DEMOGRAPHIC PROCESSES IN A SMALL, ISOLATED POPULATION OF NATTERJACK TOADS (*BUFO CALAMITA*) IN SOUTHERN BELGIUM

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In a small, isolated population of the natterjack toad in southern Belgium, some features of demography and reproductive behaviour were atypical. Fecundity (about 2000 eggs per clutch) and adult survival rate (27%, compared with typical values of 50-80%) were both very low. Population age-structure was skewed towards young toad (2-4 years) and male reproductive success was apparently independent of calling activity and the length of chorus attendance. These characteristics are interpreted in terms of isolation and small population size, and could indicate that the population is under stress.

Key words: mark-recapture, mating strategy, pond-fidelity, satellite tactic

INTRODUCTION

In the northern part of its range, the natterjack toad (*Bufo calamita* Laurenti) is adapted to habitats of early successional stages, such as heaths, dunes and alluvial areas. As such habitats are shrinking everywhere in Western Europe, the natterjack is more and more restricted to secondary habitats like slag heaps, gravel pits, sand pits and industrial ponds. Most of the 70 or so populations remaining in southern Belgium occur in such secondary habitats, seven of them being totally isolated (Percsy *et al.*, 1997; Percsy *et al.*, unpubl.).

In this paper, we report on the functioning of one such isolated population living in a former sand pit. We highlight the very small area used by calling males and we hypothesize a high frequency of satellite males (silent males attempting to intercept females attracted by the callers: Arak, 1988) as a consequence of the small area available for calling activity. Therefore, we focus on demographic parameters within this particular population (population density, sex-ratio and age-structure, individual survival and reproductive success) and their variations, compared to similar parameters from other populations (Beebee, 1979). We also investigate the consequences of the satellite parasitic behaviour for male reproductive tactics and success, as such parameters are sensitive to caller density (Arak, 1988; Tejedo, 1992a)

MATERIALS AND METHODS

THE SPECIES

The natterjack toad is a pioneer species adapted to living in unstable environments (Beebee, 1983). Its thermal requirements and susceptibility to predators and competitors in the aquatic stages often force the species to choose ephemeral ponds for reproduction (Andrén & Nilson, 1985a, b; Banks & Beebee, 1987; Griffiths, Edgar & Wong, 1991; Bardsley & Beebee, 1998; Denton & Beebee, 1997). Several demographic and behavioural adaptations have allowed the natterjack to use such habitats. The burrowing capacities of juveniles and adults allow them to use unvegetated terrestrial habitats (Beebee, 1983; Denton & Beebee, 1994). An extended breeding period (males assemble in chorus for 6-10 weeks) and the plasticity of larval growth help natterjacks cope with the risks of larval mortality due to pond desiccation (Beebee, 1983; Griffiths, 1997; Stephan *et al.*, 2001). A high female fecundity combined with high adult survival allows populations to recover rapidly, even after complete breeding failure (Beebee *et al.*, 1982).

STUDY SYSTEM

The study was performed from April to June in 1999 and 2000 in the former sandpit of Mellery (50°34'30" N, 4°34'20'' E), southern Belgium. Frequent night visits around the site in search of calling natterjacks revealed that the population of Mellery is isolated from other breeding sites by a distance of at least 10 km. In Mellery, two ponds, separated by 250 m and differing both in area and the persistence of water, were used by calling males and spawning females during the duration of the study. The aquatic part of the habitat consisted of (1) the shallower parts (about 0.12 ha total) of a small permanent lake, and (2) the ephemeral waters (for an area of aquatic habitat ranging from 0 to 0.15 ha) of an artificially-built concrete pond. Terrestrial habitat surrounding the two ponds consisted mainly of (1) intensive agricultural fields and (2) an intensive clover area on a geotextile sheet covering the ancient quarry. These were interspersed with wooded areas and agricultural roads. The total area of suitable habitats (terrestrial and aquatic) for the toads and tadpoles was found to be 2 ha and 1 ha, respectively, according to the method of Denton & Beebee (1993b).

ESTIMATE OF POPULATION SIZE

Male total population size was derived from chorus size and composition, studied by MRR (Mark-Release-Recapture). Breeding activity of male natterjacks was monitored by visiting the breeding ponds at night, at least once each week, for a minimum of 2 hrs. Toads

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were located by torchlight. Adult natterjacks were individually marked using a unique toe-clip code in 1999 or a passive integrated transponder (model TX1400, FishEagle Co., Lechlade, Gloucestershire, GL7 3QQ, England; Sinsch, 1992) in 2000. Wounds were treated with an antiseptic powder (Sulfamed, Medgenix). No formal estimate of chorus size was made in 1999 in the concrete pond because the pond dried up for several weeks during the breeding season. The number of males in 1999 is thus a minimal assessment rather than a total population estimate. During the MRR study, natterjacks were sexed and males were measured snout-to-vent (to the nearest 0.1mm) and weighed (to the nearest 0.5 g). Because toads tried to crouch when measured, we gently pressed them as flat as possible and each individual was measured twice at each capture event. Only the greatest length recorded was considered for further analyses. During handling all toads emptied their bladders, so the state of hydration was similar in all individuals. The first mass record was used for analyses.

Because no individual was found to switch between breeding ponds during one breeding season, MRR data for the two breeding ponds were analysed separately and the sizes of the two breeding assemblages were summed to give the size of the total male population. Since a given male could join and leave one chorus whenever he wanted, we consider this sampling unit to be an open system, and therefore MRR data were analysed using the Jolly-Seber (J-S) method as applied on open populations (Seber, 1982; Hines, 1988). Since all males usually participate in breeding activity every year (Sinsch & Seidel, 1995), a simple mathematical manipulation of the J-S results gives an estimate of the total number of males in each chorus. The estimate of N₁, the initial chorus size, is given by the ratio r_1/p where r, is the number of toads caught at the first date and p is the mean capture probability, calculated by the J-S method. The J-S method also gives a quantitative estimate of toad recruitment for each capture event (B_i), so we added the B_i's to the initial chorus size to estimate the total male population size in each breeding unit. The chorus sizes of each capture event were estimated using Jolly® (Hines, 1988).

MRR methods cannot be applied to females because they only stay one night in the pond to reproduce. We therefore used the census of egg clutches to assess the number of females. As other studies have shown that about 65% of female natterjacks reproduce every year (Tejedo, 1992c; Denton & Beebee, 1993*a*; Stephan *et al.*, 2001) and double clutching is very rare (Tejedo, 1992c; Denton & Beebee, 1993*a*; Sinsch & Seidel, 1995; Denton & Beebee, 1993*a*; Sinsch & Seidel, 1995; Denton & Beebee, 1996), we estimated the total female population by dividing the clutch census by 0.65.

SURVEY OF REPRODUCTIVE ACTIVITIES

In order to estimate the fecundity of females, the two sites were visited during the day every 3-4 days to search for spawn strings. Recently laid clutches were carefully taken out of water, placed in a flat, white container filled with pond water, and photographed so that eggs counts could be made from slides later on. Clutches were immediately replaced in the original location.

In 1999, the reproductive activity of each male was evaluated by (1) his arrival date in the chorus and (2) his chorus attendance. In this study, chorus attendance corresponds to the percentage of time spent in the chorus: i.e. the number of days between the first and the last capture of an individual (his minimum residence time) divided by the total length of the breeding season. In 2000, a third estimate of reproductive activity was recorded: calling activity. Each time a toad was located during the MRR study of 2000, his behaviour (calling or silent) was recorded. Calling activity is the proportion of calling behaviour for toads for which at least three observations were recorded.

In 2000, we investigated the reproductive success of males: besides the MRR study, we also visited the site every night in search of toads in amplexus. Marked males were then identified. Reproductive success is the number of females with which a male was found in amplexus during the whole season.

SKELETOCHRONOLOGY

The age of 34 toads toe-clipped in 1999 was studied by skeletochronology. Removed phalanges were stored in 70% ethanol until they were cleaned, fixed, sliced and coloured with Cresyl violet (0.05%) according to skeletochronological methods used by Friedl & Klump (1997), Sinsch (1997) and Tejedo *et al.* (1997). Slides were observed under a light microscope and growth rings were counted in order to age the toads. In southern Belgium, as in Britain and Germany, growth slows down during winter. Observations of the bone structure therefore reveal dense and light-coloured rings corresponding to winter and summer growth, respectively.

ANALYSES

Statistical analyses were carried out using SAS® (SAS Institute, 1990): "PROC UNIVARIATE" was used to test the distribution of all parameters. Morphological variables (mass and length), their ratio for the 55 to 60 mm size-class, and fecundity each showed a normal distribution. To analyse the between-year differences in mean length of males, or female fecundity, we used a t-test after testing for equality of variances (SAS®: PROC TTEST). When variances were not equal between groups, or when there were significant departures from normality (for example, behavioural attributes of males and reproductive success), we compared groups using a Kruskal-Wallis test (Chi-square approximation) on simple, linear rank statistics based on the Wilcoxon scores (SAS®: PROC NPAR1WAY). We used Kendall's τ when testing for correlation between variables on an ordinal scale, such as mass, length, age, arrival date, chorus attendance and calling activity. Multiple regressions were used to detect

the influence of morphological and behavioural attributes on chorus attendance or calling activity (in 2000 only). Logistic regressions of males' reproductive success on five potentially explanatory variables (mass, length, arrival date, chorus attendance and calling activity) were then used to detect the influence of these individual variables on reproductive success in 2000.

RESULTS

DEMOGRAPHY AND MORPHOMETRY

Both chorus composition and chorus size fluctuated during the season, and the total size of the male population in one breeding assemblage exceeded the maximal daily size of the chorus. In 1999, the male population size of the lake was estimated at 56 males, and we marked nine other males in the concrete pond. Minimum male population size in 1999 was therefore estimated at 65 individuals. For 2000, MRR data gave an estimate of the total male population of 98 individuals. During 1999, 22 clutches were laid at Mellery, while in 2000 we counted 51. Adult breeding population size, calculated following the method described above, was estimated at 98 individuals in 1999 (minimal assessment) and 176 in 2000.

Accurate estimation of density relies on precise measures of suitable habitat areas used by toads. In the particular case of the Mellery population, these measures are facilitated by the fact that the three terrestrial habitat types surrounding both sites (i.e. agricultural fields, frequently-mowed clover on a geotextile substrate, and woodland) are totally unsuitable for natterjacks. This was confirmed by frequent, fruitless searching for adult toads by night with electric torches around the two sites, according to the method of Denton & Beebee (1993b). Thus, adult density was found to be 33 individuals per ha of habitat in 1999 (minimal assessment) and 59 individuals per ha of habitat in 2000.

Mean female fecundity was 1839 eggs in 1999 (SE=198, n=11), and 2045 eggs in 2000 (SE =170, n

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FIG 1. Clutch size of Bufo calamita at Mellery. Grey bar 1999, black bar 2000.

=21). The fecundity, presented in Fig. 1, was not signifi-

cantly different between years ($t_{(30)} = 0.75$, P=0.46). In 2000, we recaptured 17 of the 62 male toads marked in 1999. Male annual survival was therefore at least 0.27. The survey of potential habitat patches in the surroundings of Mellery (>10 km radius) makes emigration unlikely as an explanation for the missing toads. On the other hand, we cannot discriminate between mortality and a possible skipping of breeding activity by some males in the population under study, though the latter behaviour is not common in the species. The estimate of male survival is, therefore, minimal.

Skeletochronology showed that a sample of 34 male toads were between 2 and 4 years old in 1999 (Fig. 2). No relationship was found between age and morphological variables (mass: Kendall's $\tau=0.125$, n=34, P=0.36; length: Kendall's $\tau=0.041$, n=34, P=0.76). Growth rate therefore varied between individuals.

Mean length of males did not vary significantly between the two seasons (mean length in 1999 = 58.2 mm, SE=0.7, n=62; mean length in 2000 = 58.8 mm, SE=0.5, n=84; $t_{(144)}=0.72$, P=0.47). However, mean mass of males was greater in 1999 (mean mass = 18.2 g, SE=0.6, n=62) than in 2000 (mean mass = 16.2 g, SE=0.6, n=93), and this difference was significant (Kruskal-Wallis χ^2 approximation = 4.89, df=1, P=0.03). Consequently, the condition of toads, as assessed by the mass-to-length ratio for the 55 to 60 mm size-class (in order to limit the effect of a possible non-linear relationship between mass and length) was significantly lower in 2000 when compared with 1999 (mean ratio in 1999 = 0.29 g/mm, SE=0.009, n=21; mean ratio in 2000 = 0.26 g/mm, SE=0.005, n=30; Kruskal-Wallis χ^2 approximation = 12.25, df=1, P< 0.001). In 2000, the mean mass



FIG 2. Age structure of the male breeding population of Bufo calamita at Mellery in 1999, expressed as the proportion of the total number of analysed males (n=34).

	Present in 1999	Mean	SE	n	Statistic (df) and value	Р
Mass (g)	Yes No	19.2 15.5	0.9 0.4	17 76	Kruskal-Wallis $\chi^2_{(1)}$ approximation=10.63	<0.01
Length (mm)	Yes No	63.0 57.8	0.9 0.5	17 67	t ₍₈₂₎ =4.48	<0.001

TABLE 1. Difference in mass and length (in 2000) for male Bufo calamita present or not present in the choruses of Mellery in 1999.

and length of toads that had been marked in 1999 were significantly greater than those of toads not observed in choruses in 1999 (Table 1).

REPRODUCTIVE ACTIVITY

Males. Breeding activity in the toad population lasted for 60 days in 1999 and 48 days in 2000. The sizes of the three choruses (one in 1999, two in 2000) fluctuated during the breeding season and reached a maximal value in each site around the mid-season (12 May in 1999, 13 May in 2000). As shown in Fig. 3, arrival dates of males in the choruses varied strongly between individuals: unmarked toads were caught each time we visited the two choruses. The effect of the morphological variables (mass and length) was tested against the arrival date. Table 2 summarizes the results of the regression analyses. Arrival date was related to length in 1999, and to length and mass in 2000. As shown in Table 2, longer males tended to join the chorus earlier in both years, whereas body mass tended to be lower among males joining the chorus later in 2000.

Chorus composition varied during both seasons: some males stayed in the chorus for the entire season, while others left after a few nights. On average, males stayed in the chorus for 33% of the season (SE =4, range 2-92%, n=62) in 1999 (permanent pond only) and for

TABLE 2. Relationship between body size (mass and length) and arrival date of male *Bufo calamita* in the chorus: summary of multiple regression analyses.

Year	Variable entered in the model (units)	Parameter estimate	SE	F for model	df _(model,error)	<i>t</i> -value	Р
1999	MASS & LENGTH			3.92	2,50		0.02
	Intercept	95.68	33.33			2.87	0.006
	Mass (g)	0.86	0.92			0.93	0.35
	Length (mm)	-1.58	0.82			1.92	0.006
2000	Mass & Length			16.81	2,81		<0.001
	Intercept	123.81	21.11			5.86	< 0.001
	Mass (g)	1.36	0.61			2.21	0.03
	Length (mm)	-2.22	0.49			4.44	<0.001

TABLE 3 Summary of multiple regression analyses for chorus attendance by Bufo calamita at Mellery. Three explanatory variables
(mass, length and arrival date) were included to predict the proportion of the total duration of the chorus for which each male was
present.

Year	Variable entered in the model (units)	Parameter estimate	SE	F for model	df _(model,error)	<i>t</i> -value	Р
1999	MASS, LENGTH & ARRIVAL DATE			9.89	3,49		<0.001
	Intercept	-1.56	0.64			-2.42	0.02
	Mass (g)	-0.05	0.02			-2.98	0.004
	Length (mm)	0.05	0.01			3.35	0.002
	Arrival date (days)	-0.01	0.00			-3.07	0.003
2000	Mass, Length & arrival date			38.87	3,80		<0.001
	Intercept	-0.28	0.49			-0.58	0.56
	Mass (g)	-0.03	0.01			-2.41	0.02
	Length (mm)	0.02	0.01			2.26	0.03
	Arrival date (days)	-0.02	0.00			-8.13	<0.001





FIG. 3. Arrival date and minimum residence time of male *Bufo calamita* at Mellery, at the Lake site in 1999, and at Lake and Pond sites in 2000. Each line represents one male, and day 0 corresponds to the beginning of male calls at Mellery each year. The arrows indicate the nights of censuses.

38% of the season in 2000 (SE=3, range 2-94%, n=92). We found no significant between-year difference in length of chorus attendance (Kruskal-Wallis χ^2 approximation = 2.03, df=1, P=0.15). We tested the effect of three variables (body mass, length and arrival date) on male chorus attendance. The arrival date was a significant determinant of chorus attendance in both years: toads that joined the chorus first showed a longer chorus attendance (Table 3). Chorus attendance was also related to the individual's length and body mass (Table 3).

Calling activity was assessed in 2000 only. Males that were observed at least three times in a chorus called in 53% of observations, on average (Fig. 4). Calling activity of males was related to length and body mass (Table 4), but neither to arrival date nor to length of chorus attendance. Longer and heavier males exhibited significantly greater calling activity than smaller males (Table 4). Toads present in the chorus in 1999 called for 69% (SE=6, n=11) of the time they spent in the choruses in 2000, whereas toads not encountered in 1999 called

FIG. 4. Calling activity of male *Bufo calamita* at Mellery in 2000. Calling activity, the proportion of observations of calling *vs* silent behaviour, was assessed for males observed at least three times in a chorus.

for only 48% (SE=6, n=32) of the time in 2000 (Table 4). The latter difference may have been due to the morphological attributes of the toads, rather than to their experience (Table 4), as the two groups differed in body size in 2000 (Table 1).

Females. In 1999, 22 females spawned between the 1st and the 48th nights and no clutches were found during the last 12 nights of the chorusing season. For those clutches that were counted, we found no significant relationship between laying date and clutch size (Kendall's τ =0.33, *P*=0.24, *n*=11). In 2000, 51 females spawned between the 6th and the 33rd nights in the permanent pond and between the 3rd and 45th nights in the ephemeral pond; calling activity of males lasted for 48 nights that year. We counted the eggs of 21 clutches and, unlike in 1999, found a significant tendency for clutch size to be smaller later in the season (Kendall's τ =0.40, *P*=0.01).

We were unable to relate clutch size to the body size of individual females. Nevertheless, we used published relationships between fecundity and length of females in

TABLE 4. Effects of morphological attributes, behaviour and previous history of male *Bufo calamita* (presence, arrival date and chorus attendance in 1999) on calling activity in 2000.

Tested variable	Statistic	τ	χ²	Р	n
Length	Kendall's correlation	0.34		<0.01	42
Mass	Kendall's correlation	0.31		< 0.01	43
Arrival date in 2000	Kendall's correlation	-0.09		0.45	43
Chorus attendance in 2000	Kendall's correlation	0.09		0.44	43
Arrival date in 1999	Kendall's correlation	-0.07		0.79	11
Chorus attendance in 1999	Kendall's correlation	0.04		0.87	11
Presence in 1999	Kruskal-Wallis test		4.55	0.03*	Present=11 Absent=32

TABLE 5. Natterjack toad clutch size recorded within the distribution of the species ¹This study; ²Beebee (1979); ³Banks & Beebee (1986); ⁴Banks & Beebee (1988); ³Tejedo (1992*b*); ⁶Tejedo (1992*c*); ⁷Kadel (1975).

Country	Range of clutch size
Belgium	700-3900 ¹
Britain	2700-7200 ^{2,3,4}
Germany	3000-7000 ²
Spain	3000-7000 ^{2,5,6}
Sweden	3200-4000 ²
Switzerland	36007

two populations in Britain (Banks & Beebee, 1986), one in Germany (Hemmer & Kadel, 1975) and one in Spain (Tejedo, 1992c) to investigate whether the relatively low fecundity we observed (Table 5) was due to the small size of the females. Predicted fecundities for females between 48 mm and 71 mm SVL (the extreme sizes at Mellery in 1999) were calculated from these four relationships. The relationship from the Spanish population predicted correctly the fecundity at Mellery (ranging from 920 to 2729 eggs per clutch in 1999), whereas the British and German relationships did not (Table 6).

TABLE 6. Expected clutch size for females ranging from 48 to 71 mm SVL, according to formulae linking clutch size to snout-tovent length (SVL): 'Banks & Beebee (1986); 'Hemmer & Kadel (1971); 'Tejedo (1992c).

Formulae	Expected clutch size (48-71 mm SVL toad)	Site - Country
$F = 99.2 \times SVL - 3204$	1558 - 3839	Cumbria – Britain ¹
F = 114.6 x SVL - 2110	3391 – 6027	Hampshire – Britain ¹
F = 158 x SVL - 4552	3032 - 6666	Germany ²
$F = 0.031 \text{ x SVL}^{2724}$	1177 – 3421	Sierra Morena – Spain ³

TABLE 7. Logistic regressions of reproductive success of males *Bufo calamita* on five potentially explanatory variables: mass, length, arrival date, chorus attendance, and calling activity.

	Parameter estimate	SE	Wald χ ²	<i>P</i> > χ²
Intercept 0	2.97	1.09	7.46	<0.01
Intercept 1	4.18	1 14	13.44	<0.001
Intercept 2	6.49	1.49	18.95	<0.001
Mass	-0.12	0.06	3.40	0.065
1.100	2000	0.000		01000
Intercept 0	8.00	3.34	5.75	0.016
Intercept 1	9.13	3.37	7.32	<0.01
Intercept 2	11.46	3.52	10.61	<0.01
Length	-0.12	0.05	4.48	0.034
Intercent ()	0.44	0.20	1 26	0.26
Intercept 0	-0.44	0.39	1.20	0.20
Intercept 1	0.94	0.43	4.05	0.03
Intercept 2	3.35	1.02	10.73	< 0.01
Arrival date	0.12	0.03	15.93	<0.001
Intercept 0	2.65	0.55	23.04	<0.001
Intercept 1	4.01	0.65	37.65	< 0.001
Intercept 2	6.39	1.15	30.61	< 0.001
Chorus attendand	ce -3.58	0.941	14.53	< 0.001
Intercent ()	0.47	0.62	0.60	0.43
Intercept 0	1.50	0.02	5.60	0.43
Intercept 1	2.60	0.07	J.02	0.02
Calling a stinit	2.0 7	1.14	10.40	< 0.01
Calling activity	0.09	1.00	0.01	0.93

REPRODUCTIVE SUCCESS OF MALES

As the number of spawning females was lower than the number of males in the choruses, we tried to identify morphological and behavioural features of successful males. Of the 98 males estimated to be present in 2000, we identified 24 in amplexus. Among the latter, eight reproduced at least twice and one three times. Five variables (body mass, length, arrival date, chorus attendance and calling activity) were used in separate logistic regressions with reproductive success as the dependent variable (summarized in Table 7). This procedure allowed us to detect effects of chorus attendance and arrival date and, to a lesser extent, the male toad's length (Table 7). Mating males were longer, joined the chorus earlier in the season, and stayed in the chorus for a long time.

DISCUSSION

The first result of our study was the very low clutch size of natterjacks at Mellery, compared with other populations (Table 5). In the natterjack, clutch size generally increases with body mass and length (Tejedo, 1992c), so the low fecundity we recorded at Mellery might have been due to the small size of the females. The females we caught were indeed as small as the males of the population (i.e. 48-71 mm in 1999). However, the comparison with other populations (Table 6) suggests that small size alone did not account for the small clutch size. This result is striking, as the ecology of Belgian natterjacks shares common features with those of British and German populations, while Spanish natterjacks differ strongly from northern conspecifics, as follows: (1) Spanish natterjacks are explosive breeders (their breeding season lasts only 2-3 weeks, compared to eight weeks in Belgium); (2) the density of their breeding populations is higher; (3) they are generally larger in size than British and German toads; and (4) their relative fecundity for comparable-sized individuals is known to be smaller (Tejedo, 1988, 1992c). As Spanish natterjacks are larger, clutch sizes as low as those at Mellery were not observed in natural Spanish populations (Tejedo, 1992b). Therefore, the low fecundity observed at Mellery cannot be entirely attributed to the youth of the females. Low fecundity could also be due to the poor condition of the females, resulting from unfavourable environmental conditions (for instance, high local density or low prey availability). We cannot at this time discriminate between the two hypotheses because the quality of the habitat and the density were not known precisely.

The minimum estimate of annual survival rate of 27% obtained in our population was very low when compared with values of 50-80% reported by Sinsch & Seidel (1995), Griffiths (1997) and Stephan *et al.* (2001). This estimated survival rate is, in fact, a between-year recapture rate. We cannot claim that all toads not recaptured in 2000 were indeed not alive at this time. The high capture probability we recorded dur-

ing MRR (we marked 95% of the estimated male population every year) excludes a low catchability of individuals at the breeding sites as an explanation for this small value. Some males may not have attended the chorus in 2000, and therefore may not have been available for capture during the MRR study, although in other studies it has been shown that male natterjacks take part in reproductive activity almost every year (Sinsch & Seidel, 1995). Another possible reason for a low recapture rate is dispersal of some individuals between years, but - given the lack of occupied potential natterjack breeding sites within a 10 km radius - this explanation seems unlikely. Moreover, adult natterjacks, particularly males, usually show high breeding site fidelity (Denton & Beebee, 1993a; Tejedo, 1992c). The hypothesis that the between-year recapture rate really reflected a low survival rate is supported by the low body condition we recorded for males. The body condition, estimated by the mass-to-length ratio for the 55-60 mm size-class $(0.26 - 0.29 \text{ g mm}^{-1})$, is at the lower end of the range of values for seven British populations, where this ratio (for the same size-class) ranged between 0.29 and 0.44 g mm⁻¹ (Denton & Beebee, 1993b). As in other species with indeterminate growth (Forsman, 1993; Civantos, Salvador & Veiga, 1999; Gotceitas et al., 1999; Morey & Reznick, 2001), the winter survival of a natterjack is likely to be dependent on its general condition and on its deposition of fat bodies. We could therefore suggest (according to Williams, 1966) that toads in poor condition have a low survival probability, and that the recapture rate we recorded truly reflects a low male survival rate at Mellery. The age structure observed for males in this study site reinforces this hypothesis. Despite the fact that only 52% of the male population was aged by skeletochronology, all sizeclasses were sampled: only the smallest and the largest we marked were not aged. Moreover, as calling males have been present at Mellery at least since 1995, we can exclude a very recent colonization of the site as an explanation of the youth of the toads.

One of the most central questions in evolutionary biology is the manner in which morphological and behavioural traits affect individual reproductive success. In our population, as in most other natterjack populations, the mean reproductive success of a male was less than one amplexus per year. Some individuals had no access to reproduction, whereas others fathered thousands of potential descendants. So, the question is: who were these reproducers and how did they succeed? As shown in Tables 2 and 3, whereas longer males joined the chorus early in the season and achieved longer chorus attendance than smaller individuals, greater male body mass was associated with late arrival and short chorus attendance. This apparently contradictory result could be interpreted in terms of "body shape" - for a given length, toads with low body mass (i.e. slim toads) show an early arrival date and a long chorus attendance, while big males came later and left the chorus quickly. This difference in reproductive effort could be

due to the general poor condition of the toads at Mellery. As their probability of survival is low, and the possibility of a future reproduction is unlikely, some toads - and particularly the slimmest - might prefer to invest more in reproduction. In the natteriack, as in other anurans, male mating success was usually positively related to the duration of chorus attendance (Halliday & Verrell, 1986; Denton & Beebee, 1993a; Sinsch & Seidel, 1995). Moreover, the calling behaviour was decisive in the reproductive success of male natterjacks: a calling male obtained at least twice as many matings as a silent (or satellite) male (Arak, 1988; Tejedo, 1992a). Chorus attendance and calling, the keys to reproduction, are expensive behaviours (Taigen & Pough, 1985; Tejedo, 1992a; Murphy, 1994). We might expect that toads calling and staying in the chorus for a long time do this in order to mate. However, the pattern of reproductive success we observed at Mellery is unusual reproductive success was independent of calling activity, and depended more on the male's arrival date and chorus attendance. This could be explained by the irregular arrival date of the females: for both years, twice as many females came to reproduce in the first half of the season as in the second. Therefore, males joining the chorus after the mid-season had less than half the breeding opportunities compared to those males involved at the beginning of breeding activity. The absence of mating gain for calling males could be understood in the light of the satellite tactic. Arak (1988) showed that, in high-density choruses, the reproductive success of calling males was reduced by the presence of satellites in their surroundings. While a small male adopting the satellite tactic increases his probability of mating, calling males are really parasitized by the presence of satellite(s), and therefore see their reproductive success reduced. Aquatic habitat area was small and the satellite tactic was largely used at Mellery, where toads called for a mean of 53% of our records, and never more than 12 callers were recorded in the concrete pond despite the presence of 30 males on some nights. We therefore suggest that satellites gained as many matings as callers and in this way decreased the reproductive success of callers. This may explain why we noticed no difference in reproductive success between caller and silent males (Table 7).

All the demographic features we observed correspond to consequences of excessive density and indicate that the population is under stress. Effective conservation measures therefore imply enlargement of existing suitable terrestrial habitats and management of ponds in the vicinity.

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