Short communication

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

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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 (Harrison 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 ± 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 determining 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 1B. 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 < 0.001). In a subsequent analysis, pairs of clones were subjected to an Anova: the FS values of all Clone M48 pairs were highly significant, except that of the couple M48/71. In a subsequent analysis, pairs of clones were subjected to an Anova: the FS values of all Clone M48 pairs were highly significant, except that of the couple M48/71.

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**Discussion**

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