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Orientation of the smooth newt (*Triturus vulgaris*) foraging on zooplankton

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The behaviour of smooth newt adult females foraging on *Daphnia* was analysed. Newts were given different-sized *Daphnia* (1.5, 2.3 and 3.8 mm), either as one-sized or two-sized prey in different densities and size ratios. The frequency distribution of angles of turns mede by newts between discrete moves during foraging bouts is a normal function peaking at approx. 0°. Increasing prey abundance or size of prey made newts turn more widely during their foraging bouts. The movements of newts during foraging bouts are directional (i.e., moving straight ahead dominates) with the exception that the first turn made after ingestion of a prey tends to be a wider arc than subsequent turns. In other words, newts move straight ahead before capturing a prey, but make random turns just after capturing the prey. A computer simulation with aggregated prey suggests that a "directional-random' turning rule (observed newt behaviour) gives the highest prey capture rate when compared to "directional-directional' (second best) or "random-random' turning rules.

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1. Introduction

Fitness in a predator depends to a great extent on the ability to locate and capture prey. The predator has to decide where to forage and for which prey to search. Foraging decisions depend, among other things, on the diversity and abundance of prey available and on the pattern of their distribution in the environment (Pyke 1984 in a recent review).

The smooth newt (*Triturus vulgaris* L.) is a common inhabitant of small ponds and pools (Steward 1969, Bell & Lawton 1975) where it encounters a diversity of prey. Zooplankton is important prey for smooth newts (Avery 1968, Pellantova 1973); for example, Dolmen & Koksvik (1983) reported that zooplankton constituted up to 75% of the diet of adult newts in central Norway. Recently Ranta & Nuutinen (1985) and Nuutinen & Ranta (1986) examined smooth newt foraging on zooplankton. In laboratory experiments newts were given *Daphnia* of varying size and abundance. The newts proved to prefer large prey over small ones.

In this paper we shall describe in more detail how smooth newts behave while they are foraging on zooplankton. Data were collected to answer the questions:

1. How do smooth newts behave once they have encountered prey?
2. How do smooth newts behave in food patches of different quality?

2. Methods

2.1. Experiments

The study was made at the Tvärminne Zoological Station, University of Helsinki. Adult smooth newt females (snout-vent body length 37 mm, range 32–42 mm) were collected from a large pond on the island Långskär. The newts in our study (made between 15 and 21 June 1983) were those previously used in the size-selectivity experiments by Ranta & Nuutinen (1985). Thus, all the newts (altogether 14) had already had experience in foraging in experimental conditions as used in the present study. Newts were kept at ambient room temperatures (20–25°C) under natural photoperiods (approx. 18L:6D), and they were fed *Daphnia* of varying sizes collected from rock-pools on nearby islands.

Prey in the single-prey experiments were *Daphnia magna* Straus, and in the two-prey experiments they were *D. magna* and *D. longispina* O. F. Müller. Prey size in the single-prey experiments was either large (body length 3.8 mm) or small (2.3 mm) *D. magna* and in the two-prey experiments 2.3 mm *D. magna* and 1.5 mm *D. longispina* (see Ranta & Nuutinen 1985, Nuutinen & Ranta 1986).

In the single-prey experiments the 3.8 mm *D. magna* were provided in two densities, 5 or 30 individuals per aquarium. The 2.3 mm *D. magna* were provided in the densities of 5, 15 and 30 individuals per aquarium. In the

Table 1. Smooth newt foraging bout duration (in seconds), length (in cm), number of turns made (mean, standard error of the mean in parentheses), correlations (r) between foraging bout lengths and numbers of turns made, and success percentage (Succ%, % of successful captures of all attempts) in single-prey and two-prey experiments

	Density	Duration	Length	Turns	r	Succ%	Captures
Single-prey							
2.3 mm *D. magna*	5	30 (3)	19 (4)	5.4 (0.6)	0.04	87	71 a
	15	22 (3)	15 (3)	4.5 (0.4)	−0.08	85	88 b
	30	23 (3)	15 (5)	5.8 (0.6)	−0.10	58	85 c
3.8 mm *D. magna*	5	41 (4)	22 (4)	8.1 (1.0)	−0.03	66	65 d
	30	54 (5)	26 (9)	10.3 (2.5)	0.04	30	38 e
Two-prey							
1.5 mm *D. longispina*	15:15	26 (3)	23 (9)	6.3 (0.9)	0.07	81	70 f
and 2.3 mm *D. magna*	5:50	30 (4)	23 (9)	6.0 (0.6)	0.01	88	64 g

In the following comparisons the difference between attempts and successful captures was statistically significant (at $P<0.001$ level, Fisher's exact test or χ^2 test): a−c, b−e, a−d, c−e, and g−d.

two-prey experiments the 2.3 mm *D. magna* and 1.5 mm *D. longispina* were provided in the ratios of 15:15 and 5:50 (Table 1). The two-prey experiments were included since we were also interested in how the newts' foraging behaviour is affected when they have to make a choice between prey of different sizes. Three to four newts were tested with each prey density and ratio. The prey sizes, densities and ratios were selected to match the experiments in our other studies of smooth newt foraging (Ranta & Nuutinen 1985, Nuutinen & Ranta 1986).

Individual newts were tested in 1−3 experiments per day (between 0900−1700 hours), depending on their feeding activity. The experimental aquarium of white polyethylene measured 37×28 cm and contained 3 litres of water from the newts' pond to a water depth of 3 cm. This essentially reduces the space available to two dimensions. Prior to the experiment a newt was placed in a similar aquarium and allowed to acclimate for 20−30 min. Meanwhile, predetermined numbers of prey were collected from our laboratory stocks and placed in the experimental aquarium. After this a newt was introduced into the aquarium. Before starting each test newts were allowed to pursue and eat 2−3 prey, then the original prey numbers were restored and the recording begun. When a prey was eaten during the experiment it was replaced with another prey of the same kind. An experimental session lasted about 12 min.

2.3. Recording and analysis

The experimental aquarium was illuminated from both ends with two 150W light bulbs placed about 60 cm above the water surface. This, together with the laboratory room lights, provided a sufficient and even light for video recording. A video camera mounted with a 1:1.8 f 12.5−75 mm zoom lens was used for documentation. The camera was mounted on a tripod with the lens about 1.3 m above the water surface.

A foraging bout is defined as begining after a newt has ingested one prey and ending at the capture and ingestion of another prey. All foraging bouts by a single newt in a given experimental design are termed a foraging session. A newt foraging bout consists of characteristic short moves, i.e. a newt moves a short distance, pauses, and moves again. The pauses were used as markers for newt turns during the bout.

The data were examined by playing the recordings on a 238×175 mm TV-monitor. A transparent film was placed above the TV-screen and newt movements (tip of the snout) were followed with a colour marking pen, with the pauses between separate moves marked on the transparency. The following data were read from the transparent films: (1) length of the foraging bouts (both in seconds and in cm), (2) turning angles between directions of subsequent moves within an accuracy of 10° (all turns due to a newt encounter with the aquarium walls were excluded), (3) we also counted the number of unsuccessful strikes newts made.

3. Results

3.1. Foraging bout

A one-way analysis of variance (original data square root transformed) suggests that foraging bout lengths (=distance moved; Table 1) differ among the seven groups ($F_{6,474}=2.38$, $P<0.05$). The difference is due to 2.3 mm *D. magna* in densities of 15 and 30 individuals per aquarium (t-tests, $P<0.05$). An analysis of covariance (Table 1; original data square-root transformed) allows rejection of the H_0 that foraging bout durations (t = time elapsed) of the seven groups are equal ($F_{6,474}=5.98$, $P<0.001$). Further, t-tests for the adjusted group means in the covariance analysis indicate that foraging bout durations in 5 and 30 3.8 mm *D. magna* differ significantly ($P<0.001$) from the other groups. The only case where *Daphnia* capture interval and sequence of prey eaten were positively correlated was with 3.8 mm *D. magna* in the density of 30 per aquarium (Table 1; $r=0.493$ ($P<0.001$). Also, the slope ($b=7.29$) deviates from zero ($t=3.07$, $P<0.001$)) indicating increased satiation and/or decreased foraging motivation.

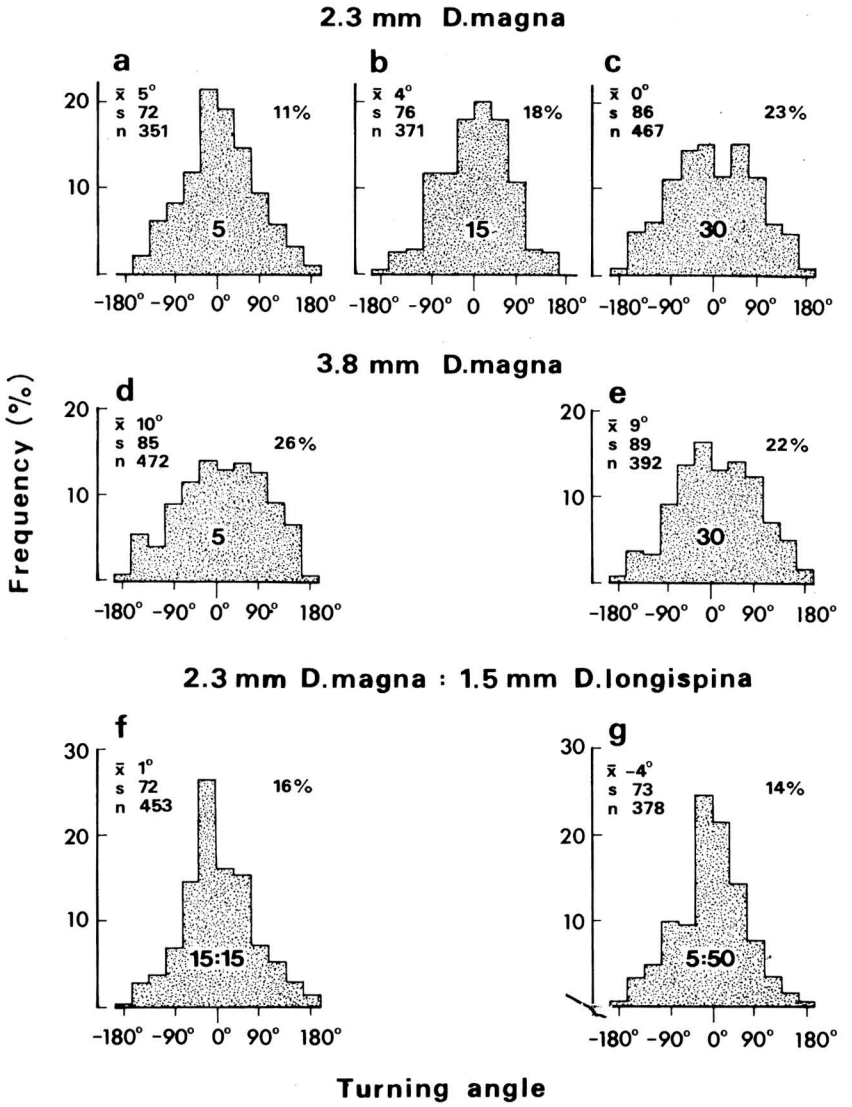

Fig. 1. Directionality of smooth newt turns (frequency distribution of left-hand (negative values) and right-hand (positive values) turns made) while foraging on different-sized *Daphnia* in different densities (figures inside the histograms) in single-prey and two-prey experiments. Mean ($\bar{x}$), standard deviation (s) and total number of turns made (n) are given for each histogram. None of the frequency distributions displayed deviate from a normal distribution (G-tests), and none of the mean values deviate significantly from 0° (t-tests). The inserted % indicates the proportion of turns made with an angle >90°. When the percentages of turns >90° are compared in pairs between the seven experiments (a−g), the following differences are not statistically significant: b−e, b−f, b−g, c−d, c−e, and f−g. All the other differences are significant at $P<0.05$ (G-tests).

Duration of a newt foraging bout averaged 20−30 sec. in our single- and mixed-prey experiments (Table 1). The 3.8 mm *D. magna* foraging bouts are an exception, lasting 20−30 sec. longer than the other foraging bouts. Handling times for 1.7 mm, 2.2 mm and 3.8 mm *D. magna* are approx. 4, 5 and 11 sec., respectively (Nuutinen & Ranta 1986). Thus, it seems likely that other factors besides longer handling time are also responsible for the significantly longer foraging bout duration for the 3.8 mm *D. magna*. Our data on the unsuccessful and successful attempts to catch a prey (Table 1) show that bigger *Daphnia* seem to be better in escaping from a foraging newt. The successful capture % is also lower in high

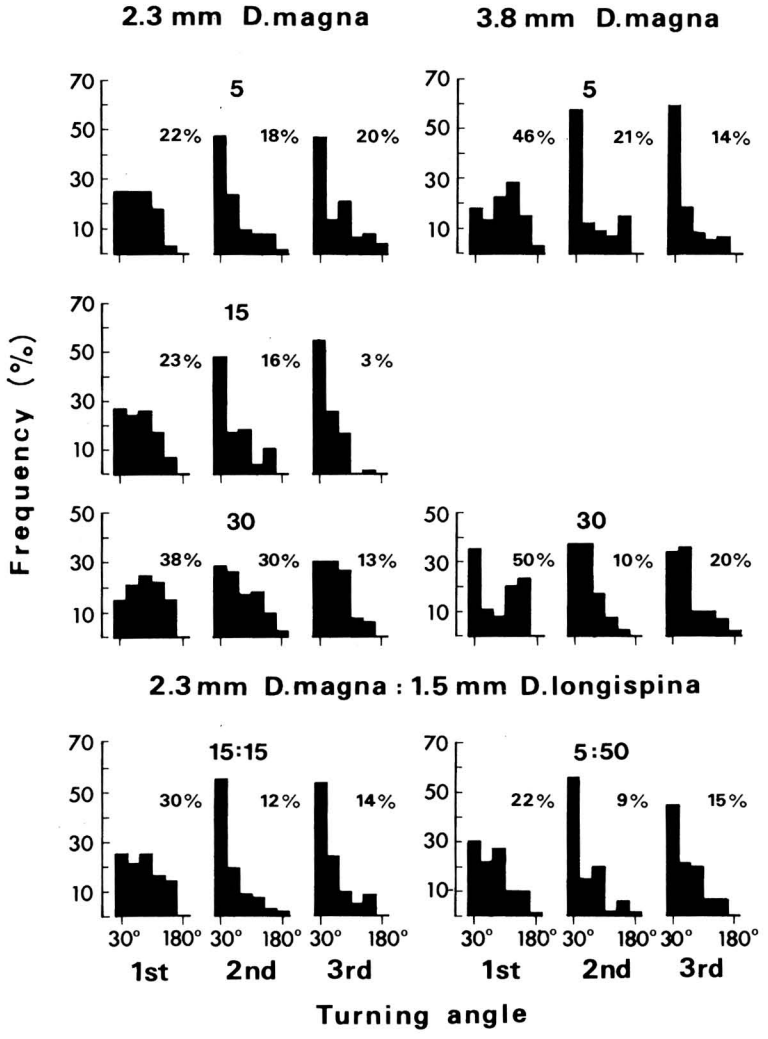

Fig. 2. Frequency distribution of turning angles of subsequent turns made within foraging bouts in different densities (numbers above histograms) of single-sized or two-sized prey. The data are displayed only for the 1st, 2nd and 3rd turn after the ingestion of a prey. The inserted % indicates the proportion of turns made with an angle >90°. In all cases the frequency distribution of angles made in the 1st turn deviates significantly (at the $P<0.05$) from the frequency distributions of angles made in the 2nd and 3rd turn (*G*-tests).

Daphnia densities (Table 1). It may also be that in high *Daphnia* densities foraging newts become confused about which prey to capture and thus make more unsuccessful strikes.

3.2. Newt directionality

Frequency distributions of newt turning angles are best characterized by normal distributions peaking at approx. 0° (Fig. 1). Newts tend to prefer a straight ahead direction while foraging, though the number of strong turns ($\geq 120°$) is always considerable (11–26 % of all angular moves made). Secondly, foraging newts responded in the 2.3 mm *D. magna* single-prey experiments to increasing prey density by increasing the angle of turns (Fig. 1 a–c). Similarly, foraging on large (3.8 mm) *D. magna* increases the angle of turns, but here no change in the shape of the histogram of turning angles was observed with increasing *Daphnia* availability (Fig. 1 d, e). Thirdly, no correlation exists between the number of turns made and foraging bout length (Table 1). Fourthly, a one-way ANOVA (original data

square-root transformed) shows that the seven groups differ in numbers of turns made per foraging bout ($F_{6,474}=3.15$, $P<0.001$). The difference is due to the numbers of turns made while foraging on 3.8 mm *D. magna* (both densities, *t*-tests, $P<0.05$).

At least two alternative explanations exist for the observed pattern of newt directionality in the experiments. Firstly, in high densities or with large prey newts make more unsuccessful attempts at capturing their *Daphnia* prey (Table 1). Secondly, encountering an abundance of prey causes newts to turn more widely in order to keep within the high quality food patch (we return to this below).

A newt foraging bout can be divided into more or less discrete parts, viz., a foraging newt moves a short distance, pauses, and moves again until a prey is captured. After a successful capture the newt pauses to ingest the prey. In our experiments newts did not move when they were eating. Within a foraging bout we numbered the moves from 1 (just after a capture) to the last move before a capture. Analysing changes in newt directionality between the moves shows that turning angles in move 1 are more evenly distributed than in the 2nd or 3rd moves, which tend to be more straight ahead (Fig. 2). An examination of the 4th and subsequent turns confirmed that the 1st turn is the only one deviating consistently from the directionality of other turns. This pattern holds for all experiments.

3.3. Area restricted search

The increased turning angle after feeding suggests that foraging newts might make attempts to stay close to the place where they managed to capture a prey. To examine this possibility we used a computer simulation to study the foraging success of predators having three different moving tactics before and after the capture of a prey. In the simulations a 'directed-directed' predator has always directed moves (i.e., prefers to move straight ahead). A 'directed-random' predator has directed moves when not encountering prey, then turns randomly just after capturing a prey. This turning tactic corresponds with the observed smooth newt behaviour (Fig. 2). A 'random-random' predator turns randomly before and after encounters with prey. In a simulation a predator moves in a 200x200 grid step by step from a node to another node with a given probability to move to any of the eight neighbouring nodes. In random turns each of the eight possibilities has a similar probability of occurrence, while for directed turns straight ahead moves have a probability of 0.51, the probability for 45° turns is 0.25, for 90° turns 0.15, for 135° turns 0.07 and 0.02 for 180° turns. These probabilities correspond to those observed by foraging newts in the present study (Fig. 2).

The simulations were run using only two densities, 128 and 512 items per the 200×200 grid. The prey were allocated either randomly or in aggregates of 2, 4, 8 and 16 items. Predators using the three moving tactics were allowed to search for prey in the grid for 500 steps, prey encountered in the grid nodes were scored and removed, but replaced elsewhere at random in the grid. Thus, prey numbers were held constant during a run. Average scores of ten replicated runs for each density and aggregate size are reported in Table 2.

In these simulations the 'directed-random' moving rule is the best of the three moving tactics in the aggregated high-prey densities and also improves in the low-densities with increasing aggregate size (Table 1), while the 'random-random' moving rule is always the worst one. When the prey are randomly dispersed both the 'directed-directed' and the 'directed-random' moving tactics do equally well.

4. Discussion

Increasing prey availability or prey size causes newts to make more and wider turns while foraging. This may indicate that newts make attempts to stay within an aggregate of food once it is encountered. Directionality of a foraging newt decreases after a successful *Daphnia* capture, while newts tend to move straight ahead before feeding. This behaviour type, klinokinesis (area restricted search), has been documented for a number of predatory and parasitoid insects (Banks 1957, Chandler 1969, Murdie & Hassell 1973, Evans 1976, Hassell 1978) and for other foragers when food is patchily distributed (Pyke et al. 1977, Pyke 1978, 1981, Heinrich 1979).

It is frequently argued that klinokinesis functions to keep a predator within a cluster of prey (Chandler 1969, Evans 1976, Hassell 1978). This behaviour is examined in theoretical terms by, for example, Murdie & Hassell

Table 2. Comparison of performances of the three foraging strategies tested in the computer simulations. The mean score with standard deviation is given for 10 runs, each lasting 500 steps. Aggregated distribution was produced by allocating a given number of prey (A) within 1600 subunits (each 5×5) in the 200×200 grid; N refers to the number of subunits having prey. The abbreviations refer to the turning tactics of a forager before and just after an ingestion of food (DD = Directed-Directed, DR = Directed-Random, RR = Random-Random); see text for more details. Differences between numbers of prey encountered are statistically always significant ($P<0.05$) between the DD−RR and DR−RR tactics. Also, with the exception of prey distributed at random, the tactics DD and DR differ at least at $P<0.08$ (Mann-Whitney U-tests).

A	N	Density	DD	DR	RR
2	64	128	0.5±0.15	0.8±0.19	0.0±0.00
2	256	512	2.7±0.53	3.5±0.89	1.8±0.41
4	32	128	0.9±0.44	0.7±0.25	0.0±0.00
4	128	512	3.1±0.41	4.5±0.98	1.3±0.66
8	16	128	0.2±0.19	1.2±0.54	0.0±0.00
8	64	512	3.5±0.70	5.8±1.42	0.5±0.35
16	8	128	0.3±0.28	1.4±0.63	0.0±0.00
16	32	512	5.0±0.63	6.4±1.55	0.0±0.00
Random		128	0.7±0.51	0.5±0.35	0.2±0.19
Random		512	3.8±1.01	3.8±0.73	2.3±0.41

(1973) and Pyke (1978). These models require also that the step length of a predator decrease together with increasing turning angle. Laboratory and field data collected from parasitoids (Chandler 1969, Evans 1976, Hassell 1978) and nectar feeding foragers (Murdie & Hassell 1973, Pyke 1978, 1981, Heinrich 1979) support the model predictions.

With computer simulations we examined the performance of three predator movement tactics, viz., the 'directed-directed' predator always having directed moves, the 'random-random' predator always moving randomly, and the 'directed-random' predator having directed moves when not encountering prey and making random turns just after encountering a prey (i.e. klinokinesis). Our computer simulations involving no step length differences showed that the 'directed-random' tactic gives the best profits (in terms of prey eaten) when prey are aggregated, while the 'random-random' tactic always scored the lowest. In environments where prey were randomly distributed both the 'directed-directed' and 'directed-random' moving rules worked equally well. The results of the computer simulation (the 'directed-random' tactic) and smooth newt orientation observed agree with each other.

During the video recordings we were unable to control the pattern of *Daphnia* distribution to any great extent. Freely swimming *Daphnia* have a tendency to aggregate rather rapidly if the illumination is not entirely homogeneous. In our experiments we avoided the most obvious aggregates by pouring *Daphnia* evenly into the aquarium and by replacing *Daphnia* eaten to areas with low *Daphnia* densities. One can suspect that the observed smooth newt orientation behaviour originates from foraging situations in their natural environments. It is likely that their food in pools and ponds is patchily distributed, and thus it pays to turn sharply after catching a prey because the chances of encountering another item in the aggregate increase. Feeding depletes the quality of the patch. Hence, if no more prey are found, it pays to move further away from the area of feeding.

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