Courtship behaviour of *Neurergus* (Caudata: Salamandridae)

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Abstract. The courtship of all four species of the salamandrid genus *Neurergus* is described. The display behaviour is similar in all species, but there are differences in the temporal organisation of tail-fanning. The behaviour of these newt species resembles that of other Old World aquatic salamandrids in its general pattern, with tail-fanning the principal movement during the display phase. The spermatophore transfer phase includes a behaviour pattern during which the male turns back side-on to the female after spermatophore deposition and arrests her in a position where her cloaca is situated over the spot where the spermatophore was put down by the male. This movement is similar to the behaviour pattern described as 'brake' in all species of *Triturus*. In cladistic terms this shared behaviour pattern forms a synapomorphy for the genera *Triturus* and *Neurergus*.

Introduction

Newts of the genus *Neurergus* are confined to Turkey and the Middle East. Presently four species are recognised (Schmidtler and Schmidtler, 1970, 1975; Schmidtler, 1994; Leviton et al., 1992): *Neurergus crocatus* Cope, 1862 from Northern Iraq and North-western Iran, *Neurergus strauchii* (Steindachner, 1887) from areas West of the Van lake in Eastern Turkey and from central Turkey (*N. s. barani*), *Neurergus microspilotus* (Nesterov, 1916) from the border area between Iraq and Iran, and *Neurergus kaiseri* K.P. Schmidt, 1952 from the surroundings of Shah-Bazan of Luristan province, Iran.

The species can be briefly characterised as follows. *Neurergus strauchii* is a large-bodied newt, reaching 18 cm in total length. The ground coloration of the dorsal and lateral sides of the trunk is black, covered with irregularly dispersed little yellow spots. With the exception of a thin orange line, the ventral side is coloured black. The lateral sides of the male's tail are coloured silver-blue during the time of reproduction. This morphological trait is unique for the species and comprises the only sexual dimorphism in colour found in the entire genus. The male cloaca is turgid and shaped like male cloacas of *Triturus* during

the breeding season. The female cloaca is not significantly different during breeding and non-breeding seasons. Like *N. strauchii*, *N. crocatus* is a large-bodied newt, reaching the same dimensions. The ground coloration of dorsal and lateral trunk is brown, covered with bigger yellow blotches than in *N. strauchii*. The ventral side is red-orange. The shape of male and female cloacas is as in *N. strauchii*. Compared to *N. strauchii* and *N. crocatus*, *N. microspilotus* is smaller, reaching 14-15 cm in total length. Coloration of the dorsal and lateral trunk closely resembles that of *N. strauchii*. Ventral coloration is as in *N. crocatus*. The shape of the male cloaca is as in the previous species; the female cloaca is slightly elongated during the time of reproduction. *Neurergus kaiseri* is the smallest species, reaching a total length of only 10 cm. The dorsal coloration is unique and rich in contrast, with a mosaic of black and white patches and orange-red dorsal stripe, legs and belly. The male cloacal anatomy resembles that of the other species; the female cloaca is extended in a tubular shape of approx. 1 cm length. The species are depicted in Steinfartz and Schultschik (1997).

On many aspects of the natural history and the biology of these species our knowledge is still very fragmented. Morphological evidence suggests that newts belonging to this genus are closely related to newts of the genus *Triturus* (for references see Schmidtler, 1994). On the basis of an examination of DNA sequences and morphological and reproductive characteristics in the family Salamandridae, Titus and Larson (1995) reconstructed a phylogeny of the family Salamandridae. According to their phylogenetic hypothesis, monophyly is well-supported for a group containing the genera *Euproctus*, *Neurergus* and part of *Triturus*. Recent work based on mitochondrial DNA data and nuclear coded allozyme data indicates monophyly of *Neurergus* within this group and allows us to distinguish two subgroups, one comprising *N. s. strauchii* and *N. s. barani* and another represented by *N. crocatus*, *N. microspilotus* and *N. kaiseri* (Steinfartz et al., 1997).

The repertoire of behaviour patterns of *Neurergus* is only partly known. The available data indicate that in its courtship display, *Neurergus* is similar to *Triturus* (Arntzen and Sparreboom, 1989; Haller, 1989; Schmidtler, 1994; Timofeev, 1997), but a more thorough description was needed to substantiate this view. The present report surveys the courtship behaviour of all four species of *Neurergus*. It is based on first-hand observation of behaviour patterns in a small number of freshly caught animals, of which the collecting locality is known (Schultschik and Steinfartz, 1996). The description is necessarily of a preliminary and qualitative nature.

Materials and methods

Neurergus strauchii barani

Ten courtship sequences (including orientation, display and spermatophore deposition) were observed in *N. s. barani*, much of which was recorded on video-tape. Our description

is based on the sexual behaviour shown by three males and five females during two days in March 1993. For the recordings a standard Grundig video-camera was used.

The animals were collected by Steinfartz and Öz at the type locality in the Turkish province of Malatya in April 1992 (Öz, 1994; Schmidtler, 1994; Steinfartz, 1995). As in the nominate race of this species, the male in breeding dress shows a silver-blue stripe on the tail.

The animals were kept in two tanks of 80 × 30 × 40 cm, one containing one male and two females, the other two males and three females. The tanks were filled with tap water to a level of 25 cm. The water was aerated and filtered by an external Eheim pump causing a strong water circulation and providing a rich supply of oxygen. Water temperature was 14°C in spring and up to 23°C in summer; the bottom was covered by a thick layer of gravel and flat stones creating corridors, hiding places and opportunities for egg deposition just under the water surface. The tank contained no vegetation and was illuminated by a 20 Watt TL light tube for 12 hours per day in the breeding season and 9 hours in the winter months. The animals were kept terrestrial in winter and aquatic in spring and summer. Food consisted of crickets and earthworms. More detailed descriptions of their maintenance are given elsewhere (Steinfartz, 1995; Schultschik and Steinfartz, 1997).

Neurergus crocatus

In *N. crocatus*, no complete courtship sequence could be recorded, but fragments of display behaviour could be video-taped in February and March 1993. One male and two females were kept and bred successfully (Steinfartz, 1995). The animals originated from Aqrah in Northern Iraq, where they were collected by C. Radspieler and others in April 1991 (Steinfartz, 1995). The animals were kept under similar conditions as *N. strauchii*.

Neurergus microspilotus

For *N. microspilotus*, our observations are only fragmentary. Notes of observed behaviour patterns were made in March 1997 on four males and two females kept in a tank of 60 x 37 x 26 cm, filled with water to a level of 18 cm and furnished with stones reaching out of the water. A small water-pump with outlet just above the water surface kept the water flowing and aerated. From November to March the animals were hibernated in a refrigerator at 4°C.

Eight males and four females were collected in the area around Quri-Qaleh (= Kermanshahan), province of Bahtaran in Iran in the first week of April 1995 (Schultschik and Steinfartz, 1996). At that time all animals were in breeding condition. Some eggs were laid during transportation to Europe.

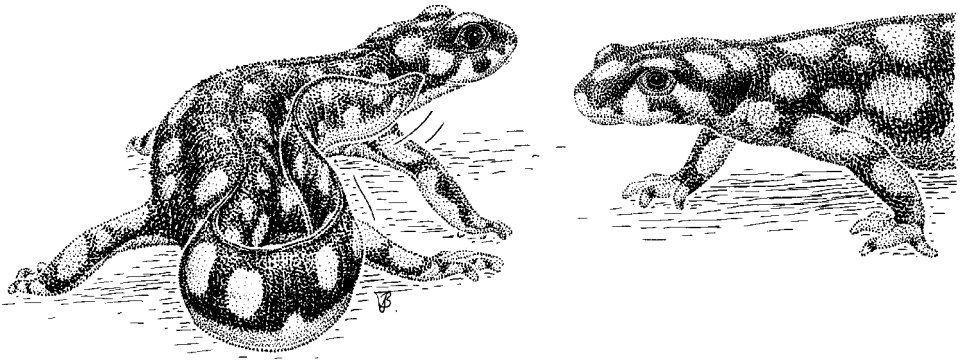

Figure 1. Tail-fanning behaviour in *Neurergus crocatus*, male left.

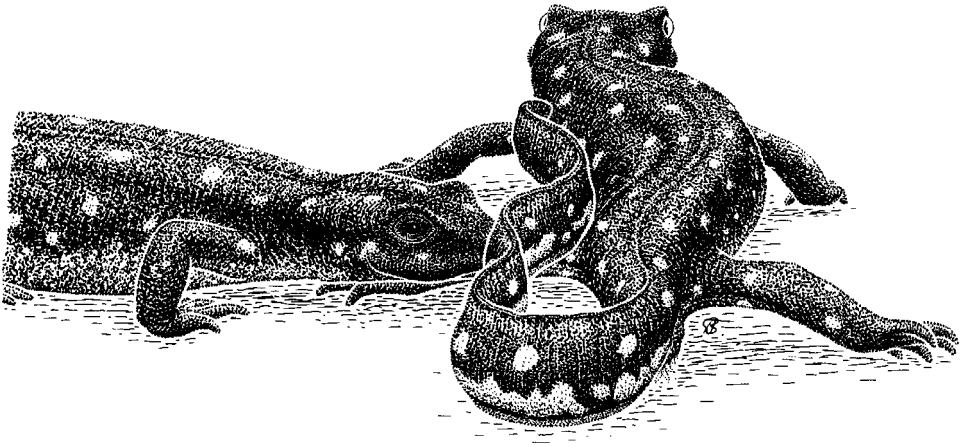

Figure 2. Brake behaviour in *Neurergus strauchii barani*, male right.

Neurergus kaiseri

In *N. kaiseri*, one incomplete and two complete courtship sequences were observed. Three males and two females were kept at a temperature of 17°C. The animals were introduced into the water at the end of February 1997. The aquarium measured 60 × 37 × 26 cm, the water level was 8 cm, the water was aerated and filtered by a Rena filter. When mating activity started, a 40 Watt heating cable was introduced, raising the water temperature to 22°C by day and 20°C by night. Sexual behaviour was observed from the first week of March until the end of the month when mating activity stopped. Observations could only be made in the evenings in darkness, assisted by dimmed torch light that was shone carefully aside the mating animals to avoid disturbance. The animals, 17 males and 10 females, were collected in the area around the type locality Shah-Bazan, in the Iranian province of Luristan in the last week of March 1995 (Schultschik and Steinfartz, 1996).

Results

Courtship behaviour

Actions performed by *N. s. barani* are labeled S, actions performed by *N. crocatus* are labeled C, by *N. microspilotus* M and by *N. kaiseri* K.

Male behaviour patterns

Alert posture. The male positions himself on the heap of stones in the water and actively surveys the surroundings; he remains at this spot and returns here after unsuccessful pursuits (M). K remains in close vicinity of its hiding place.

Pursuit. The male pursues the female, swimming or walking behind her or approaching from above and attempting to take up position in front of her and start tail-fanning (S, M, C). Very little pursuit was observed in K.

Approach. The male slowly moves in the direction of the female's head until the animals stand more or less face to face (S, C, M, K).

Fan. The male takes up a position nearly opposite the female's body, his head at some cm distance from hers. He bends his tail back against the side nearest to the female, the tail-tip reaching his flank. The tail-movements which form the fan begin at the tail-base and run to the tail-tip. With every beat of the tail-base the distal part makes an outward slapping movement. During fanning the body is bent in the middle on a horizontal plane; the male attempts to maintain his position right in front of the female, and may change his position in such a way that the fanning is performed either from the left or the right position (fig. 1) (S, C, M, K). These fanning movements may also be made from the alert posture as a reaction to a movement in or outside the observation tank (M).

The amplitude of the fan differs: in S, C and M it is large, the tail-tip making slaps of approximately 4 cm away from the male's flank; this is larger than in K, where only the distal part, approximately one third of the tail length is beaten. Fanning bouts are alternated with pauses during which the male is standing still in the fanning position with the tail bent but held motionless. In S fanning bouts last for approximately 3 s and are interspersed with breaks during which the male keeps standing in the fanning position but keeps his tail still for about 5-7 s. Frequency of tail beats during fanning is 2-3 beats per s. In C fanning bouts last up to 25 s and the frequency of tail beats is approx. 3 beats per s. In C the breaks between fanning bouts are of approx. 12 s duration. Exactly comparable data for M and K are not available. In K tail beats during fanning appear to be slightly more rapid than in S and C; the temporal organisation of fanning behaviour in K superficially resembles that of C.

Creep. The male turns away from the female and slowly walks ahead of her, his tail slightly raised and making agitated and undulating, snakelike movements. These

movements are started at the tail-base which makes rapid quivering movements on the horizontal plane (S, C, M, K).

Spermatophore deposition. The male slightly raises his undulating tail and deposits a spermatophore in front of the female (S, C, M, K).

Brake. After spermatophore deposition, the male creeps on approximately one body length and pivots about one foreleg, making a 90° turn so that he comes to stand in a position perpendicular to the female's body with his tail folded back and making slow worm-like movements, mainly on a horizontal plane, but occasionally waving above the male's back (fig. 2) (S, C, K).

Male sexual interference. A male may interrupt an on-going courtship by moving in-between a courting pair at all stages of courtship. He may then take over courtship and by so doing usurp a female (thus far seen in S only; males scrambling for a female have been observed in M).

Female behaviour patterns

Stand still. While the male approaches the female and starts tail-fanning display, the female remains standing motionless (S, C, M, K).

Follow. When the male has turned away from the female after having displayed to her, the female, if responsive, will follow the creeping male, orienting towards his undulating tail. Occasionally she is undulating or slowly fanning her tail while following the male (S, C, M, K).

Touch-tail. While following the creeping male, the female touches his tail with her snout several times (S, C, K).

Spermatophore pick-up. The female moves over the spermatophore deposited in front of her and the spermatophore sticks to her cloaca (S, C, K).

Egg-deposition. The female deposits her eggs singly or in small clusters on the underside of stones or in hollows and crevices. Egg assemblages are found under flat stones (S, C); single eggs or small assemblages are laid in narrow hollows and crevices on the lower surface of stones (M); eggs are laid singly on rough surfaces, away from the light but not necessarily on the underside of stones (K).

Female sexual interference. A female moves in between a creeping male and following female, pushes the first female away and instead follows him herself (only seen clearly in S).

Static flamenco. A female holds her tail stretched and slightly raised (observed after spermatophore pick-up in S and K).

Temporal relations

The following description of the temporal organisation of courtship is mainly based on 21 videotaped encounters of S and five in C. The male takes up position in front of the female, his body at an approximate right angle to that of the female or more or less opposite and facing her. Fanning is executed from this position, either from the left or the right side, and always directed towards the female's snout.

If the female remains standing still, the male continues fanning in short bouts, interrupted by pauses. By moving forward towards the male the female signals that she is responsive. The male retreats by making a few steps backward while attempting to keep his orientation towards the female. Then he turns through 180° and starts to creep ahead of the female, his tail making undulating, snake-like winding movements. The female follows him closely and from time to time touches his tail. The male halts after a few seconds and stops making undulating tail-movements until he receives further tail-touches. Every time the female touches his tail with her snout, this stimulates the male to advance further. It induces him to make a little spurt forwards, quiver his hind-body and undulate his tail vigorously.

Subsequently, after a number of tail-touches, the male deposits a spermatophore, his tail slightly raised and making slow undulating movements. The male continues to creep forward, but at a slower pace than before and the female keeps following him, her snout pressed against the lower part of the male's tail (the area which in S is coloured bluish in the breeding period). While creeping on, the male slowly folds his moving tail against one side of his body, the tail-tip occasionally waving over his back, and slowly makes a 90° turn, which brings him back into a position perpendicular to the female's body. He halts, thereby stopping (braking) the female in her progress at a point when she has moved forward about one body length and her cloaca is situated above the place where the spermatophore was deposited. This behaviour was found to be similar in S, C and K. For M there are no precise observations.

After taking up the brake position, the male may revert to the creeping direction, continue creeping ahead of the female and deposit further spermatophores, or he may revert to fanning. In S, C and M, males were capable of depositing several spermatophores during one evening. Data for K are insufficient to make a statement.

Out of 21 courtship encounters recorded for S, 14 ended with the creep stage and eight with spermatophore deposition. In three instances more than one spermatophore was deposited, on one occasion a total of four were put down in one sequence of about 10 min duration. The static display phase — fanning bouts alternating with pauses during which the couple stood still in fanning position — took up 281 s, the first creep including first spermatophore deposition took 42 s, brake 12 s, second creep 80 s, brake 18 s, third creep 31 s, brake 36 s, fourth creep 74 s, brake 60 s. Then another animal interfered with the courtship causing the partners to swim away. The third spermatophore was picked up successfully. Each spermatophore deposition was followed by the male taking up the

brake position, after which he continued to creep, mostly in a direction different from the preceding creep. The male did not revert to tail-fanning between the subsequent spermatophore depositions.

Discussion

The four species of *Neurergus* appear to have a broadly similar repertoire of courtship behaviour patterns. Tail-fanning is similar in *N. strauchii*, *N. crocatus* and *N. microspilotus*, where fanning is a rather large amplitude movement. There is a clear difference between fanning bout duration between *N. strauchii* and *N. crocatus*, with *N. crocatus* showing fanning bouts of considerably longer duration than *N. strauchii*. The frequency of two to three tail-beats per second is comparatively low. In *N. kaiseri* the fanning movement is of smaller amplitude, with mainly the distal part of the tail making the fanning movement. On the whole, the display of *Neurergus* is rather calm and static. Tail-fanning is the only behaviour pattern observed thus far during this phase of courtship.

The behaviour during which the female stretches her tail and holds it up (termed 'static flamenco' by Denoël, 1996, who described this behaviour in *Triturus alpestris*) was occasionally shown by *N. strauchii* and *N. kaiseri*. It looks like a kind of signal-posture such as is known for instance in both sexes of *Euproctus asper* (Thiesmeier and Hornberg, 1990; Nöllert and Nöllert, 1992, p. 161). Further observations are needed to interpret this behaviour.

Sexual interference was observed in both sexes, especially in *N. strauchii*. These behaviour patterns were commonly seen when more animals were sexually active in the same tank. Their appearance was similar to some of the behaviour patterns described for *Cynops* (Sparreboom, 1996) and *Triturus* (Waights, 1996).

The spermatophore transfer phase appears to be similar in all four species, although more observations are needed especially for *N. microspilotus* and *N. kaiseri*. Thus far the observations suggest that spermatophore deposition is invariably followed by a type of behaviour that is practically identical to a behaviour pattern described for *Triturus* and was termed 'brake' (Halliday, 1974). The male pivots about one forelimb, turns side-on to the female with his tail folded against his body at the side facing the female, and by so doing blocks the female's progress. Preliminary observations by breeders that this behaviour is also shown by *Neurergus* (Arntzen and Sparreboom, 1989; C. Radspieler in Schmidtler, 1994), can now be confirmed (fig. 2).

Comparison with behaviour patterns in other salamandrid genera places *Neurergus* in close proximity to *Triturus*, especially *T. alpestris* which is the *Triturus* species with the least complex display movements (Halliday, 1977; Arntzen and Sparreboom, 1989; Denoël, 1996). Whereas there are notable species-specific differences in display behaviour patterns among *Triturus* species, the spermatophore transfer phase is very similar throughout the genus and more stereotyped than the initial display behaviours

(Halliday, 1977, 1990). All *Triturus* species show the brake behaviour after spermatophore deposition and all but *T. cristatus* (Arntzen and Sparreboom, 1989) may add a further refinement to this behaviour: While the male is standing in brake position, he pushes the female back by unbending his tail and allows her to approach him again. As a result of this behaviour, her cloaca moves backward and forward over the place where the spermatophore was deposited. Various explanations have been proposed for this 'push-back' behaviour; probably it serves to increase reliability of sperm-transfer (Halliday, 1974, 1990; Denoël, 1996). The salamandrid genera *Cynops* and *Paramesotriton* have a mating pattern that is similar to *Triturus* (Tsutsui, 1931; Arnold, 1972; Rehák, 1984; Sparreboom, 1983, 1984, 1994), but in these genera neither brake nor push-back behaviour has been observed. After spermatophore deposition, the male just marches ahead, without turning round and spending more time and energy on each spermatophore, and may deposit several more spermatophores in one sequence. Observations on *Pachytriton labiatus* suggest that this species is similar in this respect to *Cynops* and *Paramesotriton* (Sparreboom and Thiesmeier, 1999). So with regard to this brake behaviour, *Neurergus* falls somewhere in between the European and East-Asian species groups. In cladistic terms, within the Salamandridae brake is synapomorphic for all species of *Triturus* and *Neurergus*.

Our observations on sexual behaviour appear to be largely in concordance with conclusions based on molecular and morphological analysis (Titus and Larson, 1995), that *Neurergus* is more closely related to *Triturus* than to *Cynops* and *Paramesotriton*, and probably other taxa such as *Pachytriton*. Behavioural data suggest furthermore that within the clade comprising species of *Triturus*, *Euproctus* and *Neurergus*, *Neurergus* is closer to *Triturus* than is *Euproctus* with its amplectic courtship modes and direct sperm transfer. In the light of the non-monophyly of *Triturus* that was found by Titus and Larson (1995), it is of interest that the brake behaviour we found in *Neurergus* is found in all *Triturus* species alike (Arntzen and Sparreboom, 1989). So unless brake is considered a homoplaseous character, this finding does not fit in with the non-monophyly of *Triturus* hypothesised by Titus and Larson (1995) and further limits the options for a robust phylogeny.

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