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Short communication

An estimation of the heritability of phototaxis in *Daphnia magna* Straus

Luc De Meester
Laboratory of Animal Ecology, State University of Ghent, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

Summary. The phototactic responses of four clones of *Daphnia magna* were experimentally analysed. Broad-sense heritability of this behavioural character was estimated through an analysis of variance, and it was very high under the standardised experimental conditions of this study.

Key words: *Daphnia magna* – Phototaxis – Vertical migration – Heritability

Diel vertical migration of zooplankton (sub)populations is a well documented and very widespread ecological phenomenon. Typically, the major fraction of the zooplankton population is found in deeper water during daytime than during the night (Cushing 1951). The overall importance of light stimuli in governing vertical migration is illustrated by field studies (e.g. Clarke 1934; McNaught and Hasler 1964) as well as by experimental results. Harris and Wolfe (1955), working with *Daphnia magna*, succeeded in inducing vertical migration cycles of varying length by merely changing light intensities. The results of Ringelberg (1964) indicate that the relative change of light intensity is the real stimulus initiating phototactic responses. However, it must be stressed that the pattern of vertical migration may be influenced by a complex of ecological parameters. Thus, Bayly (1986) concluded that the sporadic occurrence of reverse migration (deeper in the water column at night) can not be assigned to one single factor.

Many studies have focused on the possible adaptive significance of vertical migration in zooplankton. Predator avoidance (Zaret and Suffern 1976), photo-damage (Hairston 1978) and niche segregation (Lane 1975) are possible ultimate causes for the evolution of vertical migration.

Using *Daphnia magna* as the experimental animal, females characterised by different phototactic behaviours could be isolated (Dumont et al. 1985; De Meester and Dumont 1988). As *Daphnia magna* reproduces by apomictic parthenogenesis under favorable culture conditions (Hebert and Ward 1972), experiments on the resulting clones are indicative for the relative importance of genotype versus environment with respect to the variability of the observed behaviour. In this way, working with clones provides a straightforward method for the estimation of heritability in the broad sense (Falconer 1981).

Materials and methods

Daphnia magna was used as the experimental animal. Most experimental studies on vertical migration have been done on this species, it being easy to culture and manipulate. Though it is a pond species, it exhibits diurnal vertical migration in nature (unpublished data).

Test animals were reared in one liter jars. For culture methods, we refer to Dumont et al. (1985) and De Meester and Dumont (1988). Preliminary tests showed the need for animals to be in good condition when tested for their behavioural responses (see also De Meester and Dumont 1988). About eight days before an experiment, 15 to 20 test animals were placed as juveniles in suitable culture medium; they were fed (*Scenedesmus acutus* + horse manure extract) every two days. In this way, the test animals grew under optimal and fairly standardised conditions: at low density and with abundant food. In this study, only adult females were used as test animals. The occurrence of mixis was prevented by culturing at long day photoperiod (14 h/10 h light/dark; Stross and Hill 1965).

The experimental set-up consisted of a small perspex column (25 cm height, 5 cm internal cross-section), placed in a darkened box, and illuminated from above with a 150 W fiber light source (type Schott). The bottom of the column was covered by small black pebbles, so that light reflection was minimised. The column was externally divided in an upper compartment of 10 cm height, a lower compartment of 3 cm height, and a middle compartment of 12 cm height (these boundaries were set after examination of experimental distributions of many different clones). The whole set-up was placed in a temperature buffered ($20 \pm 2°$ C) culture room.

Experiments were carried out with 4 to 10 animals each. The test animals were placed in dechlorinated tap water three hours before the experiment. The experimental column was also filled with dechlorinated tap water. Once in the experimental column, five minutes dark adaptation was given, after which the fiber light source was lit. Each experiment lasted ten minutes. At one-minute intervals, the position of the test animals was recorded. A percentage positively phototactic behaviour can be assigned to the number of animals in the upper compartment, while a percentage negatively phototactic behaviour can be defined for the lower three centimeters of the column. For our present analysis, the observations of the second five minutes of

the experiment were averaged. The value used for mathematical analysis was the logarithmic transformation of the following ratio: animal-observations upper + middle compartment/animal-observations middle + lower compartment $[(U+M)/(M+L)]$.

The obtained data were analysed via a single classification Anova (Sokal and Rohlf 1981). For determing heritability in the broad sense, the method of Parsons (1973) was followed.

Results

Experimental results are tabulated in Table 1. At first glance, large differences between the clones are apparent. The animals of clone 71 were predominantly found in the upper compartment, whereas clone M48 and clone Y animals stayed near the bottom of the experimental column. The experimental distribution of clone E animals was more scattered, with most of the animals in the middle compartment. The values obtained through logarithmic transformation of the ratio $(U+M)/(M+L)$ (animals in upper + intermediate compartment/animals in intermediate + lower compartment) were tested for independence (runs test), homoscedasticity (Fmax test, Bartlett's test) and normality (Kolmogorov-Smirnov test for goodness of fit) and proved suitable for parametric analysis of variance (Sokal and Rohlf 1981). A single classification Anova was carried out on the data of the four clones; the resulting Anova-table is presented in Table 1 B. The variation between the clones is much more substantial than the variation within each set of experiments on a single clone. The FS value is highly significant ($p \ll 0.001$). In a subsequent analysis, pairs of clones were subjected to an Anova: the FS values of all pairs were highly significant, except that of the couple M48/Y (not significant at the 0.5 level).

The data of the Anova-table can be used to estimate heritability of the character studied. Total phenotypic variance has a genetic as well as an environmental component. For the present purpose, interactions between genotype and environment are assumed to be negligible, so $V_p = V_e + V_g$ (V_p = phenotypic variance; V_e = variance due to environmental influences; V_g = variance due to the involvment of several genotypes). Within each group, only one genotype is considered, thus the observed variation is entirely environmental in origin. We note that interference of mutations with our results can be excluded, as no permanent changes, lasting for several generations, have been met. Thus, the mean square within groups can be identified with V_e. The mean square between groups has environmental as well as genotypic components, and is identified with $V_e + rV_g$ (with r the number of replicates in each group; Parsons 1973).

Considering the four clones, $V_e = 0.33938$ and $V_g = (12.59156 - 0.33938)/13 = 0.94248$. Heritability in the broad sense is defined as the relative importance of the genotypic variance component to the total phenotypic variance: $h_B^2 = V_g/(V_g + V_e)$. In the present analysis, the obtained h_B^2 value is approximately 0.735.

We note that, when heritability is calculated for the three clones E, 71 and M48 only, the obtained h_B^2 value is 0.827.

Discussion

The resulting estimate is merely intended to indicate the high degree of heritability of phototaxis of *Daphnia magna*,

Table 1. A) Experimental data. U = animal-observations in the upper compartment; M = middle compartment; L = lower compartment

Date (1987)	No. of ind.	% U	% M	% L	log [(U + M)/(M + L)]
Clone E					
12/05	10	44	56	0	0.252
13/05	10	36	38	26	0.063
27/05	8	20	80	0	0.097
28/05	10	24	76	0	0.108
23/06	10	36	52	12	0.138
6/07	5	84	12	4	0.778
3/08	10	50	46	4	0.283
7/10	4	25	40	35	−0.062
12/10	10	30	52	18	0.069
14/10	5	40	36	24	0.103
15/10	5	8	72	20	−0.060
15/10	10	0	40	60	−0.398
3/11	10	14	74	12	0.010
Clone 71					
30/06	10	78	22	0	0.657
17/07	10	66	28	6	0.441
3/08	10	74	22	4	0.567
7/08	5	80	18	2	0.690
5/10	10	90	10	0	1.000
5/10	10	100	0	0	2.000
4/12	10	100	0	0	2.000
16/12	10	98	2	0	1.699
16/12	10	98	2	0	1.699
16/12	10	82	18	0	0.745
16/12	10	98	2	0	1.699
16/12	10	100	0	0	2.000
17/12	10	88	12	0	0.921
Clone M48					
20/05	10	8	46	46	−0.229
20/05	10	4	18	78	−0.638
21/05	10	0	12	88	−0.921
28/05	10	0	18	82	−0.745
23/06	10	0	0	100	−2.000
16/07	5	0	12	88	−0.921
16/07	5	0	4	96	−1.398
16/07	4	0	20	80	−0.699
3/08	10	0	8	92	−1.097
28/08	10	8	30	62	−0.387
4/09	10	0	0	100	−2.000
6/09	5	8	20	72	−0.523
12/10	10	14	2	84	−0.745
Clone Y					
12/05	10	4	48	48	−0.266
12/05	10	16	40	44	−0.176
12/05	10	8	38	54	−0.260
6/07	5	0	8	92	−1.097
3/09	8	0	10	90	−0.959
7/10	5	16	40	44	−0.176
12/10	10	2	18	80	−0.690
14/10	5	0	0	100	−2.000
15/10	8	0	0	100	−2.000
15/10	8	0	0	100	−2.000
20/10	10	30	56	14	0.090
30/10	10	34	26	40	−0.028
12/11	5	20	44	36	−0.097

B) Anova-table; 4 clones (E, 71, M48 and Y)

	SS	DF	MS	FS
Between groups:	37.7747	3	12.59156	37.1021
Within groups:	16.2901	48	0.33938	

as it is largely dependent on the population (clones) studied and on the experimental standardisation (Parsons 1973; Falconer 1981). The experimental procedure in the present study was highly standardised, thereby reducing environmental variation to a minimum. The observed within group variation is therefore by no means a good estimation of behavioural plasticity under natural conditions.

The heritability estimation based on the data of clones E, 71 and M48 ($h_B^2 = 0.827$) can be thought to indicate a maximum heritability, as the screening of many clones did not reveal the existence of more than three well defined experimental distributions. Crossings of *Daphnia magna* clones are currently being performed in order to clarify the nature of the genetic inheritance of phototactic behaviour.

In previous studies (Dumont et al. 1985; De Meester and Dumont 1988), it was shown that clones of *Daphnia magna* could be isolated that respond differently to high light intensities. Using a simpler but more quantifiable experimental set-up, the results presented here illustrate the repeatability of these findings. The consistent differences in phototactic behaviour of the clones tested, shown highly significant through an analysis of variance, further corroborates the statement that the behaviour studied has a large genetic component.

It is admitted that one should be cautious in extrapolating experimental results on phototaxis of zooplankters to vertical migration in nature. However, Weider (1984) points to a correlation between genotype and vertical distribution in a natural population of *Daphnia pulex*.

The fact that vertical distribution/migration is largely genetically determined is of far-reaching ecological importance. The observation of a particular diel vertical migration pattern in a natural population can then be viewed as the result of natural selection. Metabolic advantages of non-migrants (Stich and Lampert 1984) are balanced to photodamage (Hairston 1978) and visual predation (Gliwicz 1986; Zaret and Suffern 1976). Furthermore, as competition is often highly developed in the poorly structured freshwater habitats (Hutchinson 1967; Neill 1975), vertical migration may evolve for the purpose of habitat partitioning and niche differentiation (Weider 1984; Lane 1975). The diversity in migration patterns in the starting gene pool is thereby structured to the observed spatial/temporal distribution of the zooplankton population(s) in each particular case.

In this way, we believe that considering a genetic background of vertical migration patterns results in a constructive viewpoint in face of the overwhelming variety of field results.

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