo bufo* - mortality - scramble competition - survivorship.

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INTRODUCTION

A pivotal trade-off around which life histories are thought to evolve, is between allocating limited energy reserves to current reproduction, that may hinder growth and survivorship, or to somatic growth, that may increase the chance of future reproduction (Williams 1966, Harshman & Zera, 2007). The cost of breeding in male vertebrates has been studied in fish (Kawabata *et al*., 2015), amphibians (Davies & Halliday, 1979; Grafe *et al.,* 1992; Tejedo, 1992; McLister, 2003; Hettyey *et al*., 2009, 2012), reptiles (Olsson, Madsen & Shine, 1997), birds (Moller, 1991) and mammals (Kovacs *et al*., 1996; Yoccoz, *et al*., 2002; Galimberti *et al*., 2007; Lane *et al*., 2010; Tennenhouse *et al*., 2012; Meise *et al*., 2014; Foley *et al*., 2018).

In amphibians the majority of these studies have focused on quantifying the energetic cost of breeding, usually measured in terms of biomass allocated to testes development and gamete production (Hayward & Gillooly, 2011; Hettyey *et al*., 2012), loss of body mass during the breeding season (Ryser, 1989), and in measuring the metabolic cost of breeding activities, such as calling to attract a mate (Tejedo, 1992; Grafe & Thein, 2001) and amplexus (McLister, 2003), rather than measuring the cost of reproduction on an individual's subsequent survival and breeding success (Pianka, 1976; Clutton-Brock, 1984), as it is via these two processes that natural selection operates (Pianka, 1976). Most have also investigated the impacts of breeding within a single breeding season (Gastón & Vaira, 2020) rather than assessing the potential long-term effects over an individual's lifetime. The need for longer and more detailed studies of wild populations to investigate potential long-term costs for individuals, and populations, as a result of breeding, has been acknowledged for many years (Partridge & Harvey, 1985; Halliday & Verrell, 1986; Hettyey *et al*., 2009, 2012).

The common toad (*Bufo bufo* L) is an 'explosive' breeder arriving at their breeding sites once a year in the early spring, immediately following emergence from hibernation (Reading & Clarke, 1983; Reading *et al*., 1991). In southern England the breeding season can start as early as late January and end as late as early April and male mate competition for females is intense (Davies & Halliday, 1979). During a forty-two year ongoing study of a common toad population at their breeding site in southern England (1979-2020) the timing of breeding, changes in body condition, and survivorship were studied in relation to environmental temperature and climate change (Reading & Clarke, 1995; Reading, 1998; Reading, 2001; 2007). Between 1993 and 2014 male toads were individually marked and their breeding history recorded from their first to their last breeding season, presenting a unique opportunity to investigate the possible long-term impact of current breeding on their body condition, survivorship and future breeding success.

MATERIALS AND METHODS

STUDY SITE

The common toad breeding pond is located in a flooded clay pit (approximately 0.34 ha) situated to the north of the Purbeck Hills in south Dorset, UK (50°38’N, 2°07’W). All the vegetation from the immediate surround of the pond was cleared during the winter of 2005/2006 subsequently resulting in largely open rough grassland with some limited low scrub cover (regenerating *Rhododendron ponticum* L., gorse *Ulex europaeus* L. and heather *Calluna vulgaris* L.). Beyond the cleared area is mixed deciduous woodland. Between 1980 and 2020 the overall mean annual temperature was 11.3°C (range: 9.8-12.4 °C) whilst during the study period (1993-2014) is was 11.4°C (range: 10.1-12.4 °C).

DATA COLLECTION AND ANALYSIS

Annually, between 1979 and 2020, daily searches were completed for toads arriving at the breeding pond, from the arrival of the first toad to two days after the capture of the last toad. Daily captures were achieved by completing two slow searches in the water, around the perimeter of the pond, and collecting all paired and single toads that were either seen close to the water surface, or detected by touch under the surface. The second search was completed after processing the toads from the first search. Pairs in amplexus were separated before being processed and then re-paired prior to release. All captured toads were released at their respective collection sites after processing the toads from the second search. The time lapse between searches varied depending on the time taken to process the toads captured during the first search. All captured toads were measured (snout-vent length (SVL) mm: millimetre ruler), and weighed (g: Salter model 12 spring balance). As part of this ongoing study, between 1993 and 2014, all captured toads were also individually marked with a PIT tag (Passive Integrated Transponder: Trovan ID 100) and the identity of all males and females in amplexus was recorded each time they were captured during each breeding season up to the last recapture of a PIT-tagged toad in 2017.

The body condition (BC) of all PIT-tagged male toads was determined in two ways, both validated for use in amphibians (Băncilă *et al*., 2010; MacCracken & Stebbings, 2012), to address possible discrepancies occurring between indices. First, using the residuals from an ordinary least squares (OLS) regression analysis of $\log_{10}$ body mass (g) against $\log_{10}$ body length (SVL: mm) using Minitab 18.1 software (Minitab 18). Second, using the scaled mass index (SMI), standardised for mean SVL, as described by Pieg & Green (2009, 2010).

$$\text{Male SMI} : \widehat{M}_{\mathrm{i}} = M_{\mathrm{i}} (\mathrm{L}_0/\mathrm{L}_{\mathrm{i}})^{\mathrm{b}_{\mathrm{SMA}}} \text{ where } \mathrm{b}_{\mathrm{SMA}} = \mathrm{b}_{\mathrm{OLS}} / \mathrm{r}.$$

$\widehat{M}_{\mathrm{i}}$ = predicted body mass of individual *i* when the SVL was standardised to L_0; M_i and L_i = body mass and SVL of individual *i*; L_0 = mean SVL of all males within each breeding category between 1993 and 2017; $\mathrm{b}_{\mathrm{SMA}}$ = scaling exponent estimated from the standardised major axis (SMA) regression of Log$M$ on Log$L$; $\mathrm{b}_{\mathrm{OLS}}$ = regression coefficient of Log$M$ on Log$L$; r = Pearson’s correlation coefficient.

Each year males were allocated to a breeding category (1st - 8th time breeders depending on their individual breeding history) and also to one of four categorical groups, within each breeding category, depending on whether or not they had paired with a female that year, and whether or not they returned to the breeding pond the following year. The groups were 1: Unpaired/No Return (UnP-NoRet); 2: Unpaired/Returned (UnP-Ret); 3: Paired/No Return (P-NoRet); 4: Paired/Returned (P-Ret). The BC of males in each of these four groups were compared after first testing for normality within the data sets (Anderson-Darling test statistic: AD) and homoscedasticity (Levine's test). Data that were not normally distributed were analysed using the Mann-Whitney test (W-statistic). Data that were normally distributed, with equal variances, were analysed using the 2-sample t-test (t-statistic).

Since the BC of paired males may have been influenced by fights with unpaired males trying to replace them, an annual 'male competition factor' was estimated (1993-2014) by multiplying the annual sex ratio (♂:♀) by the overall length of the breeding season (days).

Over the 22 year study period the number of paired or unpaired males that either returned or failed to return in subsequent years was analysed using the Pearson χ^2 test for association between these categorical variables for 1st to 4th time breeders.

The overall survivorship of males visiting the pond to breed on multiple occasions (years) was determined after first removing, from the 1993 data set, all those males that had been captured in previous years. First-time breeders were those arriving at the breeding pond for the 1st time in any particular year whether or not they were captured multiple times within the same breeding season. Second to eighth time breeders were those that had arrived at the breeding pond in 1-7 previous years. Only 1st time breeders were used in the analysis for 1993. Some males were not captured each year ('Not Found') but were known to have been alive as they were captured in subsequent years. Each year the number of males in this category was counted and added to the total number of captured males as they were assumed to have been at the breeding pond. Survivorship for each breeding category (1^{st}-8^{th} time breeders) was estimated using the sum of the total number of tagged males in each category, including those 'Not Found', captured in year 'i+1' divided by the number found in year 'i', also including males in the 'Not Found category.

In all statistical analyses a *p*-value of 0.05, was the threshold for significance.

RESULTS

MALE BODY CONDITION (BC)

The overall BC data estimated from regression analysis residuals (OLS) for all 1^{st}-3^{rd} time breeding groups (Table 1) were not normally distributed (AD test: $p<0.05$) whilst that for 4^{th} time breeders were (AD test: $p>0.05$). The overall BC data estimated using the Scaled Mass Index (SMI) for 1^{st} and 2^{nd} time breeders were not normally distributed (AD test: $p<0.05$) whilst that for 3^{rd} time breeders was (AD test: $p>0.05$). Three of the BC data sets for 4^{th} time breeders were normally distributed and three were not.

Both BC estimates (OLS and SMI) showed that 1^{st} time breeding males that successfully paired (Fig. 1a), but didn't subsequently return (P-NoRet), had a significantly ($p<0.001$) lower BC than those that didn't pair and either subsequently returned (UnP-Ret) or didn't return (UnP-NoRet; Table 1). Males that paired and returned (P-Ret) had a significantly ($p=0.007$) lower BC than those that didn't pair and returned (UnP-Ret), as determined from the OLS, but were not significantly different ($p>0.05$) using the SMI. The OLS showed no significant ($p>0.05$) difference between those that paired and either did (P-Ret) or didn't (P-NoRet) return whilst the SMI showed that paired males that didn't subsequently return (P-NoRet) had a significantly lower ($p<0.001$) BC than those that paired and did return (P-Ret). Overall, 1^{st} time breeding males that failed to subsequently return had a lower BC than those that did return irrespective of whether or not they had paired (Fig. 1a, Table 1).

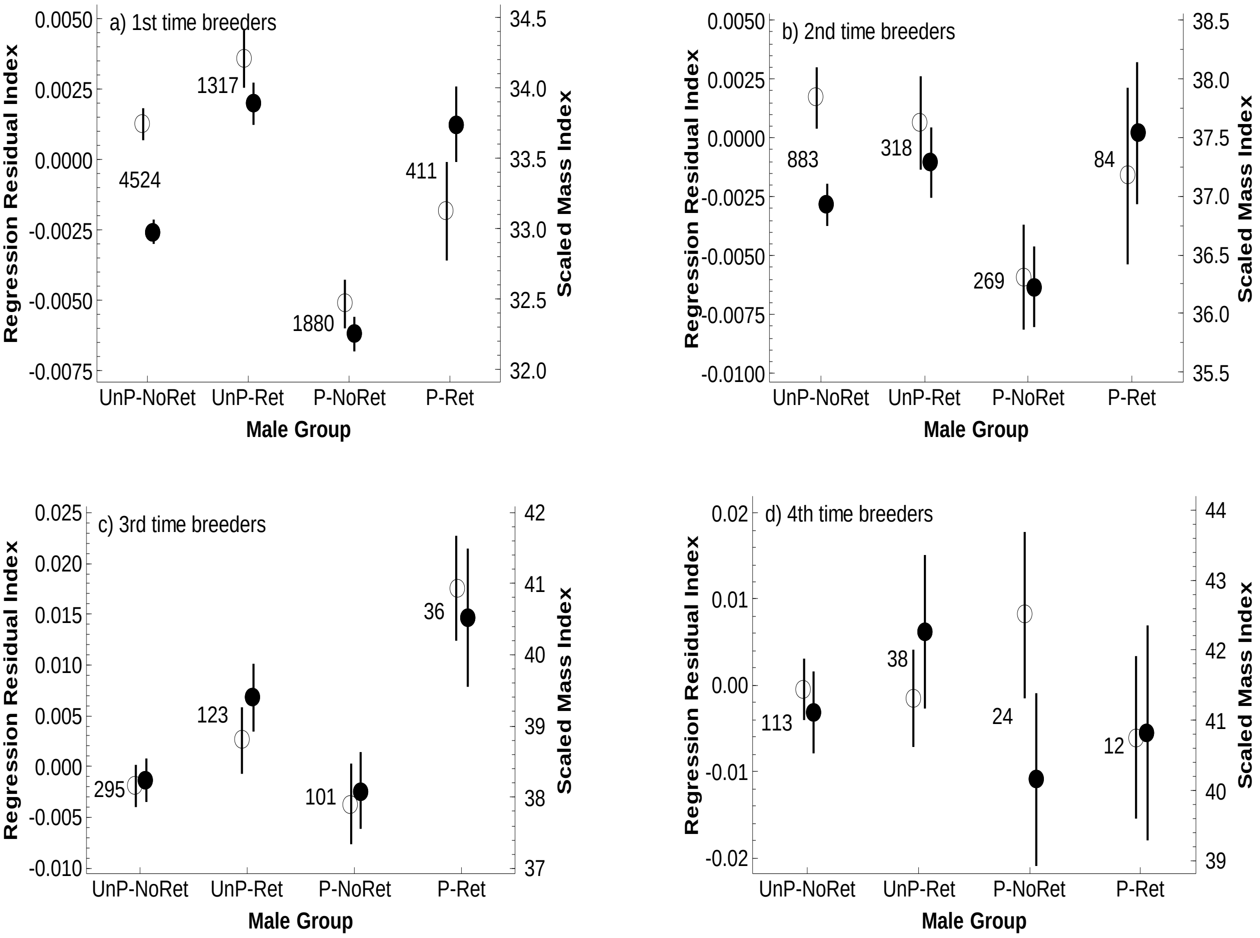

Figure 1. The estimated mean body condition ± SE (regression residual index: OLS: ○; Scaled Mass Index: SMI: ●) for male toads within each of the four groups visiting the breeding pond for the 1st-4th time between 1993 and 2014. (UnP-NoRet: Unpaired-No Return; UnP-Ret: Unpaired-Returned; P-NoRet: Paired-No Return; P-Ret: Paired-Returned). N is shown for each male group.

Table 1. Comparison of body condition estimates (OLS and SMI) for males in each of the four groups (Fig.1: UnP-NoRet: Unpaired-No Return; UnP-Ret: Unpaired-Returned; P-NoRet: Paired- No Return; P-Ret: Paired-Returned) and the number of years they were recorded at the breeding pond, using either the Mann-Whitney Test (W) or two-sample t-test (t) with *df* in parenthesis. Significant values (P<0.05) are shown in bold.

	Regression Residuals (OLS)		**Scaled Mass Index (SMI)**	
	1st Time Breeders			
Comparing	**Test statistic**	***p***	**Test Statistic**	***p***
UnP-NoRet vs UnP-Ret	**W**=13109764.0	**0.052**	**W**=12935876.5	**<0.001**
UnP-NoRet vs P-NoRet	**W**=14928962.5	**<0.001**	**W**=14812798.0	**<0.001**
UnP-NoRet vs P-Ret	**W**=11211601.0	0.094	**W**=11090133.5	**0.007**
UnP-Ret vs P-NoRet	**W**= 2283773.0	**<0.001**	**W**= 2318575.5	**<0.001**
UnP-Ret vs P-Ret	**W**= 1162325.0	**0.007**	**W**= 1142520.0	0.653
P-NoRet vs P-Ret	**W**= 2131463.0	0.058	**W**= 2092356.0	**<0.001**
	2nd Time Breeders			
Comparing	**Test statistic**	***p***	**Test Statistic**	***p***
UnP-NoRet vs UnP-Ret	**W**=533336.0	0.617	**W**= 524811.5	0.268
UnP-NoRet vs P-NoRet	**W**=520647.5	**0.015**	**W**= 519561.5	**0.028**
UnP-NoRet vs P-Ret	**W**=429102.5	0.479	**W**= 425525.5	0.450
UnP-Ret vs P-NoRet	**W**= 96653.5	0.123	**W**= 99239.0	**0.005**
UnP-Ret vs P-Ret	**W**= 64530.0	0.633	**W**= 63928.5	0.876
P-NoRet vs P-Ret	**W**= 47122.5	0.548	**W**= 46041.0	**0.054**
	3rd Time Breeders			
Comparing	**Test statistic**	***p***	**Test Statistic**	***p***
UnP-NoRet vs UnP-Ret	**W**=60499.0	0.247	**t**= 2.08 (416)	**0.039**
UnP-NoRet vs P-NoRet	**W**=58926.5	0.711	**t**= 0.24 (394)	0.812
UnP-NoRet vs P-Ret	**W**= 7259.5	**0.002**	**t**= 2.42 (329)	**0.016**
UnP-Ret vs P-NoRet	**W**=14494.0	0.174	**t**= 1.85 (222)	0.065
UnP-Ret vs P-Ret	**W**= 9272.0	**0.020**	**t**= 1.11 (157)	0.271
P-NoRet vs P-Ret	**W**= 6385.5	**0.004**	**t**= 2.25 (135)	**0.026**
	4th Time Breeders			
Comparing	**Test statistic**	***p***	**Test Statistic**	***p***
UnP-NoRet vs UnP-Ret	**t**=0.17 (149)	0.862	**W**= 8520.0	0.772
UnP-NoRet vs P-NoRet	**t**=0.92 (135)	0.357	**t**= 0.70 (135)	0.485
UnP-NoRet vs P-Ret	**t**=0.49 (123)	0.623	**t**= 0.16 (123)	0.875
UnP-Ret vs P-NoRet	**t**=0.93 (60)	0.358	**W**= 1227.5	0.665
UnP-Ret vs P-Ret	**t**=0.31 (48)	0.759	**W**= 987.0	0.691
P-NoRet vs P-Ret	**t**=0.85 (34)	0.402	**t**= 0.32 (34)	0.747

For 2nd time breeding males (Fig. 1b, Table 1), both OLS and SMI estimates of BC showed that those that paired and didn't return (P-NoRet) had a significantly (*p*=0.015; *p=0.028*) lower BC than those that didn't pair and didn't return (UnP-NoRet). Only the SMI showed that returning males that hadn't paired the previous year (UnP-Ret) had a significantly higher (*p*=0.005) BC than those that had previously paired but didn't return (P-NoRet). Males that paired and returned (P-Ret) had a significantly (p=0.054) higher BC, estimated from the SMI, than those that paired and didn't return. Overall, second time breeding males that paired and failed to subsequently return (P-NoRet) had a lower BC than those from the other three groups (UnP-NoRet, UnP-Ret, P-Ret).

For 3rd time male breeders (Fig. 1c, Table 1), those that returned (UnP-Ret, P-Ret) the following year had a significantly (p<0.05) higher BC than those that didn't return (UnP-NoRet, P-NoRet) irrespective of whether or not they paired. There were no significant (p>0.05) differences in the BC of any of the four groups in 4th time breeding males (Fig. 1d, Table 1).

Over the study period the annual sex ratio varied between 1.7:1 and 7.0:1 (mean = 4.2:1, n = 22) whilst the length of the breeding season ranged between 8-26 days (mean = 14.8 days, n = 22) and were used to estimate a 'male competition factor'. No significant relationships (p>0.20), determined by linear regression analysis, were found between the mean BC of either paired or unpaired males, and the sex ratio, the length of the breeding season or the 'male competition factor'.

MALE BREEDING FREQUENCY

The proportion of each group (1st-8th) that successfully paired declined as the number of times they arrived at the breeding pond increased (Fig. 2). Males arriving for more than six consecutive years failed to pair.

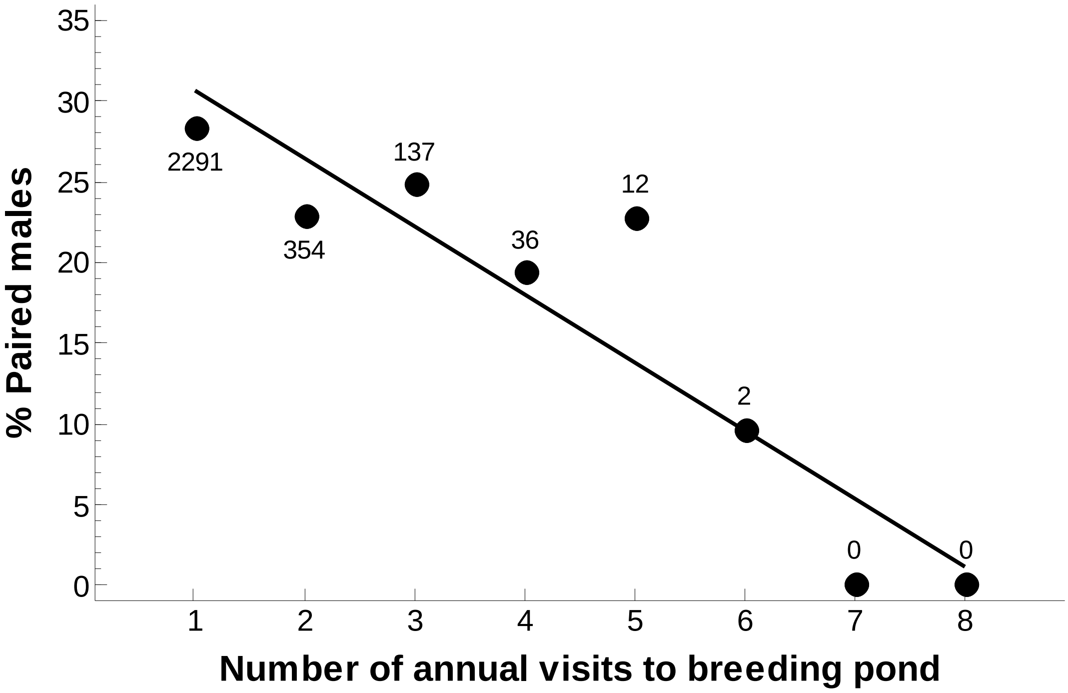

Figure 2. Pairing success (%) of marked males in relation to the number of times they visited the breeding pond (1993-2014). Total number of pairings are shown against each point. % Paired = 34.81 – 4.692 Visits to pond; $r^2 = 84.5\%$, p=0.001, n = 8.

MALE SURVIVORSHIP

Over the 22 years, 195 males (2.4%) were recaptured after missing one (179 males), two (15 males) or four (1 male) consecutive years at the breeding pond.

Between 1993 and 2017, when the last PIT-tagged male was captured, a total of 8,132 individual males were captured. Including males in the 'Not Found' category there was a 21.2% survival rate for those that arrived at the pond to breed for the first time and subsequently returned the following year with higher rates (28.3-37.0%) for those returning up to five times (Fig. 3). Due to the low survivorship of 1st time breeding males compared to those that had arrived for up to three previous years, the pair and return data for these four groups were re-analysed separately.

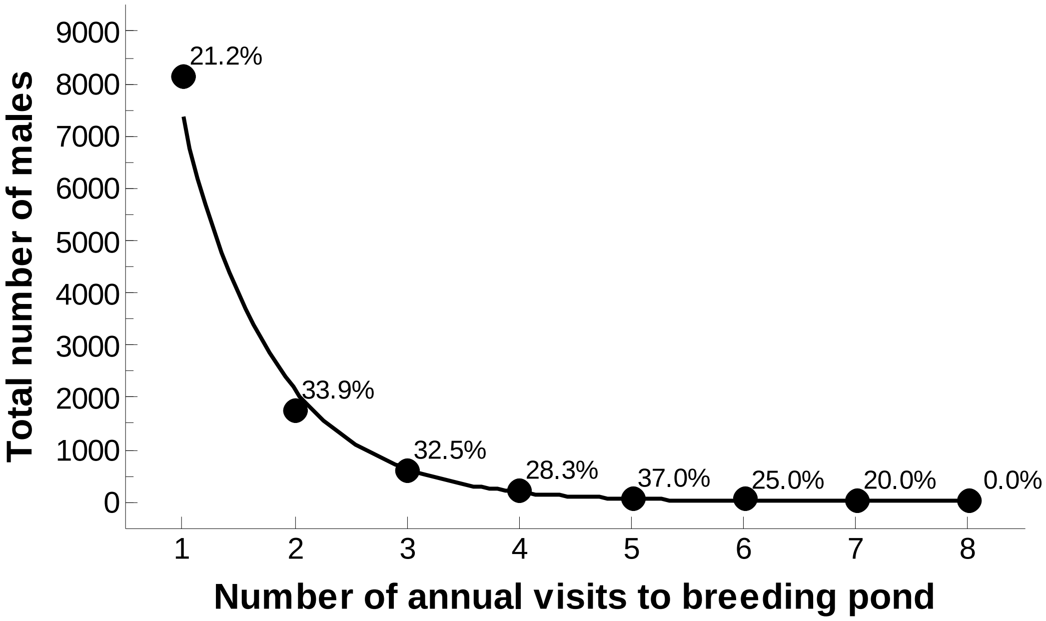

Figure 3. The number of male toads visiting the pond once (1) and then subsequently returning (2-8 times). Group survival rates (%) to next group are shown against each point. Log_{10} Total No. males = 4.404 - 0.5360 Visits to pond, $r^2 = 99.67\%$; $p<0.001$; n = 8.

For 1st time breeding males the probability of returning to breed in subsequent years was dependent on whether or not they paired in the current year. No significant association between these categorical variables was found for 2nd-4th time breeding males (Table 2).

The observed number of 1st time breeding males that subsequently returned to the breeding pond (P-Ret) was significantly lower than expected with a contribution to the overall χ^2 value of 56.6%. The observed number of unpaired males that subsequently returned (UnP-Ret) was significantly higher than expected accounting for 20.2% of the overall total χ^2 value whilst significantly more paired males, than expected, failed to return (P-NoRet) contributing 15.3% to the overall total χ^2 value. Together, the contribution by these three male groups to the overall χ^2 value was 92.1%.

Table 2. Pearson Chi-square analysis for the number of males arriving at the breeding pond for the 1st - 4th time that paired (P), didn't pair (UnP), returned in subsequent years (Ret) or failed to return (NoRet). The contribution to the overall χ^2 values by each of the four male groups (UnP-NoRet, UnP-Ret, P-NoRet, P-Ret) are shown in parenthesis. obs: observed count; exp: expected count.

	1st Time Breeders		**2nd Time Breeders**	
	No Return (NoRet)	Return (Ret)	No Return (NoRet)	Return (Ret)
Unpaired (UnP)	obs: 4524 exp: 4600 (*1.250*)	obs: 1317 exp: 1241 (*4.632*)	obs: 884 exp: 891 (*0.053*)	obs: 319 exp: 312 (*0.150*)
Paired (P)	obs: 1880 exp: 1804 (*3.187*)	obs: 411 exp: 487 (*11.810*)	obs: 269 exp: 262 (*0.179*)	obs: 85 exp: 92 (*0.511*)
	χ^2 = 20.878, *df* = 1, ***p*<0.001**		χ^2 = 0.894, *df* = 1, *p* = 0.344	

	3rd Time Breeders		**4th Time Breeders**	
	No Return (NoRet)	Return (Ret)	No Return (NoRet)	Return (Ret)
Unpaired (UnP)	obs: 297 exp: 300 (*0.032*)	obs: 123 exp: 120 (*0.081*)	obs: 113 exp: 111 (*0.051*)	obs: 38 exp: 40 (*0.140*)
Paired (P)	obs: 101 exp: 98 (*0.099*)	obs: 36 exp: 39 (*0.247*)	obs: 24 exp: 26 (*0.214*)	obs: 12 exp: 10 (*0.586*)
	χ^2 = 0.458, *df* = 1, *p* = 0.498		χ^2 = 0.990, *df* = 1, *p* = 0.320	

Although the analyses for the 2nd and 3rd time breeding males were not significant their return capture pattern followed that of 1st time breeding males with higher than expected numbers of males recaptured in the UnP-Ret and P-NoRet groups and lower than expected numbers captured in the UnP-NoRet group.

For 1st time breeding males 17.9% of those that paired subsequently returned compared to 22.5% of those that didn't pair. With the exception of 4th time breeders (4th: Paired = 33.3%, Unpaired = 25.2%) similar survival patterns were found in males that had returned to the pond for two to three consecutive years (2nd: Paired = 24.0%, Unpaired = 26.5%; 3rd: Paired = 26.3%, Unpaired = 29.4%). Overall, the survival rate of paired males increased as the number of breeding seasons they participated in increased.

DISCUSSION

To the best of our knowledge this is the first study of a potentially negative impact of pairing (amplexus) on male survivorship of any wild amphibian species encompassing multiple reproductive cohorts, and using individual based data in which the mating history of each male was known. The analysis has shown that over a 22 year period male common toads that paired with a female had a significantly lower BC than those that didn't pair. However, although males found in amplexus with a female does not automatically mean that they successfully spawned with that female, it is safe to assume that the majority (≈85%) did (Reading, 2001), and that searching for a female, forming amplexus, and then repelling rival males trying to dislodge them, does represent energy expensive activity (Gittins *et al*., 1980; Arak, 1983; Ryser, 1989; McLister, 2003; Dittrich *et al*., 2018) irrespective of whether, or not, pairing culminated in spawning.

Breeding success was highest in 1st time breeding males and lowest in the oldest males. Indeed, the male that arrived for eight consecutive years was never found paired with a female despite being one of the oldest males found at the breeding pond. The opposite was reported for the Omei treefrog (*Rhacophorus omeimontis*) where older males had a higher mating success than younger males (Liao & Lu, 2011).

In our study the 1st-3rd time breeding males with the lowest BC were also those with the lowest return rate whilst although the difference in the survival rates between paired and unpaired males were relatively small (4.6-2.5%) they were, nevertheless, indicative of the relationship differences between BC and survival rate.

In an evolutionary context, the role that these consequences of pairing might have for individual male common toads is unclear. In common frogs (*Rana temporaria*) small males are less discriminative about female size, when attempting to find a mate and can move faster than larger males, thereby increasing their chance of pairing, particularly if they do so by intercepting females before they arrive at the breeding site (Kovar & Brabec, 2007; Dittrich *et al.*, 2018). Larger males also arrive at the breeding site earlier than smaller males who are breeding for the first time (Dittrich *et al.*, 2018). At our study pond 1st time breeding males arrive later than males that have previously bred (Reading *et al.*, 1991). Although small male common toads invest as much energy in reproduction as larger males (Hettyey *et al.*, 2012) they may also be more physiologically stressed due to pairing when compared with unpaired males, as found in the Yungas Red-belly toad (*Melanophryniscus rubriventris*) in Argentina (Gastón & Vaira, 2020).

The estimation of a 'male competition factor', as a correlate for energy expenditure, is fraught with problems making its usefulness questionable. The biggest problem concerns the estimation of the operational sex ratio (OSR) which constantly changes throughout the breeding season so that the 'competition factor' must also vary on at least a daily basis depending on the number of new males and females arriving at, or leaving, the breeding pond. Thus, the daily OSR should be considered, rather than the overall breeding season sex ratio. However, this is difficult to estimate with any degree of confidence, particularly if spawning occurs at more than one site within a pond and males move between them in search of a mate. Also, the length of time that a male stays at the breeding pond is likely to vary considerably between individuals and is likely to be longer than that for females, who, once spawned, will leave the pond (Reading & Clarke, 1983). In addition, females arriving at the pond at the start of the breeding season spend longer at the pond before spawning, than those arriving later in the season (Reading & Clarke, 1983). An increase in male competition, over females, may have a negative impact on their BC, particularly in 1st time breeding individuals which tend to be younger and smaller than those that have bred in previous years, as they probably have lower initial energy reserves (Tejedo, 1992).

Male common toads, exposed to high summer temperatures and/or mild winter temperatures, have a lower BC due to a lack of prey in summer (Reading & Clarke, 1995), for storing adequate energy reserves for hibernation. The over-utilization of these reserves during warm winters, compared to cold ones, will further reduce the BC of males migrating to the breeding pond immediately following hibernation (Reading & Clarke, 1995). The stored energy reserves of small males may therefore be used at a faster rate than those of larger males if proportionately more indiscriminate inter-male fighting occurs, over females, as reported for *R. temporaria* (Dittrich *et al*., 2018) and this may explain, in part, why 1st time breeding males are less likely to survive to the following year than older males (Loman & Madsen, 2010). Given the overall high annual mortality rate of male common toads, particularly those visiting the breeding pond for the first time (78.8%), then it may be more advantageous for them to attempt breeding once sexual maturity is attained rather than wait an extra year and possibly failing to breed at all (Höglund & Robertson, 1987; Hettyey et al., 2010). It also appears unlikely that male toads would miss a breeding season once sexually mature, as suggested by Loman & Madsen (2010). A more prosaic explanation for the observed apparent missing of a breeding season, by a small number of males in the current study, is that they were present at the breeding pond but were not captured.

The results of this long-term study of individually marked male common toads have indicated that reproduction is correlated with a high immediate cost, a reduction of male BC, and a subsequent high long-term cost, an increase in male mortality, so that the likelihood of paired males returning to breed in subsequent years is significantly reduced compared to males that didn’t pair.

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