

The homing behaviour of displaced smooth newts *Triturus vulgaris*

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Abstract. Homeward orientation of passively displaced smooth newts *Triturus vulgaris* was tested in four arena experiments at release sites 213m to 3,270m distance from their breeding pond. Newts were unable to assess the home direction from test sites which were located outside the area of familiarity. However, at the shortest displacement distance the mean direction chosen by the newts did not differ from the home direction and the mean vector length was significantly different from zero. It is hypothesised that *T. vulgaris* uses olfactory beaconing to orientate within its area of migratory experience.

Introduction

True navigation is the ability of an organism to orient towards a goal following displacement to an unfamiliar site, without outward journey information and sensory contact with the goal (Able 1980). This ability requires the use of a spatial map and of a compass and has been demonstrated for several vertebrates, including the newt *Notophthalmus viridescens* (Phillips et al. 1995; review: Sinsch 2006). Another four species of newts (*Taricha rivularis*, *T. granulosa*, *Triturus alpestris*, *T. marmoratus*) were shown to actually home following long-distance displacements or to choose the homeward direction in experimental releases (Twitty 1959; Twitty et al. 1964; Diego-Rasilla and Luengo, 2002, 2004; Diego-Rasilla 2003; Diego-Rasilla et al. 2005). Home orientation is hypothesised to rely on a geomagnetic map and celestial and geomagnetic compasses (Fischer et al. 2001; Phillips et al. 2002a, b).

The ability of five newt species pertaining to three genera to navigate home from unfamiliar sites may suggest that this a feature common to all newts. Therefore, we used smooth newts (*Triturus vulgaris*) to test experimentally this hypothesis. Adult smooth newts stay usually within a distance of 20-60m from their breeding pond and only few individuals have been found to move as far as 400m (Baker and Halliday 1999). The maximum dispersal distance of juveniles amounted about 1km (Cabela and Girolla 1994). Early experimental tests suggested that short-distance orientation is based on olfactory cues combined with geotactic behaviour

(Czeloth 1931). In a series of four experiments, we displaced reproductive newts to test sites which were 213-3,270m distant from their breeding pond and monitored their directional choice (= initial orientation) *in situ* in an arena. We expected that at least the less distant test site was within the area of previous migratory experience of most individuals, whereas the most distant site was far outside of the natural migratory range. Aims of this study were to quantify the effect of familiarity on directional choice and to look for indications of a navigational ability.

Material and Methods

Groups of at least 25 adult newts were captured at the breeding pond (Schmittenhöhe, Rhineland-Palatinate, Germany; Sinsch et al. 2003) one day before testing and each group was displaced to a test site with full access to magnetic, olfactory and visual cues during the outward journey. At the test site, they spent the complete night and part the next day within moist plastic boxes and full sensory access to local cues including sky. Boxes (34 x 24 x 10 cm) were shaded during day to prevent overheating. Four test sites were chosen which varied in distance to the breeding pond and were distributed along a south-west axis: (1) 266° (home direction), 213m (distance to home), June 11th, 2005 (date of test); (2) 240°, 496m; (3) 233°, 773m, May 27th, 2005; (4) 239°, 3,270m, May 16th, 2005. After the testing period newts were returned to their breeding pond. All tests were performed during the newts' reproductive period.

Tests consisted in a series of 20 consecutive releases of one individual each in an open unstructured, visually symmetrical plastic arena (80cm diameter, 30cm high) which was placed on flat ground and aligned to the N-S axis. The floor and arena walls were thoroughly wiped with a damp cloth between trials to eliminate directional olfactory cues (Fischer et al. 2001), and then they were wiped dry. All tests were done between 10am and 5pm under a clear day time sky without alteration of the local geomagnetic field. Prior to testing, newts were transferred for at least 10min to a plastic box (34 x 24 x 10 cm) half-filled with water from the newts' breeding pond. Newts were then placed in the arena center under an opaque, cylindrical plastic container (10cm diameter, 15cm high) that served as a release

device. Newts were held in the container for 5min to overcome effects of handling. The release device was then lifted, and the newts were allowed to move freely. Two observers stood motionless at the north and the south pole of the arena and monitored the newt's movements during 5min. An individual trial ended at the first contact of the newt with the arena perimeter. Directional choice (to the nearest 1°) and decision time of 20 newts per test site were recorded.

Directional data were analysed using standard circular statistics (Batschelet 1981). The direction of the mean vector was calculated by vector addition and tested for significance using the Rayleigh test for a non-random distribution. A 95% confidence interval was used to test whether the newts' mean directional choice was significantly different from the homeward direction at the test sites. Sex-specific decision time and median decision time at the four test sites were compared using the Mann-Whitney *U*-test and the Kruskal-Wallis test, respectively. Shapes of distributions were tested for differences by the Kolmogorov-Smirnov test. The level of statistical significance was set at 0.05. All calculations were performed using the program package STATGRAPHICS Centurion.

Results

Independent from the specific test site, orientation behaviour of newts consisted in an initial raising of the head and staying almost motionless in the centre of the arena for 10-40s. Newts gave the impression that they were smelling. Then, newts moved either in rather straight or more often twisted paths to the perimeter of the arena. Males ($n=37$) and females

($n=43$) did neither differ significantly with respect to median decision time (63s, range: 13-153s versus 64s, 7-280s; Mann-Whitney *U*-test, $P=0.59$) nor with respect to the shape of data distribution (Kolmogorov-Smirnov test, $P=0.78$; Fig. 1). Site-specific medians of decision time did not vary either (overall median: 63s; Kruskal-Wallis test, $P=0.44$).

The mean vector length of initial orientation obtained for the three releases at less than 1km distance increased with decreasing displacement distance (Fig. 2): (1) test site: 266°, 213m; mean vector length: 0.388, mean direction: 296.0° ($n=20$, Rayleigh-test, $P=0.043$); (2) test site: 240°, 496m; mean vector length: 0.283, mean direction: 293.7° ($n=20$, Rayleigh-test, $P=0.21$) (3) test site: 233°, 773m; mean vector length: 0.116, mean direction: 351.1° ($n=20$, Rayleigh-test, $P=0.75$). At the site of presumed unfamiliarity, initial directional choice did not differ significantly from random: 239°, 3,270m; mean vector length: 0.359, mean direction: 13.3° ($n=20$, Rayleigh-test, $P=0.073$). Thus, only newts displaced to the close vicinity of the breeding pond were significantly oriented and chose a mean direction, which was not significantly different from the home direction.

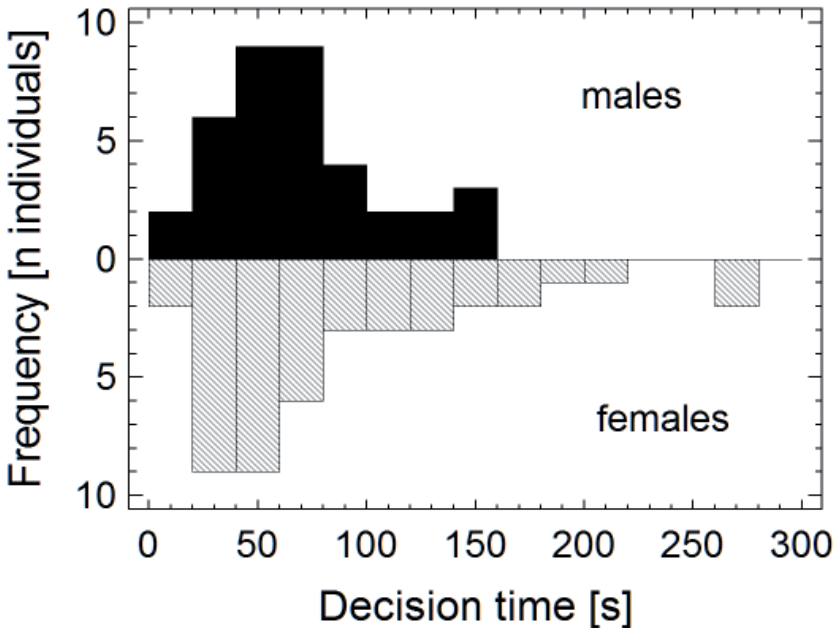
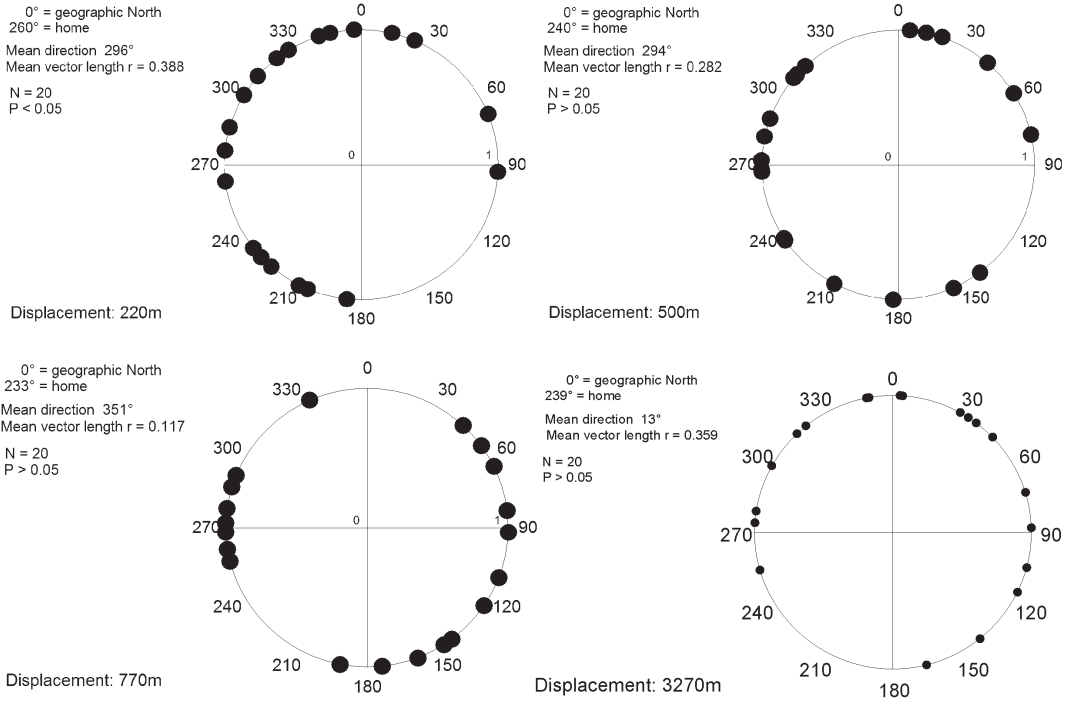


Figure 1. Sex-specific distribution of individual decision time (period between the start of an individual release to the first contact of the individual with the arena wall). Statistical details in text.

Figure 2. Circular diagrams of four tests with increasing distance to home pond. Statistical details are given in the text. Each dot represents the bearing of one individual, the radius of the circle was set to 1.



Discussion

Smooth newts were not able to assess the home direction, if displaced to sites outside their natural migratory range. Not even full access to outward journey information and to local cues at the test sites did improve initial orientation. This result permits to reject the hypothesis that the ability to navigate is feature common to all newts. It is, however, in full agreement with previous studies on the homing ability of displaced *T. vulgaris*. Blab (1986) estimated the maximum displacement distance which allowed successful homing at 550m in males (homing accomplished after 37d) and at 600m in females (after 48d).

Successful homing in smooth newts possibly requires direct sensory contact to the goal, for example by smelling pond odours as suggested by the behaviour of the newts when released in the arena, and by earlier experiments by Czeloth (1931). Close-up releases of alpine newts (*T. alpestris*) also indicated that their homeward orientation over distances of 45-110 meters was based on olfactory cues emanating from the breeding pond (Joly and

Miaud 1993). Thus, olfactory beaconing seems to be a common feature of the orientation system of *T. alpestris* and *T. vulgaris* for short distance homing (Sinsch 2006).

In contrast, the long distance homing ability has only been demonstrated for *T. alpestris* and *T. marmoratus*, but not for *T. vulgaris* (Diego-Rasilla 2003, Diego-Rasilla and Luengo 2002, this study). Pond odours seem to be unsuitable cues for homing from distant unfamiliar sites because the availability of these cues will be affected by wind direction, distance from the pond, and turbulence at ground level (e.g. Sinsch 1987, Baldocchi 1989). Map-based orientation is the most probable mechanism used for homing from unfamiliar sites (e.g. Fischer et al. 2001). The absence of the ability to navigate in *T. vulgaris* may also be related to the fact that the genus *Triturus* is not monophyletic (e.g. Grossenbacher and Thiesmeier 2003; Carranza and Amat 2005). Each of the studied species pertains to another clade which had separated from each other about 14 Myr ago (Carranza and Amat 2005). Therefore, the evolutionary origin of the navigation ability remains

obscure, it may have been secondarily lost in the clade of *T. vulgaris*, or evolved independently in the clades of *T. alpestris* and *T. marmoratus*.

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