Modelling the extinction risk of isolated populations of natterjack toad *Bufo calamita*

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Many local populations of the natterjack toad *Bufo calamita* in Germany are endangered. Due to the fragmentation and destruction of natural habitats by man, toads have often been forced to switch to secondary habitats. The permanent existence of these habitats is uncertain. Habitat and area requirements have been investigated in various parts of Germany in recent years. Our study uses field observations from sites in Halle (Saxony-Anhalt) and List (Schleswig-Holstein) as a basis for analyses of the population dynamics under different environmental conditions. Deterministic trends of these populations are calculated with the help of a Leslie matrix consisting of average parameters for mortality and reproduction. For a more thorough analysis we use a stochastic simulation model in order to assess survival probabilities of local toad populations. This model also takes into account environmental fluctuations affecting mortality and reproduction. Using scenarios from different locations, a sensitivity analysis of the parameters indicates which management options are the most promising to preserve a population. Our results indicate that the mortality rates of juveniles and the availability of spawning ground have the greatest influence on a population's survival. Consequently, habitat management should focus on these aspects. In addition, we investigate the risk of extinction for different reproductive strategies. Natterjack toad populations observed in the field actually follow a strategy with three breeding periods. We find that this strategy supports the survival of the population better than strategies with less periods, which are more likely to result in a complete breeding failure during one season.

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Declines in amphibian populations have been reported from many parts of the world during the past decades (Barinaga 1990, Blaustein and Wake 1990). There is little evidence for a single global cause, but many possible local reasons for these declines like habitat destruction, land use changes, introduction of exotic species, pesticide pollution, pathogens, acid rain or predation by humans. Global factors, such as increased ultraviolet radiation exposures or climate changes (Sherman and Morton 1993) may have contributed to the actual situation as well as natural stochastic effects (Blaustein and Wake 1990).

Within central Europe the natterjack toad inhabits alluvial pioneer sites which have been severely changed by river corrections and other anthropogenous influences. As natterjacks can dodge onto secondary sites, natural habitats are nowadays very uncommon (Günther and Meyer 1996). Unlike the dynamics of a natural riverine area, the persistence and quality of an anthropogenous secondary

habitat are not guaranteed (Grosse et al. 1996). The abandonment and change of designated land uses, succession and recultivation are factors serious endangering these pioneer communities. To some extent, natterjack toads represent these communities, which makes them an interesting object of study. We investigated their habitat and spatial requirements. Data concerning the biology and ecology of the species have been collected in field investigations since 1991. We studied three populations of different sizes and different habitat types (Meyer and Grosse 1997, Meyer et al. 1997). The most intensive study was done for the population in the nature reserve "Brandberge" near Halle (Meyer 1993). Some results of this study are summarized in Table 1.

Data from these investigations were used as a basis for the parameters of a computer simulation model and a theoretical model. Our goal is to assess risk factors threatening toad populations in the cultural landscape. Models are a helpful instrument to assess the actual status of a population and to support management decisions. Theoretical examples of stochastic modeling providing a basis for practical case-studies can, for example, be found in Stephan and Wissel (1994) and Wissel et al. (1994). Two interesting case studies, with intentions quite similar to those presented here, are described in Märtens et al. (1996) and Wiegand et al. (1998). A model for predicting the persistence of amphibian populations has been presented by Halley et al. (1996). They use a metapopulation approach which approximates the dynamics of local populations.

The two models in this paper describe local populations, as there is no evidence for a metapopulation structure from our field observations. Firstly, a theoretical model describes the mean changes in the size of a population by evaluating the Leslie matrix. We determine the net growth rate which can be used as an indicator whether a population is prone to extinction or not. If the growth rate is only slightly larger than one, stochastic effects may drive a deterministically surviving population towards extinction. Therefore, we use a simulation model in order to include stochasticity. Simulations track the fate of each single individual. As every simulation depends on chance events, we evaluate 1600 simulations for each parameter set in order to obtain reliable results.

We assess the survival probability and mean survival time of natterjack populations under different circumstances. Three main scenarios are tested, representing populations investigated in the field. In a second set of scenarios, we vary the number of breeding periods in order to study different reproductive strategies. An overview of the model, its limitations, its parameters and rules, and a detailed description of the scenarios are given in the following section. The parameters of the theoretical model are derived from those in the more complex situation model which is described first.

Model overview

Limitations

The exact carrying capacities of the natterjack habitats investigated here are not known. Within source populations, the carrying capacity will sooner or later be exceeded and the surplus in juveniles can be absorbed by sink populations (rescue effect; Sinsch 1992, 1997). When speaking of carrying capacities in our model, we always refer to numbers of adult females (see paragraph about sex ratios in the section below).

The maximum age of natterjack toads is set at seven years. All the animals reaching this age are automatically killed in the next winter. In practice, the adult survival rates given in the model would allow only a very small proportion ($\approx$ 5%) of the population to reach a higher age. Therefore, cut-off at seven years does not substantially change the dynamics of the population.

The population consists of strongly connected subpopulations which can be regarded as one local population. We assume that the population is isolated within a wider range. If neighbouring populations interact, our model will work properly if the immigration rates equal the emigration rates. From 1992–1999 we could not find any exchange of individuals between the Brandberge study site and a neighbouring population in Heide/Nord in Halle.

In our model, females can reproduce once per year at most. This corresponds with field observations from central Europe where double clutching has never been ob-

Table 1. Field data overview from 1992–1999 for the Brandberge study site. Breeding success shows the numbers of spawn strings where metamorphs emerged from versus the total number of strings. The survival rate given is a low estimate – averaged over all age classes – assuming all survivors of the preceding year being captured.

Year	1992	1993	1994	1995	1996	1997	1998	1999
Breeding success	4/10	5/9	1/9	3/19	4/16	3/9	4/9	2/9
Captured individuals	28	57	54	44	29	26	25	29
New individuals		39	27	23	12	15	11	11
Survival rate		0.64	0.47	0.39	0.39	0.38	0.54	0.72

served (Sinsch 1997). This rule does not hold for natter-jacks at the edge of their geographic range, e.g. in southern England (Denton and Beebee 1993) and Sweden (Silverin and Andrén 1992).

The aquatic life stage of natterjack larvae is not explicitly considered. Similarly to Halley et al. (1996), we assume a density-dependent regulation at the larval stage. The regulation leads to an average number of offspring per female surviving until winter which is used as a model parameter. Beebee et al. (1996) observed density to be primarily regulated at the average rate of metamorphic success, which supports this assumption. Furthermore, we assume mortality to depend on environmental conditions occurring in winter. As summer mortality is lower, and more or less constant over the years, it can be subsumed in winter mortality.

Understanding the dynamics of natterjack toad populations requires long-term field studies over wider areas. However, these two criteria are not met in actual scientific practice. Using different plausible scenarios for data at the individual level, a modeling approach can help to expand our knowledge at the level of population dynamics.

The annual cycle of the simulation model – standard parameters

The simulation model works with annual time-steps. The modelled processes, which make up a complete time-step and thus form an annual cycle, are shown in Fig. 1. Each cycle starts with an update of the actual population size.

In the next stage, the environmental conditions in summer – important for reproduction – are chosen by a random generator. Our standard parameter-set assumes prob-

abilities of 0.2, 0.6, 0.1 and 0.1 for the occurrence of good, medium, bad and very bad conditions respectively. These probabilities correspond to the number of successful breeding periods – a maximum of three successful breeding periods is assumed in our basic scenario. Thus three successful breeding periods constitute good conditons, the case of no successful breeding period refers to very bad conditions. A more detailed explanation is given in the next section, the data mentioned can also be found in Table 3.

Next, the number of offspring surviving until winter is determined. According to the actual environmental conditions, every adult female is marked as breeding or non-breeding. Under good weather conditions all females breed – but if, for instance, the actual weather conditions are bad (only one successful breeding period), there is only a 33% chance for a female to become a breeder. For each breeding female, the number of surviving offspring is drawn from a random distribution which is also given in Table 3. We estimate this distribution as being in accordance with our observations, but we cannot provide "hard" data. The mean of the distribution is eight and it follows the shape of a normal distribution with a standard deviation of two. This procedure adds juvenile individuals to the adult population. As adult summer mortality is negligible, this stage of the model ends up with the population consisting of juveniles (age class 0), subadults (age class 1) and adults (age classes 2–7) before winter sets in.

Modelling winter survival completes the annual cycle. Again, different environmental conditions come into play. In our basic scenario, the stages good, medium, bad, very bad occur with probabilities of 0.2, 0.6, 0.1 and 0.1. Analogous to the processes mentioned above, a random generator determines the actual environmental condition in winter. Survival rates depending on this condition and on the age of an individual are then applied to each individual, i.e. it is randomly determined whether the individual survives this stage or not. After this procedure the population size is updated and the next cycle starts.
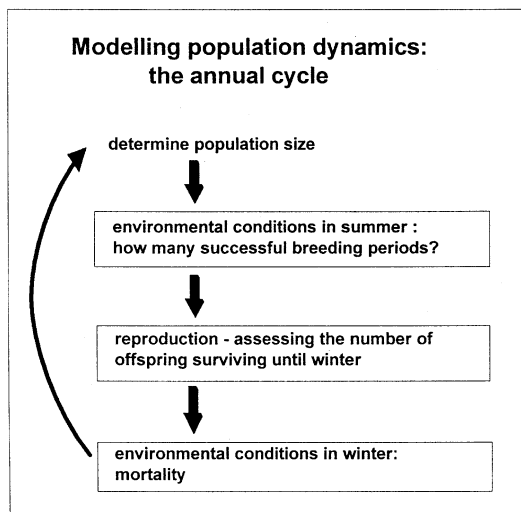
Model parameters in different scenarios

In this section we describe the parameters choice for different scenarios. Parameters are derived from own field observations (see Table 1) and estimations combined with data from the literature. Table 2 provides an overview of the different (sub-) scenarios with definitions of codes which are used when referring to a scenario in the text. Scenarios have two letter-codes where the first letter describes the type of the scenario (e.g. B = basic, E^+ = optimal environment) and the second letter stands for the location (S = small pool, B = Brandberge, L = List). An overview of all parameter values is presented in Table 3.

As mentioned above, our model assumes a maximum age of seven years for each animal. Reproduction starts at

Fig. 1. Flow chart of the model simulating natterjack toad population dynamics.

Table 2. Scenario overview for the stochastic simulation model. Different environmental conditions and different survival rates were investigated for all three basic scenarios, variations in the number of breeding periods were limited to the Brandberge scenario.

	List	Brandberge	Small pool
Basic scenario	BL	BB	BS
Optimal environment	E⁺L	E⁺B	E⁺S
Pessimal environment	E⁻L	E⁻B	E⁻S
High survival rates	S⁺L	S⁺B	S⁺S
Low survival rates	S⁻L	S⁻B	S⁻S
Two breeding periods	–	2B	–
One breeding period	–	1B	–

the age of two years. These parameters are valid for all scenarios. In our basic scenarios, there are three breeding periods within one season. Each of these periods is used by approximately one third of breeders. Breeding failure is possible for any breeding period as natterjack toads lay their eggs into shallow ponds which may dry out within a few days. As it is unlikely that ponds will dry out in every period, at least part of the population should reproduce successfully. A strategy involving, say, only one breeding period would substantially enhance the risk of complete breeding failure within the season. On the other hand, a single breeding period offers a better chance for a large number of offspring if the good weather conditions prevail throughout. Good weather conditions over three breeding periods are less likely.

For our investigation concerning the influence of different reproductive strategies, we choose three scenarios with different numbers of breeding periods (see Table 2). The basic (realistic) scenario BB works with three periods, the others with two (2B) and one (1B), respectively. Adult females are divided into equally-sized cohorts. Each of these cohorts makes use of one breeding period. BB assumes 20% probability of three successful breeding periods (good years – all adult females breed successfully), 60% of two successful breeding periods (medium years – two thirds of adult females breed successfully) and 10% each of one (bad years – only one third breeds successfully) and no (very bad years – no breeding success at all) successful breeding period. These data are estimations based on field observations at the Brandberge study site from 1992–1999. They provide an average breeding success of 63%. An equivalent scenario with one breeding period (1B) can thus be constructed by assuming a 63% probability of success (good years – all females breed successfully) and 37% of failure (bad years – complete breeding failure) in this single breeding period. We also investigate an intermediate scenario 2B assuming a maximum of two breeding periods: 39% probability of two successful periods (good years – all adult females breed successfully), 48% of one successful period (medium years – half the adult females breed successfully) and 13% (bad years) of complete failure. Again, this scenario leads to an average breeding success of 63%. Our 63% assumption is in accordance with Denton

and Beebee (1993) who found 44%–64% of breeding females in a five-year study of a female-biased natterjack population at Woolmer, U.K.

We assume a sex ratio of 1.3 males per female for newborns. This corresponds to the sex ratio found at the sites in Halle. Field investigations concerning this point do not present a consistent picture. Data in the literature vary from 0.84:1 to 11.2:1 (Günther and Meyer 1996). The high surplus of males found in some experiments is probably caused by methodological difficulties. An exceptionally high surplus of females of ca 3:1 was found in a British population at Woolmer, perhaps a consequence of selective predation by the snake *Natrix natrix* (Denton and Beebee 1993, Banks et al. 1993). However, under the usual circumstances of male surplus, the sex ratio does not have a significant effect on the number of offspring if the number of females is given. In order to avoid any difficulties, we thus refer to the number of reproductive females as "carrying capacities" in the analyses of our model simulations. Males are still present in our simulations though – and the population will go extinct if no male is left. The model of Halley et al. (1996) completely focuses on the female breeding population, implicitly assuming that the number of males is always higher than the number of females.

Annual survival rates of toads depend on age and environmental conditions. As for reproduction in summer, we distinguish between four types of winter environmental conditions that determine the survival of individuals. We estimate that these different conditions (good, medium, bad, very bad) occur with probabilities of 0.2, 0.6, 0.1, 0.1.

For our analysis of the influence of differences in survival rates, we use three basic scenarios developed from our field observations in Germany, in the areas of Halle, Saxony-Anhalt (no. 1, no. 2) and List, Schleswig-Holstein (no. 3): 1) "Small pool" (BS) with low winter survival probabilities, particularly for juveniles and sub-adults. Winter survival for juveniles (sub-adults) is between 0.2 and 0.05 (0.4 and 0.1), depending on environmental conditions. 2) "Brandberge", (BB) describing a medium-sized population, where winter survival rates of juveniles (sub-adults) range from 0.4 to 0.1 (0.6 to 0.1). 3) "List" (BL) – a large viable population with a range from 0.4 to 0.1 (0.7 to 0.1).

The survival rates for adults are more or less the same

Table 3. Parameter overview for the stochastic simulation model.
Maximum age: 7 yr. Age of maturity: 2 yr

Probabilities for environmental conditions influencing reproduction and number of breeding periods

No. of breeding periods		3				2			1	
No. of successful periods	3	2	1	0		2	1	0	1	0
Probability	0.60	0.20	0.10	0.10		0.39	0.48	0.13	0.63	0.37

Probabilities for number of offspring per successfully breeding female surviving until winter

2	3	4	5	6	7	8	9	10	11	12	13	14
0.002	0.009	0.027	0.065	0.121	0.176	0.200	0.176	0.121	0.065	0.027	0.009	0.002

Sex ratio of newborns m/f : 1.3

Probabilities for environmental conditions influencing survival rates

	good	medium	bad	very bad
Optimistic sub-scenarios	0.30	0.60	0.05	0.05
Basic scenarios	0.20	0.60	0.10	0.10
Pessimistic sub-scenarios	0.20	0.50	0.15	0.15

Probabilities for annual age-dependent survival rates for different sites and environmental conditions, basic scenario

site	List				Brandberge				Small pool			
conditions	good	med.	bad	v. bad	good	med.	bad	v. bad	good	med.	bad	v. bad
age 1	0.40	0.40	0.30	0.10	0.40	0.40	0.30	0.10	0.20	0.10	0.10	0.05
age 2	0.70	0.65	0.40	0.10	0.60	0.45	0.30	0.10	0.40	0.20	0.20	0.10
age 3	0.70	0.70	0.50	0.30	0.70	0.60	0.50	0.30	0.70	0.60	0.50	0.30
age 4	0.90	0.85	0.70	0.50	0.90	0.85	0.60	0.50	0.90	0.85	0.60	0.50
age > 4	0.90	0.85	0.85	0.85	0.90	0.85	0.85	0.85	0.90	0.85	0.80	0.70

for all three scenarios. Significant differences are assumed to occur only under bad and very bad environmental conditions, with the BS scenario having lower survival rates than the other two. The "standard" adult survival rate (medium weather, scenarios BL, BB and BS) of 0.85 corresponds to the survival rate of adult females in the Woolmer population (Banks et al. 1993). Halley et al. (1996) assume a survival probability of 90% for mature animals of the common toad *Bufo bufo* in their model. The estimates of survival rates given in Table 1 are lower as they include juveniles and sub-adults. Apart from that, the estimates assume all suvivors of the preceding year being captured which is rather unlikely.

Furthermore, we vary the parameters within these basic scenarios in order to compare the influence of changes in environmental conditions and survival rates. We investigate four additional series of sub-scenarios, two of them with better and two with worse average survival rates than the basic scenarios. Better average conditions can be ob-

tained in two ways: 1) Better average environmental conditions in winter (E^+) – we change the probabilities (good, medium, bad, very bad) to 0.3, 0.5, 0.1, 0.1. These sub-scenarios are denoted as E^+S, E^+B and E^+L. 2) Direct increase in the survival rates (S^+) – we increase them such that the net growth rate of the model population equals the rate in the first sub-scenario. This is done by the help of the theoretical model discussed below. The notations of the subscenarios are S^+S, S^+B and S^+L. 3) Worse conditions are studied analogously. The probabilities for environmental conditions are changed to 0.2, 0.5, 0.15, 0.15 in a third series of sub-scenarios (E^-); a fourth series with the same net growth rate directly uses lower survival rates (S^-). Thus we receive six further sub-scenarios, denoted as E^-S, E^-B, E^-L and S^-S, S^-B, S^-L.

As Table 3 is already rather large, we did not show the explicit values of survival rates for the optimistic and the pessimistic sub-scenarios S^+ and S^-. They are respectively ca 10% above and below the rates for the basic scenarios and B.

For all scenarios we investigated carrying capacities K from 20 to 100 adult females. This range is chosen as it is realistic for the population at the Brandberge study site (see Table 1).

Theoretical model

The model presented above looks rather complex and requires many computer simulations in order to obtain reliable results. It might be argued that a purely theoretical model is sufficient to handle the extinction problem. For instance, stochasticity will be relatively unimportant if a population already declines deterministically and is thus doomed to extinction. Therefore, we present a theoretical alternative in this section, represented by a Leslie matrix. We use the same parameters as in the simulation approach if it is possible – wherever the construction of the theoretical model does not allow this, we use adjusted parameters describing the mean behaviour of the stochastic simulation model.

As we assumed a maximum age of seven years for natterjacks, our population can be described by a vector $(N_0, N_1, N_2, N_3 ... N_7)$. The deterministic growth (or decline) of the population can be calculated from the Leslie matrix which consists of birth and survival rates. Birth rates have to be adjusted to a "mean individual", taking into account that only females give birth. Furthermore, both birth and survival rates are weighted averages over the environmental conditions, which are used in the simulation model. The Leslie matrix looks as follows

$$
\begin{bmatrix}
0 & 0 & b & b & b & b & b & b \\
s_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & s_1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & s_2 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & s_3 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & s_4 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & s_5 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & s_6 & 0
\end{bmatrix}
$$

$s_0, s_1, ... s_6$ are the mean survival rates of individuals in the corresponding age class. Their values are given in Table 3.

b is the number of offspring produced by a mean individual. It depends on the sex ratio q and the number of offspring b_i under different environmental conditions which occur with probabilities p_i:

$$b = \frac{1}{q} \sum_{i=1}^{4} p_i \cdot b_i$$

With p_i, q and b_i given in Table 4 we obtain b = 2.20.

The theoretical model can compare scenarios with different mean mortality and birth rates. The leading eigenvalue λ of the Leslie matrix gives the net growth rate of the population. A value below unity indicates a declining population, which often will go extinct rather quickly, whereas a value above unity indicates a deterministically growing population. How stochasticity affects this average growth can be seen by analyzing the simulation model.

As the parameters of the Leslie matrix are mean values derived from the simulation model, the theoretical model cannot analyse differences between reproductive strategies which originate in different levels of stochasticity. On average, the sub-scenarios 1B and 2B are equivalent to the basic scenario BB and cannot be distinguished from each other. Of course, the Leslie matrix also does not distinguish the sub-scenarios E^+ from S^+ as well as E^- from S^-. As mentioned above, S^+ and S^- are constructed such that their net growth rates equal the rates of E^+ and E^-, respectively. In order to achieve this goal, we vary the survival rates of the basic scenarios until the eigenvalues of the Leslie matrices (i.e. the net growth rates) are adjusted to those of either the E^+ or the E^- scenario.

Results

Theoretical model

The "small pool" scenario does not lead to a viable toad population in the long-term. The net growth rate for the standard scenario is $\lambda = 0.72$, which is far below unity. The sub-scenarios do not lead to substantial changes. Under the optimistic scenarios E^+ and S^+ this rate goes up to 0.76 whereas the pessimistic scenarios lead to $\lambda = 0.71$. With such an annual decline, 100 adult females would be reduced to less than one female in 15 yr (basic scenario), 17 yr (optimistic) or 14 yr (pessimistic).

The "Brandberge" scenario shows a population which is deterministically almost stable. For the basic scenario we find $\lambda = 1.01$, the value for the optimistic scenario is $\lambda = 1.05$ and for the pessimistic scenario $\lambda = 0.98$. Starting with 100 adult females, the population would be reduced to less than one individual in ca 230 yr using the pessimistic scenario. The other scenarios do not lead to deterministic extinction.

The "List" basic scenario shows a deterministically growing population which is associated with $\lambda = 1.09$. For the optimistic case we obtain $\lambda = 1.14$ and for the pessimistic case $\lambda = 1.05$. For all scenarios, an initial small population will grow until it reaches carrying capacity and will never die out.

Simulation model

For all scenarios investigated, the mean lifetimes of toad populations were calculated using carrying capacities K from 20 to 100 adult females. For the BS scenario we find that even the most optimistic case of K = 100 (rather unre-

Table 4. Parameter overview for the Leslie matrix model. Mean rates are calculated as weighted averages over the environmental conditions (see text).

Mean survival rates for different scenarios and sites

Site	List			Brandberge			Small pool		
Scenario	opt.	basic	pess.	opt.	basic	pess.	opt.	basic	pess.
s_0	0.380	0.360	0.340	0.380	0.360	0.340	0.127	0.115	0.112
s_1	0.625	0.580	0.540	0.470	0.430	0.405	0.255	0.230	0.225
s_2	0.670	0.640	0.610	0.610	0.580	0.560	0.610	0.580	0.560
s_3	0.840	0.810	0.785	0.835	0.800	0.770	0.835	0.800	0.770
s_4, s_5, s_6	0.865	0.860	0.860	0.865	0.860	0.860	0.855	0.840	0.830

Reproductive parameters

No. of successful breeding periods	3	2	1	0
Probability p_i	0.60	0.20	0.10	0.10
Number of offspring b_i	8	5.33	2.67	0

Sex ratio q = 1.3

Mean number of offspring b = 2.20

alistic for a small pool) results in a mean population lifetime of only 15 yr. After 20 yr, the survival probability of the population is 96% and after 30 yr there is no significant difference from 100% anymore. The mean lifetime results are in good accordance with the findings from the theoretical model. In this case, extinction is dominated by deterministic processes which are well described by a Leslie matrix. The mean lifetimes for various carrying capacities are plotted in Fig. 2, together with the other basic scenarios BB and BL.

The Brandberge scenario BB has a net growth rate of λ = 1.01, i.e. the population ought to be deterministically stable. As stochastic factors come into play, the extinction of the population is possible, especially at low carrying capacities (see Fig. 2). For a capacity of K = 100, we find a mean lifetime of T = 131 yr and an extinction probability of 43% after 100 yr; a small population with K = 20 has a mean lifetime of 61 yr and will die out with 86% probability within the next 100 yr. In the long run, a population of this type is not viable even though the survival probabilities of single individuals are high enough to obtain a deterministically stable population.

Naturally, of the basic scenarios investigated here, the "List" scenario BL providing the highest individual survival rates for juveniles and sub-adults shows the lowest probabilities of extinction and the highest mean lifetimes. From the theoretical model we have found that the net growth rate of the population is λ = 1.09, i.e. the population has the potential of a 9% increase per year on average. However, this potential is limited by the carrying capacity and by stochastic events that may drive the population to extinc-

tion. At low carrying capacities of, say, K = 20, these stochastic forces are rather strong. Although the mean lifetime is 173 yr (Fig. 2) and thus longer than in the BB scenario where K = 100, the extinction probability after 100 yr is 42%, almost equal to the BB scenario discussed above. Higher carrying capacities – as they are likely for the List site – have a much stronger effect now: as extinction times were approximately doubled when going from K = 20 to 100 in the BB scenario, we now find T = 1010 yr for K = 100 (Fig. 2), which is about six times higher than for K = 20. The extinction probability after 100 yr is reduced to 8%. We see that extinction is still possible within this time
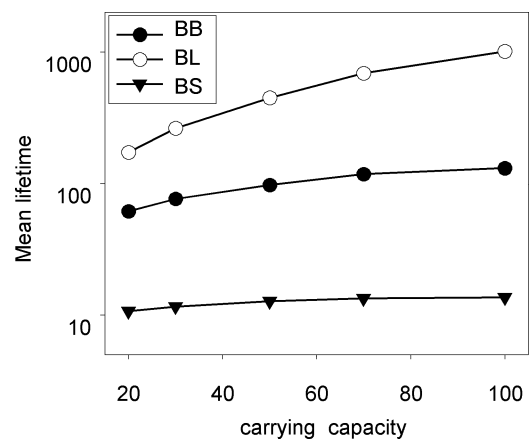

Fig. 2. Mean lifetime vs carrying capacity (adult females) for natterjack toad populations in three different locations, namely "List" (BL), "Brandberge" (BB) and "Small pool" (BS).

frame – not even this scenario can give an absolute guarantee for the survival of the natterjack toad population. Nevertheless, the risk has substantially diminished compared to the scenarios discussed earlier.

Figure 3 presents an overview of the "Brandberge" scenarios. As mentioned above, we varied the average environmental conditions and the individual survival rates in winter to obtain two optimistic (E^+B, S^+B) and two pessimistic (E^-B, S^-B) sub-scenarios. Figure 3 shows the mean lifetime of the population plotted against the carrying capacity of adult females for these scenarios. In the following text, we refer to the optimistic carrying capacity of 100 adult females unless otherwise stated.

As expected from the theoretical model ($\lambda = 0.98 < 1$), we find that the pessimistic scenarios cannot sustain a viable population in the long term. Even relatively large populations with a carrying capacity of 100 adult females have mean lifetimes below 60 yr. The probability of being extinct after 50 yr are 45% (S^-B) and 54% (E^-B). After 100 yr, in both scenarios, the population has a likelihood of > 90% of being extinct.

The basic scenario has already been discussed above. Although the net growth rate is slightly larger than one, the population is not safe in the long-term. It is no surprise that the optimistic scenarios (E^+B, S^+B) show the lowest extinction risks and the highest mean lifetimes. However, as we can guess from the discussion of the BL scenario above ($\lambda = 1.09$), a net growth rate of $\lambda = 1.05$ does not guarantee the long-term survival of the population. Although the mean lifetime for the S^+B scenario is 350 yr, there is still an 18% chance of extinction within the next 100 yr. E^+B gives the best results: the mean lifetime is 987

yr and the probability of extinction within 100 yr is reduced to 6.6%. This is even less than in the BL scenario (which has a higher net growth rate) and spotlights the high importance of good environmental conditions.

Our analysis of different reproductive strategies is based on the "Brandberge" scenario BB. General trends in the results remain unchanged with the List scenario BL. The small pool scenario is not appropriate for any further investigation as it dooms any population to extinction within a few years. We find that the risk-avoiding strategy with three breeding periods leads to the lowest extinction risk. Figure 4 shows the mean lifetime of a natterjack population vs. the carrying capacity of adult females for the three strategies described in the section above. The results for K = 100 are as follows: The mean lifetime of 131 yr in the basic scenario is reduced to 91 yr if we allow two breeding periods, while a further reduction to 65 yr follows if only one breeding period is possible. Correspondingly, the probability of extinction after 100 yr rises from 43% (three periods) to 68% (two periods) and 84% (one period).

Discussion

The extinction probabilities vary greatly between the different locations. Although this was more or less expected, there are some interesting aspects: firstly, the parameter values we chose for different locations in the three scenarios mainly vary in survival rates for juveniles and sub-adults. As we have learned from these scenarios, high survival chances for single individuals, particularly juveniles and sub-adults, have a strong positive influence on the sur-
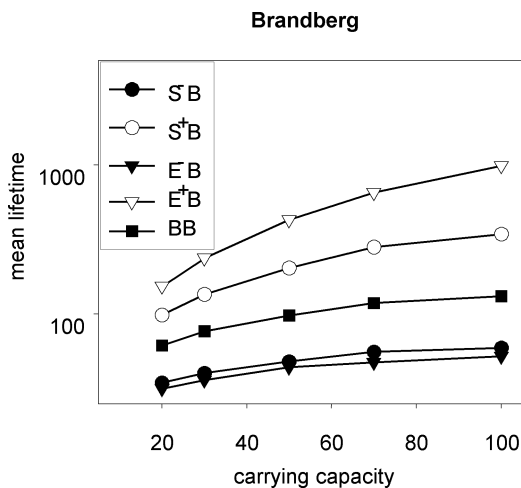

Fig. 3. Mean lifetime vs carrying capacity (adult females) for various sub-scenarios of the natterjack toad population model. Sub-scenarios are derived from the basic "Brandberge" scenario BB. S^-B stands for pessimal survival rates, E^-B for a pessimal environment, S^+B for optimal survival rates and E^+B for an optimal environment.
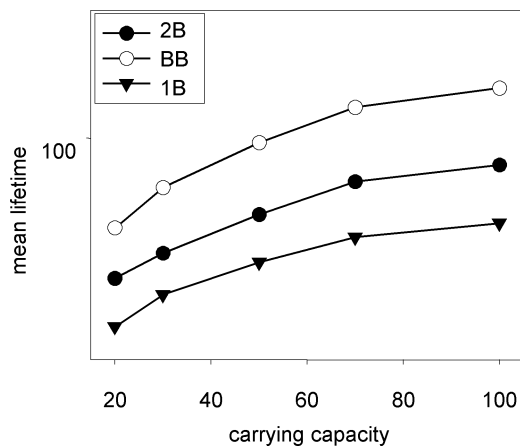

Fig. 4. Mean lifetime vs carrying capacity (adult females) for natterjack toad populations with different reproductive strategies. The scenario with three breeding periods corresponds to the BB scenario. 2B has two and 1B has one breeding period.

vival of the whole population. Secondly, for a fixed location, improving the average environmental conditions has the most beneficial effects on the population's survival. Providing better environmental conditions seems to be the most effective way of increasing the average survival of individuals and consequently increasing the population's chance of survival. Thirdly, the influence of carrying capacity – which is related to habitat size – is relatively weak in deterministically declining or stagnant populations. Populations with a clearly positive net growth rate show a much stronger dependence. Long-term studies and knowledge about habitat requirements in connection with the model results presented here support the following recommendations for successful management and conservation: 1) Natural primary habitats and their dynamics should be conserved and restored. 2) Secondary habitats should play an additional role, but alone they are unable to ensure long-term survival of natterjack toad populations.

Our results concerning reproductive strategies help elucidate this behaviour. Evolution has evidently favoured this division into different breeding cohorts. Results from Sinsch (1997) support the hypothesis that the integration of first breeders to a specific breeding cohort is genetically controlled in central European natterjacks. The results we obtain indicate that this individual trait seems to be beneficial for the population as a whole. Natural environmental fluctuations are effectively reduced by choosing different breeding periods.

The main problem for a pioneer species like the natterjack toad is that it is beset by unstable succession stages. We suggest that active habitat management should preserve the desired successional stages and thus avoid further habitat area losses. Such kind of habitat management has been performed for about two decades in southern Britain at Woolmer. Banks et al. (1993) state that this population has developed rather successfully, but "it seems unlikely that without intervention the population would be at its current size; indeed, it seems more likely to have become extinct". After Beebee et al. (1996) management of small isolated toad populations should focus on maintaining adult numbers at the highest practicable densities in order to retain regular reproductive success. Less attention should be necessarry for other parts of the lifecycle, such as juvenile and adult mortality. The first statement fits in with our results shown in Fig. 3 and Fig. 4 as "regular" reproductive success is equivalent to improving environmental conditions (scenario E$^+$B) or at least reducing environmental fluctuations – a goal which natterjacks achieve by dividing up the reproductive effort into different breeding periods. However, we cannot fully agree to the second part of their statement. The model results indicate that maintaining high survival rates for juveniles also has a great effect on the population's survival as higher juvenile survival rates will generally result in a higher number of reproductive adults. Whether management efforts in this direction are effective, will depend on what quantitative improvements of survival rates are possible at a given site.

Up to our knowledge, a simulation modelling approach for local toad populations has not been published yet. This is probably due to the lack of reliable data on reproduction and survival. The clumped distribution of toads in the field leads to great difficulties in analyzing mark-recapture data. Furthermore, even with a ten-year long-term study, there remains a lot of uncertainty about quantifying environmental variations. Of course, our data-set contains many uncertainties, but the construction of different scenarios and a careful interpretation of the results seem to be a good way to deal with this problem.

We regard our approach as a complement of the work of Halley et al. (1996) who focused on spatial aspects of amphibian populations, e.g. the dependence of local extinction probabilities upon the distance to a source population. They use a stochastic difference equation in order to approximate local population dynamics. As our study is confined to a local population, a simulation approach without these fairly complex mathematics seems superior. For instance, approximations like focusing on the female breeding population are not necessary. On the other hand, the effort of performing thousands of stochastic simulations may be too high if the status of the population is obvious. Therefore, we have combined our simulation approach with a deterministic Leslie matrix model. The deterministic model shows that there is no long-term survival chance for the small pool scenario. For the other scenarios, the theoretical model is not sufficient to deal with extinction problems and a more thorough analysis by the help of simulations is needed.

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