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Female–male activity and zooplankton foraging by the smooth newt (*Triturus vulgaris*)

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Behaviour of smooth newt females and males foraging on zooplankton was studied. Diel activity patterns of the sexes differed in both movement and feeding activities. Female newts moved slightly more at night and in early morning hours while males had their highest swimming activity around midday. Feeding activities were at greatest around noon for both sexes, lasting longer at a more intense level in females than males. Both sexes clearly preferred larger prey over smaller ones in size–selectivity experiments. No significant differences in numbers of prey eaten were found between female and male newts.

Allowing a female and a male to forage together resulted in clear behavioral differences between the sexes. Females were more interested in foraging while males displayed more interest in courtship. Increasing hunger, however, modified the sequence of male activities. With lengthened food deprivation courtship interests were increasingly followed by feeding, while well fed males almost ignored foraging compared to the response of females. The level of hunger also altered the time sequence of newt activities. With no food deprivation, feedings occurred rather evenly throughout the trials whereas increasing hunger led to most of the feedings taking place at the beginning of the experimental sessions.

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1. Introduction

The smooth newt, *Triturus vulgaris* (L.), is a predator in small freshwater pools and ponds (Steward 1969, Dolmen 1983c). A great variety of aquatic invertebrates in these habitats are potential prey for the newts (Avery 1968, Pellantova 1973, Dolmen & Koksvik 1983). Our objective is to gain an understanding of the behaviour of smooth newts while they are searching for prey (Ranta & Nuutinen 1985, Nuutinen & Ranta 1986, Ranta et al. 1986). This paper describes a set of experiments used to detail to what degree smooth newt female and male foraging behaviour agrees. To our knowledge, there are no published results where feeding behaviour of female and male smooth newts have been compared in controlled situations. We focused on diel activity pattern and prey size selection by both sexes of smooth newts. In order to build on results of previous studies (Ranta & Nuutinen 1985, Nuutinen & Ranta 1986, Ranta et al. 1986) *Daphnia* of different size classes were again used as prey in similar experimental design. This parallel design allows us to test the generality of our earlier results.

2. Material and methods

2.1. General

Adult smooth newts were netted from a large pond on the island Långskär, close to the Tvärminne Zoological Station (University of Helsinki), southern coast of Finland. In the laboratory their snout–vent body lengths and live body weights were measured. The newts were kept separately in 28×18×10 cm containers with 3 l of water from the newt pond at ambient room temperature (20–25°C, which corresponds to water temperatures recorded from newt ponds in the Tvärminne area) and natural photoperiod. The food deprivation and activity experiments were run from 15 May – 6 June, 1984 and the diel activity and size–selectivity experiments from 3–26 June, 1985. In no cases were newts kept longer than two weeks in the laboratory.

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For the experiments we fed newts different size classes of *Daphnia magna* Straus. Discrete size classes were achieved by separating the *Daphnia* through a series of sieves (mesh sizes: 3.0, 2.5, 2.0, 1.5, 1.0 and 0.5 mm). In the 1984 experiments we used the *Daphnia* which remained on the 2.5 mm sieve (body length without tail spine 3.8±0.2 mm). In the 1985 experiments the small prey used were *Daphnia* remaining on the 1.0 mm mesh and the large ones were those remaining on the 1.5 mm mesh (body lengths 1.7±0.1 and 2.2±0.1 mm, respectively). If not otherwise stated newts were deprived of food for 8–12 h before the trials, and allowed to feed ad libitum on *Daphnia* of all sizes after the experiments. Throughout the study we used experimental aquaria of 38×28 cm white polyethylene filled with 3 cm of pond water.

2.2. Diel activity

Activity of the newts was tested every four hours over a 24 hour period (00, 04, 08, 12, 16 and 20, GMT hours) under natural light conditions (ca. 19L:5D) in the laboratory. Newly collected newts (collecting dates and hours of beginning of recording: 4 June 12.00; 17 June, 20.00; 25 June, 12.00) were introduced into containers with an abundance of 2.2 mm *Daphnia*. They were allowed to acclimate for 2–3 hours before the experiment began.

The bottom of the experimental aquaria were marked into ca. 2×2 cm grids. Each newt was acclimated for 15 min. in a holding aquarium and then transferred to the experimental aquarium having a constant 30 2.2 mm *Daphnia*. For a period of 10 min. we counted the (1) number of grid unit crossings (movement activity), (2) number of strikes made towards *Daphnia* (feeding activity), and (3) visits to the water surface to breathe. After each recording session was over the newts were returned to their containers and given unlimited food. Our data refer to the activity of non–deprived newts.

2.3. Size–selectivity

In these experiments *Daphnia* of 1.7 mm and 2.2 mm were introduced in a ratio of 30:30 into the aquarium. The experimental aquarium was lit (ca. 200 lux at the water surface), and the experiments were run between 9.00–17.00 hours. Before each 10 min. experiment newts were introduced into a similar aquarium to acclimate for about 20–40 min.

After the introduction of a newt into the aquarium the recording was started when the newt fed on its first *Daphnia*. We recorded in sequence the number and size of prey eaten as well as unsuccessful strikes. Any prey eaten were replaced with *Daphnia* of their size so that our observations refer to feeding rates at constant prey densities and size ratios.

We ran additional experiments to score the number of 1.7 mm prey eaten per 10 min. observation time at prey densities of 30, 60 and 120 *Daphnia*.

2.4. Food deprivation and female–male activity

The experiment (run in late May, 1984) was designed to distinguish possible differences between females' and males' choice of behavior when given *Daphnia* to feed on. A random pairing of newly caught newts, a female and a male, was placed together into an aquarium containing 30 3.8 mm *Daphnia*. For the next 22 min. we video recorded their behaviour. During the experiment *Daphnia* eaten were replaced in sets of 5 to keep the prey density approximately constant.

We subjected the newts to three levels of hunger manipulation. First, their activity was studied when they had

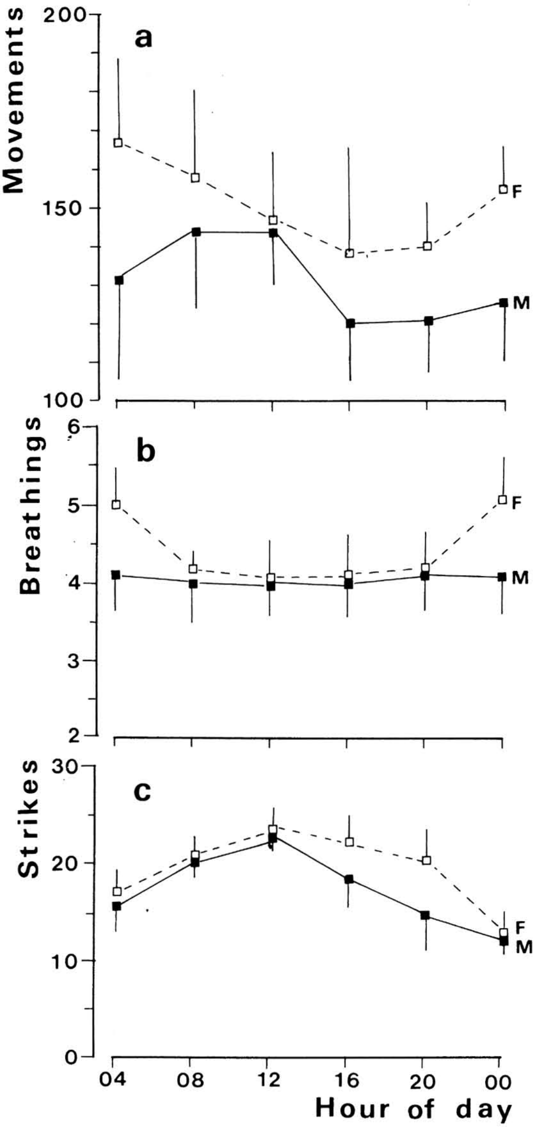


Fig. 1. Diel activity of smooth newt females (F) and males (M; mean with standard error), a = movements per 10 min. observation period (see p. 000), b = visits to water surface to take fresh air, c = feeding activity as measured by total number of strikes made on 1.7 mm *Daphnia*.

had an ad libitum access to *Daphnia* during the previous 12 hours. After the video recording the pairs were deprived of food for 24 hours, and then their activity was once again recorded in the experimental aquarium. In the final stage the same newts were deprived of food for 48 hours before recording.

The level of breeding interest in newts is difficult to measure given only their outer appearance (especially in females), and so our experimental design provides only for newt pairs with three levels of hunger: (a) no food deprivation, (b) 24 h deprived, and (c) 48 h deprived animals. The video equipment broke down during the experiment and so we have 14, 12 and 7 (a, b and c, respectively) replicated runs for the three levels of food deprivation.

The video tapes were used to read the duration (with an accuracy of one second) of the following activities: feeding, breathing, and encounters of the other sex. For males we also recorded if the encounter led to active following of the female, and if the following turned out to more pronounced courtship activities. These fine–tuned behavioural events are described in full detail by Halliday (1974, 1975b, 1976, Halliday & Sweatman 1976). In our experiments the newts did not complete the full sequence of courtship behaviour. This was most likely due to females not responding as expected by males. Thus, for the present we have pooled all the courtship sequences under 'sniff, whip and fan' (see Halliday 1975b: 295).

3. Results

3.1. Diel activity

The diel activity comparisons revealed some differences between the sexes (Fig. 1). The Tvärminne newts seem to have a slight peak in movement activity during the night and early morning hours (Fig. 1a), with females active earlier and displaying slightly higher activity levels than males. A two–way analysis of variance (*sex*, *time of day*, and *experiment date* as grouping variables; original data log-transformed) shows that only sex ($F_{1,5}$ = 4.30, $P<0.05$) is a significant factor in the general model explaining the observed variation.

The number of times when newt sexes surfaced to breathe averages slightly above four per 10 min. (Fig. 1b). No clear diel pattern was observed in number of breathings, though females do have slightly elevated levels of activity in the mid–night hours. A clearly different pattern became apparent when the diel activity was measured in terms of strikes made on the *Daphnia* (Fig. 1c). In both sexes the activity peaked between 0800 and 2000 hours. In this case both sex ($F_{1,5}$ = 11.14, $P<0.001$) and time of day ($F_{5,5}$ = 3.09, $P<0.05$) contributed as statistically significant factors to the two–way ANOVA. That is, females are slightly more active in feeding, especially in the late afternoon and evening hours, than males (Fig. 1c).

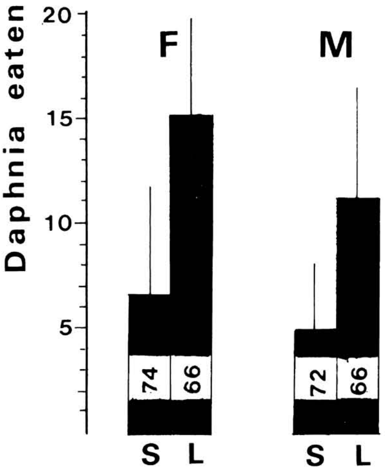


Fig. 2. Number of 1.7 mm (S) and 2.2 mm (L) *D. magna* eaten (mean with standard deviation) by smooth newt females (*F*, *n* = 19), and males (M, *n* = 17; numbers within columns indicate percentages of successful strikes of all strikes made on corresponding prey sizes).

3.2. Size–selective predation

Allowing smooth newts to forage in a constant ratio of 30:30 items of 1.7 and 2.2 mm *D. magna* showed that both sexes took a disproportionally greater share of the large prey (70% of *Daphnia* eaten both in females and males) (Fig. 2; *G*-test against the 1:1 expectation, females G = 37.99, males G = 24.34, $P<0.001$ in both cases). Thus, in terms of size–selective predation there are no differences between the smooth newt sexes.

We did not find any sex dependent differences in numbers of *Daphnia* eaten in the experiments where the newts were foraging on 1.7 mm *D. magna* in three differing densities (Table 1). An examination of the mean values of *Daphnia* eaten suggests that in these prey densities the functional response of the smooth newt sexes has already levelled off to the ± constant level frequently observed in type II functional responses (Ranta & Nuutinen 1985 give more detailed examples). However, prey density affects the foraging success of smooth newts, with the percent of successful strikes decreasing with increasing prey density (Table 1). This pattern agrees with our earlier observations (Nuutinen & Ranta 1986).

Table 1. Rate (prey/10 min.) of 1.5 mm *Daphnia* feeding by smooth newt females and males at three different prey densities. For the statistical analysis the original data were square-root transformed (feeding rate) or square-root-arcsin transformed (% strikes).

	Females			Males				Two-way ANOVA			
Density:	30	60	120	30	60	120		Sex	Density	Sex&dens.	Error
Feeding rate											
Mean	20.1	23.0	20.5	16.2	21.7	23.6	*F*	0.56	0.54	1.40	
SD	7.8	10.0	8.1	4.3	10.0	10.1	*P*	0.458	0.587	0.256	
Percentage of successful strikes											
Mean	69	60	61	71	62	56	*F*	0.01	3.31	0.21	
SD	15	12	9	18	17	16	*P*	0.910	0.044	0.810	
n	13	5	10	13	10	10	*df*	1	2	2	55

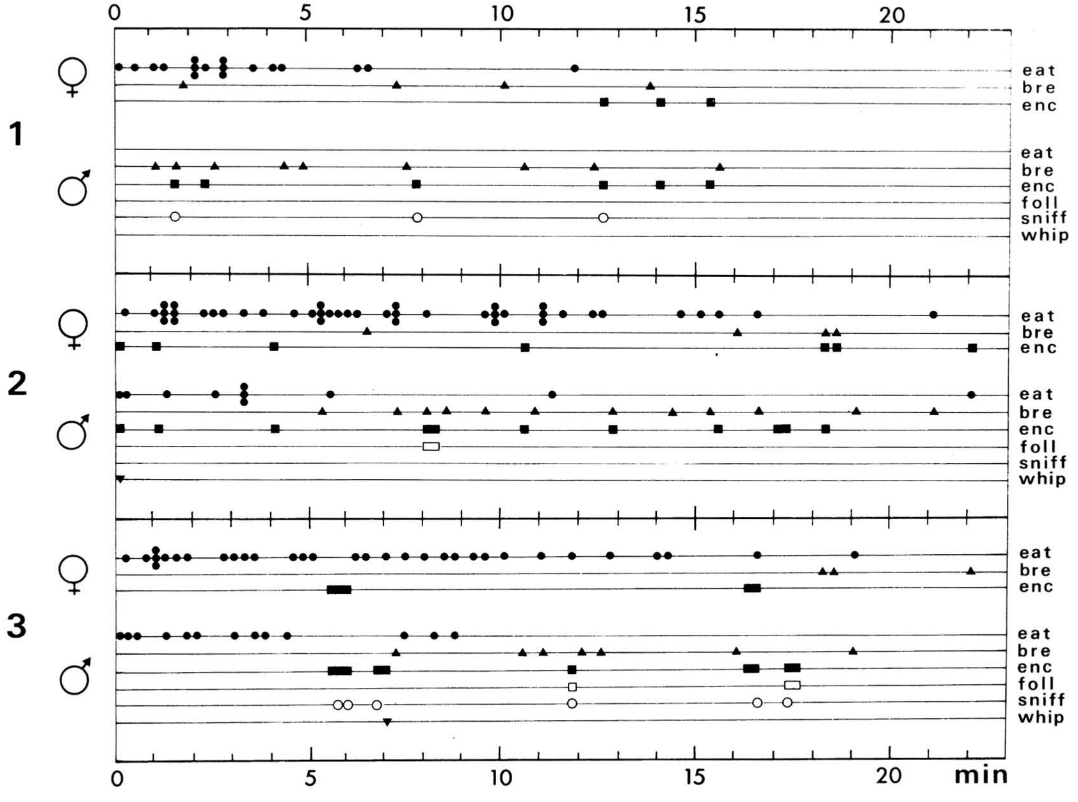
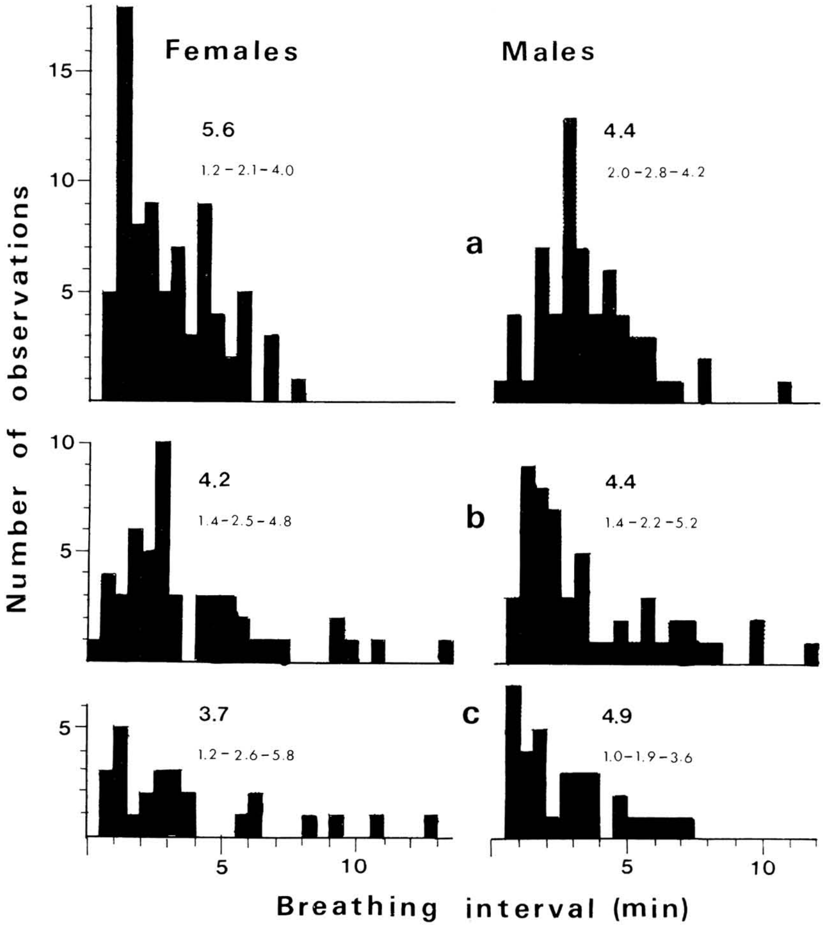


Fig. 3. An example of activity of a female (no. 13) and male (no. 8) smooth newt with three levels of hunger: (1) no food deprivation, (2) 24 h food deprivation and (3) 48 h food deprivation. Beginning and end of the activities (eat = *Daphnia* feeding, bre = breathing, enc = encounter with the opposite sex, foll = the male follows the female, sniff (sniffing the female cloaca) and whip (whipping or fanning with the tail) are courtship behaviour terms after Halliday (1976) are shown with an accuracy of 15 sec. (in cases of feeding, overlapping occurrences in this time scale are shown).

Fig. 4. Breathing intervals (time elapsed between subsequent breathings) by smooth newt females and males with different levels of food deprivation (a = no deprivation, b = 24 h deprivation and c = 48 h deprivation). The topmost number in each histogram indicates the mean number of breathings per newt, median and lower–upper quartiles of the frequency distributions are also inserted.



3.3. Females and males foraging together

The behaviour of smooth newt females and males foraging together was analysed both in terms of foraging and courtship behaviour (see Halliday 1974, 1975b, 1976 for a thorough description of the courtship behaviour). As we were unable to manipulate sexual activity of the foraging pair we manipulated their level of hunger. We used newts with no food deprivation, with 24 h, and with 48 h food deprivation. An example of the data to be discussed here is shown in Fig. 3.

The median breathing interval in females was 2–2.5 min (Fig. 4), and it was independent of the level of hunger (Kruskal–Wallis one–way ANOVA $H = 1.43$, *df* 2, $P>0.1$). The corresponding values for males range from 2.8 min (no food deprivation) to 1.9 min (48 h food deprivation) and the differences between the three treatments are statistically significant ($H = 6.01$, $P<0.05$).

For both sexes the time intervals between subsequent feedings are skewed to the right (Fig. 5) indicating that the newts alternate between eating a few *Daphnia* in a short period, switching to some other behaviour (e.g., breathing) and then resuming feeding. The hunger level manipulations depict interesting differences between females and males (Fig. 5). First, with no food deprivation at all, male newts seem to be less interested in foraging (mean number of *Daphnia* eaten per male = 2.1) than in other activities (Table 3), while females showed much higher food intake (6.3 *Daphnia* per female). With 24 h and 48 h food deprivation the average intake rates are 13.5 and 13.4 *Daphnia* per male, respectively, and 20.0 and 23.3 *Daphnia* per female (all the differences between sexes in corresponding

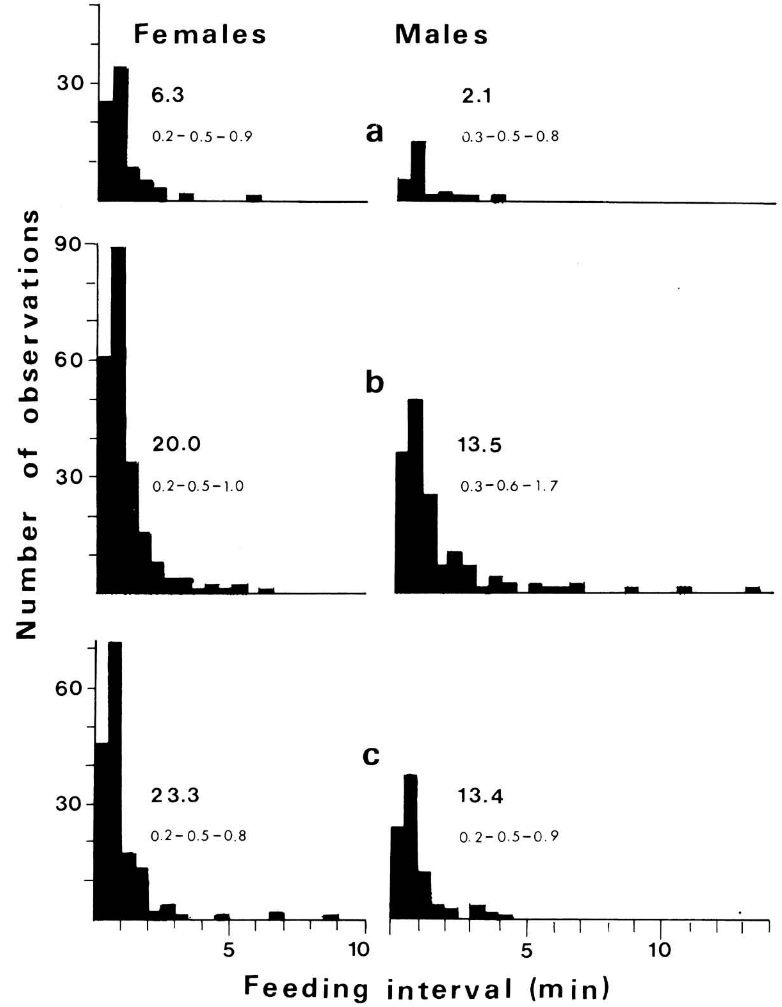


Fig. 5. Feeding intervals (time elapsed between subsequent *Daphnia* feedings) by smooth newt females and males with different levels of food deprivation (a = no deprivation, b = 24 h deprivation and c = 48 h deprivation). The topmost number in each histogram indicates the mean number of *Daphnia* eaten per newt, median and lower–upper quartiles of the frequency distributions are also inserted.

levels of hunger are statistically significant; Mann-Whitney *U* tests, $P<0.05$). Feeding interval differences due to hunger levels in females ($H = 11.21$, $P<0.01$) and males ($H = 17.74$, $P<0.001$) are statistically significant.

An examination of the frequency distributions of feedings and breathings in time (by dividing the experiment time into three parts, 1st, 2nd and 3rd third segments of the total time, ca. 22 min, available in the recordings) reveals the following points (Fig. 6). With no food deprivation, feedings and breathings are rather evenly distributed over the experiment time for both sexes. However, with increasing hunger, feedings tended to occur more and more at the beginning of the experiments and breathings took place increasingly during the last two thirds of the experiments (Fig. 6).

The pattern of changing activities both due to level of hunger and within the experiments is shown in Tables 2 (females) and 3 (males). The data displayed are first order transition matrices, i.e., they show which single behaviour type follows a given behaviour. For example, in females with no food deprivation feeding usually follows feeding, and the pattern goes rather evenly throughout the experiment. However, increasing the level of hunger makes the feeding–follows–feeding category (Table 3) to be strongly dominant in the beginning of the experiment, and less and less likely towards the end of the experiment.

The same is also more or less true in males (Table 3), though here the behaviour was split into finer fractions. We took the two actions, active female following and 'sniffing & tail whipping–fanning'

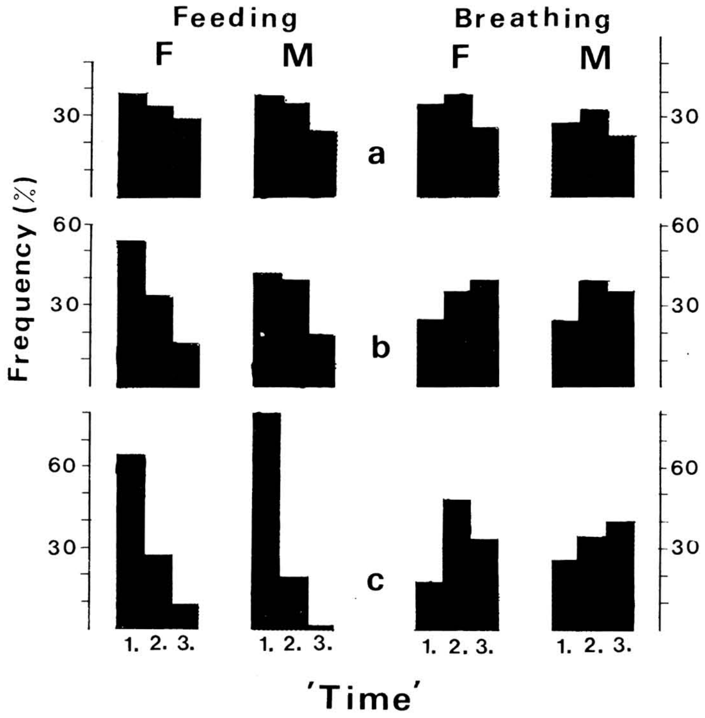


Fig. 6. Frequency distributions of feeding and breathing events by smooth newt females and males with three different levels of food deprivation (a = no deprivation, b = 24 h deprivation and c = 48 h deprivation). The experiment time is divided into the 1st, 2nd and 3rd third of the total time (ca. 22 min for each recording). Statistically significant differences between sexes are found as follows: feeding b, feeding c; breathing c (*G*-tests, at least $P<0.05$). In females the histograms b and c differ from a both in feeding and breathing, in males feeding c differs from feeding a and b, and breathing c differs from breathing a (*G*-tests, at least $P<0.05$).

Table 2. Transition matrices for female smooth newt behaviour in the three food deprivation levels (no deprivation, 24 h and 48 deprivation). FE = feeding, BR = breathing, EN = encounter with a male, *n* = number of events. The observation time was divided into three parts, 1st refers to the first third, 2nd to the second third and 3rd to the last third of the time elapsed (see text). Matrix entries are percentages rounded up to the nearest integer.

Preceding behaviour	Following behaviour								
	1st third			2nd third			3rd third		
	FE	BR	EN	FE	BR	EN	FE	BR	EN
No food deprivation									
FE	39	4	4	24	7	1	23	2	2
BR	6	15	13	4	18	22	4	23	18
EN	4	13	3	0	17	7	0	12	18
			n = 101			*n* = 72			*n* = 57
24 h food deprivation									
FE	61	5	10	55	12	4	36	7	5
BR	7	1	1	12	6	4	10	11	10
EN	10	3	3	5	4	0	4	10	7
			n = 157			*n* = 108			*n* = 81
48 h food deprivation									
FE	70	2	9	50	11	1	20	9	9
BR	5	0	0	6	6	10	9	9	9
EN	8	3	3	4	9	3	9	9	20
			n = 122			*n* = 70			*n* = 35

Table 3. Transition matrices for male smooth newt behaviour in the three food deprivation levels (no deprivation, 24 h and 48 deprivation). FE = feeding, BR = breathing, EN = encounter with a female, FO = active following of female, SW = 'sniff', or 'whip of the tail' (signs indicating courtship activity), n = number of events. The observation time was divided into three parts, 1st refers to the first third, 2nd to the second third and 3rd to the last third of the time elapsed (see text). Matrix entries are percentages rounded up to the nearest integer.

Preceding behaviour	Following behaviour														
	1st third					2nd third					3rd third				
	FE	BR	EN	FO	SW	FE	BR	EN	FO	SW	FE	BR	EN	FO	SW
No food deprivation															
FE	4	0	1	0	0	4	0	1	0	0	0	1	1	0	0
BR	0	2	5	1	1	1	3	6	2	1	1	1	5	0	2
EN	0	2	0	5	5	0	2	2	4	4	1	2	5	4	6
FO	0	2	4	3	4	1	4	3	6	2	1	3	5	4	4
SW	5	10	10	17	19	3	12	9	18	9	1	12	16	9	18
					n = 281					n = 33					n = 218
24 h food deprivation															
FE	16	2	5	0	0	16	10	3	3	1	10	3	3	1	1
BR	2	0	2	0	1	3	2	5	0	0	3	4	5	0	1
EN	1	1	1	2	6	1	2	0	1	5	3	3	2	2	5
FO	3	0	2	1	1	2	2	0	1	3	3	3	3	3	2
SW	20	4	6	7	17	16	8	9	5	13	10	7	9	6	9
					n = 190					n = 266					n = 281
48 h food deprivation															
FE	22	2	4	0	1	14	1	4	0	0	0	0	1	0	0
BR	2	1	0	0	0	2	4	2	0	0	0	5	8	2	0
EN	2	0	0	2	4	1	1	1	1	5	0	5	1	3	8
FO	6	0	1	1	2	3	2	2	0	1	0	3	5	1	1
SW	27	2	4	5	13	19	8	9	5	14	2	17	17	5	16
					n = 252					n = 487					n = 109

(FO and SW in Table 3) to indicate the level of sexual interests in males, and then compared in what proportions they are followed by feeding (an activity less likely to indicate courtship interests). We found that with no food deprivation the percentages for the 1st, 2nd and 3rd part of the experiment are 5.3, 3.8 and 1.9%. Increasing the level of hunger makes the corresponding percentages range from 13% to 32% (Table 3; the 3rd part of the 48h deprivation with 1.8% is an exception). In other words, male newts have rather high sexual interests almost regardless the level of hunger, but as females do not respond positively, they resume feeding, especially when the level of hunger is high.

The data given in Tables 2 and 3 clearly demonstrate that the behaviour of both sexes are greatly dependent on their level of hunger, which naturally decreases as they feed more with elapsing time in the experiments. This makes fine-tuned behavioural patterns (e.g, second and higher order conditional transition sequences) difficult if not impossible to analyse.

4. Discussion

Diel rhythms of the aquatic phase of the smooth newt have been studied in central Europe (Himstedt 1971), central Norway (Dolmen 1983a, b) and southern England (Griffiths 1985). Usually a crepuscular peak of activity has been found, being more pronounced in females than males. In this study the diel activity of the smooth newt females and males differs if we look at movement and feeding activity. Female newts move most around in the aquarium during the night and early morning hours, while males have the highest movement activity around the noon. Feeding activities, however, are at highest around noon for both sexes, lasting at elevated level in females longer than in males. Contrary to this study Griffiths (1985) observed that in English ponds smooth newt feeding occurs at night time only.

Dolmen (1983b), while trapping newts, observed that male newts are rather evenly active both in early and late season, while in the middle they may even display bimodal activity (low phase during dark hours). In females he reports a peak of activity at about midnight in early season, but rather even diel activity during late season. In southern England the smooth newt movement activity peaks between 1600 and 2200 hours, although different populations do display differing activities (Griffiths 1985). The reasons for the differences between the reported cases are somewhat uncertain. Some likely sources of variation are differences in methods recording the activity, geographic and seasonal differences, differing weather and light conditions.

In the size–selectivity tests we did not find significant differences in prey size choice between females and males. Both sexes clearly preferred the larger *Daphnia* over the smaller ones, and they also ate the two prey sizes in the same proportions.

These data tell us that both female and male newts use the same criteria while deciding whether or not to accept the prey in vision. Also, no differences due to sex were found when the newts were foraging in constant densities of the 1.7 mm *Daphnia.* We can conclude that the results of feeding rate and diet selection by Ranta & Nuutinen (1985) and Nuutinen & Ranta (1986) are applicable for both sexes of the smooth newt.

When smooth newt females and males are allowed to forage together males do show less interest in feeding than do females. This held true even when the level of hunger was increased. However, the ordering of the behavioural events is likely to change with increasing number of prey eaten. For example, feeding is concentrated more at the beginning of the experimental session, while breathing bouts show the opposite trend. An obvious explanation for this is that foraging, occurring in short bursts, has the highest priority in hungry animals. While feeding, the oxygen reserved are exhausted (or the air bubble stored in the mouth is gradually lost) and needs for fresh air increase.

Halliday (1974, 1975b) has thoroughly described the movement sequence male newts display in courtship. In smooth newts the female must respond positively to the courting male in order to elicit the complete sequences of behaviour. This is difficult to observe in laboratory experiments without manipulating the female responses (see Halliday 1975b: 294). The present data show that males kept trying to complete courtship even though female responses were minimal. Males showed rather high interest in sexual activities even in the experiments where food deprivation continued to 48 h. Hunger did modify the transition probability of the behavioural sequences. With increasing hunger displays indicating 'sexual' interests were increasingly followed by feeding. Nevertheless, after feeding on a few *Daphnia*, males resumed their courtship sequences in the pattern observed in the experiment without food deprivation.

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