Structure and dynamic of a natterjack toad metapopulation (Bufo calamita)

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Summary. The migratory and reproductive behaviour of Bufo calamita was studied at four neighbouring breeding sites in the northern Rhineland, Germany, from 1986 to 1991. Radio telemetry and marking systems based on toe-clipping and on microchips were used to follow the tracks of toads and for individual recognition. Emphasis lay on estimates of (1) the exchange of reproductive individuals between neighbouring sites, and (2) the reproductive success at each site. Allozyme electrophoresis served to assess the genetic diversity of local populations. More than 90% of all reproductive males showed a lifelong fidelity to the site of first breeding, whereas females did not prefer certain breeding sites. Due to the female-biased exchange of individuals among neighbouring sites the genetic distance between local populations was generally low but increased with geographical distance. This pattern of spatial relations is consistent with the structure of a metapopulation. Moreover, up to three mass immigrations of males per breeding period, replacing previously reproductive individuals, suggested the existence of temporal populations successively reproducing at the same locality. Genetic distances were considerably greater between temporal populations than between local ones, indicating partial reproductive isolation. In fact, an exchange of reproductive individuals between the temporal populations at each site was not detected, but gene flow due to the recruitment of first-breeders originating from offspring other than their own seems probable. Thus, natterjack metapopulations consist of interacting local and temporal populations. The reproductive success differed considerably among the four sites and also between the temporal populations. Three out of four local populations had low reproductive success as well as the latest temporal population. The persistence of these populations depended entirely on the recruitment of juveniles from the only self-sustaining local population. This "rescue-effect" impeded local extinction. The discussion focuses on the modifications required to fit the classical metapopulation concept to the empirical findings and their consequences for the dynamics of amphibian metapopulations.

Key words: Bufo calamita – Metapopulation – Migration – Allozymes – Genetic diversity

In Amphibia, groups of individuals of the same species which reproduce simultaneously at the same site are frequently referred to as populations. This definition is particularly useful for explosive breeders such as Bufo bufo (Heusser 1969) and Rana temporaria (Savage 1961) with a lifelong site fidelity to the natal pond. Both species establish fairly closed populations geographically limited to the areas around the breeding pond. The rather strict site fidelity leads to a long-lasting genetic continuity and the development of significant diversity even between nearby populations due to gene drift and the low interpopulational exchange of individuals (Reh 1988, Reh and Seitz 1990, Sherif 1990). However, in most amphibian species it is considerably harder to define the term population due to the complexity of migratory and reproductive behaviour.

In several species individuals may not reproduce in the natal pond but join distant breeding assemblages. Therefore, in toads such as B. woodhousii (Breden 1987) the continuous exchange of individuals by immigration and emigration reduces the genetic differentiation between different sites of reproduction. Newts (Notophthalmus viridescens; Gill 1978a, b) and frogs (R. lessonae; Sjögren 1991) establish metapopulations consisting of interacting and unstable local populations. Populations at suboptimal sites do not produce sufficient offspring and remain in a state of permanent recolonization by roaming individuals of neighbouring populations. The genetic consequences of these interactions have not been studied yet. In terrestrial-brooding species central sites of reproduction do not exist (Duellman 1985), and populations cover large areas only limited by geographic barriers interrupting the genetic flow.

Besides the difficulty of assessing the geographical extension of a population prolonged breeders (Wells 1977) such as Bombina variegata and Bufo melanostictus
provide a further complication to amphibian population ecology. The annual breeding period lasts several months, whereas the individual reproductive activity is considerably shorter (Jorgensen et al. 1986, Kapfberger 1984). Consequently, the temporal spacing of individual reproduction may lead to genetic differentiation into early and late breeders. Thus, study of the population ecology of an amphibian species requires detailed information on the migratory and reproductive behaviour of the individuals of a breeding assemblage, and also of the interactions among neighbouring breeding assemblages.

A pilot study on the prolonged breeder *B. calamita* in 1987 demonstrated spatial and temporal interactions between local breeding assemblages (Sinsch 1988a, 1989). Spatial interactions are primarily based on roaming females whereas males showed a rather strict site fidelity to the breeding site (Sinsch 1992a). The consecutive immigration and emigration of three distinct groups of males to and from the breeding sites between April and August of a single year indicated at least partial reproductive isolation between the individuals of the early, main and late breeding periods. These unexpected findings led to a thorough analysis of the structure and dynamics of the population until the present time. The aims of this study are (1) to monitor the migratory behaviour of reproductive natterjacks in order to assess the exchange of individuals among the local populations; (2) to estimate the recruitment of juveniles and, thus, the stability of each population; and (3) to estimate the genetic diversity among the local and temporal populations by allozyme electrophoresis. The discussion focuses on the consistency of results with the current concepts of metapopulations (Gill 1978a, b, Gilpin and Hanski 1991, Schoener 1991) and proposes modifications for species inhabiting unstable biotopes.

Materials and methods

Study site

The study was conducted in the northern Rhineland near Siegburg, Federal Republic of Germany, at altitudes between 52 and 58 m. The study area of about 8 km² was inhabited by 3000-10000 natterjack toads (*Bufo calamita*) which reproduce in four spatially separated groups of potential breeding ponds. These groups of 6-20 neighbouring ponds are referred to as breeding areas, numbered consecutively I to IV from north-east to south. A detailed description of the study site has been published elsewhere (Sinsch 1988a, b). The number and the position of single ponds often varied from year to year within each breeding area. Therefore, the terms breeding assemblage and local population do not refer to the toads of single ponds but to all individuals simultaneously advertising and/or reproducing in a given breeding area.

Monitoring of the migratory behaviour

The annual pattern of migrations was studied from 1 June 1986 to 30 September 1991. Three methods were used to detect movements of toads: direct observation, tagging and recapture, and radio telemetry.

Direct observations during the night served to detect mass migrations (> 50 males or > 10 females per night) and to assess the dominant direction of migration (towards or away from the breeding area). An indirect measure to detect and to quantify the migrations of reproductive females was the presence and the number of spawn strings deposited. The frequency of observations (2-4 h each, beginning 30 min following sunset) ranged from daily during the reproduction period to 3-6 per month during the rest of the activity period.

In April/May 1987 a total of 133 males were site-specifically toe-clipped in area I, 24 males in area II, and 89 males in area III. In 1988 another 58 males were tagged in area III. Based on the recapture rates of marked toads the numbers of reproductive males present in the breeding area were estimated (see Ritter, 1989). Abrupt changes in the absolute numbers of recaptured males and the estimated total indicated emigration and/or immigration (Sinsch 1988a). The spatial distribution of recaptures of marked toads outside their breeding area was also used to estimate the migratory range of males.

In April/May 1991 254 males and 175 females were individually tagged using passive integrated transponders (PIT tags) which emit a ten-space, alpha-numeric code after activation by a hand-wand scanning device. PIT tags (size: 10 x 2.1 mm, mass: 63 mg) consist of a microchip encased in glass. They were placed into the lateral lymphatic sacs of the toads (further details are given in Sinsch, 1992b). The presence of tagged toads within area III and their reproductive activity was determined during 50 censuses in the period from May to September 1991.

Twenty-one males and 12 females were radio-tracked for periods ranging between 9 and 167 days. Single-stage transmitters (Custom Electronics, Urbana, Ill., mass of transmitter package: 2.5 g) were implanted into the abdominal cavity of the toad following the procedure described in Sinsch (1988a, 1991). Toads were released at the capture site within the next 3 h and tracked with a CE 12 receiver (Custom Electronics) and a 3-element-Yagi antenna. The range of the transmitters varied from 40 m in burrowed toads to 200 m in toads migrating on bare ground. Ten toads at most were tracked simultaneously and their locations recorded once per day. At the end of the tracking period the transmitters were removed through a contralateral incision.

Recruitment of juveniles in each breeding area

The development of the spawn strings to larvae and to tadpoles was continuously monitored in all temporary pools of the study area. Records consisted of (1) the number of spawn strings lost by desiccation before producing free-swimming tadpoles; (2) the number of spawn strings in pools which dried up before the tadpoles finished metamorphosis; and (3) the remaining number of spawn strings which produced tadpoles. The number of successfully developed strings was used as a measure for the recruitment of juveniles in each breeding area. This measure is obviously a rough one because the number of eggs per spawn string (1700-6500; Kadel 1975; Banks and Beebee 1988) and the number of potential predators varied considerably from pond to pond. Nevertheless, these sources of variance were similar in each of the breeding areas and, therefore, the total number of successfully developed spawn strings per area represents a useful base for an inter-area comparison.

Allozyme electrophoresis

Blood from a total of 164 reproductive males was sampled in April and June, 1989, and again in April, May and June 1990, in breeding areas I, III and IV. The number of individuals per date and site ranged from 8 to 15. Approximately 60 µl of blood was collected into heparinized capillaries from the vena angularis of each individual (Nöller 1959). Blood cells were separated from plasma in a COMPUR microcentrifuge at 11500 rpm for 3.33 min. Blood cells...