

## Clutch size in *Daphnia*: even versus odd?

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With 1 figure and 1 table in the text

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**Abstract:** It has recently been hypothesized for *Daphnia* that even numbers of eggs per clutch are more common than odd numbers, because of the paired nature of the ovaries. This effect has important consequences for the production of optimal egg sizes. To test the hypothesis, we have analysed data sets containing information for a total of 12,504 clutches, from two inter-specific hybrids and six species of *Daphnia*. We did not find strong patterns in the data. Even-sized clutches were more common in some of the data sets, and not in others. We therefore conclude that trends towards the production of eggs in pairs are weak, and unlikely to have a significant effect on optimal clutch and offspring sizes.

### Introduction

It is generally assumed that reproductive strategies evolve to maximise the fitness of the parent. Most models of optimal clutch size also assume that there is a fixed amount of energy expenditure per reproductive event, and that offspring fitness increases with offspring size (e.g., SMITH & FRETWELL 1974, STEARNS 1992, CARRIÈRE & ROFF 1995). A trade-off between clutch size and offspring size should exist, and larger offspring should be produced under poorer environmental conditions. These assumptions are largely supported by work with the freshwater crustacean *Daphnia* (GLIWICZ & GUISANDE 1992, EBERT 1993).

A new dimension to optimality models is introduced when one considers the fractional clutch-size problem (RICKLEFS 1968, NUSSBAUM 1981, EBERT 1994). Clutch size is a discretely varying trait, but optimization of egg size may require a non-integer number of eggs. In this case, the animal must produce either the next highest or the next lowest integer number of eggs, resulting in sub-optimal clutch and egg sizes.

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A further confounding influence on the optimal clutch size has been proposed by BOERSMA (1995). In a laboratory study, he found significant differences between the number of odd and the number of even clutch sizes produced by *D. galeata*. Even-sized clutches were the more common, especially at the lower end of the clutch size distribution, and BOERSMA suggested that this may be due to the paired nature of the ovaries in *Daphnia* (ZAFFAGNINI 1987). If this finding holds true, optimal egg sizes are even harder to achieve.

In this study we test the even/odd clutch size hypothesis by asking the following questions: do *Daphnia* generally produce even numbers of eggs more often than odd numbers? Is this effect more pronounced in small clutches? We make the distinction between large and small clutch-sizes because it may be easier to observe biases towards even-sized clutches when reproductive investment is low (slight relative differences between the ovaries could obscure the effect when larger numbers of eggs are produced), and because the relative effect of deviation from optimality is greater for individual offspring from small clutches. Additionally, we quantify the effect of the hypothesis, which is essential in judging its significance for *Daphnia* evolution and ecology.

## Materials and methods

We looked at clutch-size data from various studies on two inter-specific *Daphnia* hybrids and six *Daphnia* species (*D. galeata* × *D. hyalina*, *D. galeata* × *D. cucullata*, *D. cucullata*, *D. hyalina*, *D. magna*, *D. galeata*, *D. pulex*, and *D. pulicaria*). For each taxon, clutches from different instars were pooled; but data coming from different environmental conditions (e.g. food levels, temperature) or different field samples were analysed separately. Results thus obtained were used to calculate overall means for each taxon.

Firstly, we calculated the observed frequency of each clutch size. Then, the mean frequency of clutch sizes 1 and 3, 2 and 4, 3 and 5, 4 and 6 and so forth were calculated. These means were our expected frequencies for clutch sizes 2, 3, 4, 5 etc. The expected frequency values were then subtracted from the observed frequency values to produce values we refer to as frequency differences (FD's). For example, suppose that in a particular data set for a particular species we observed 10 clutches containing two eggs, 12 clutches containing three eggs and 20 clutches containing four eggs. Our predicted data set in this case would assume that there should be 15 clutches containing three eggs (i.e. the mean of the previous and following clutch size frequencies); the FD between the observed and the predicted value is therefore -3. If the FD for a particular clutch size was a positive value, then more than expected of those clutch sizes were observed. Conversely, if the FD was a negative value, then the frequency of that particular clutch size was less than expected. Note that we did not use single egg clutches in the analysis since we could not calculate a predicted value (we had no information on the occurrence of zero sized clutches).

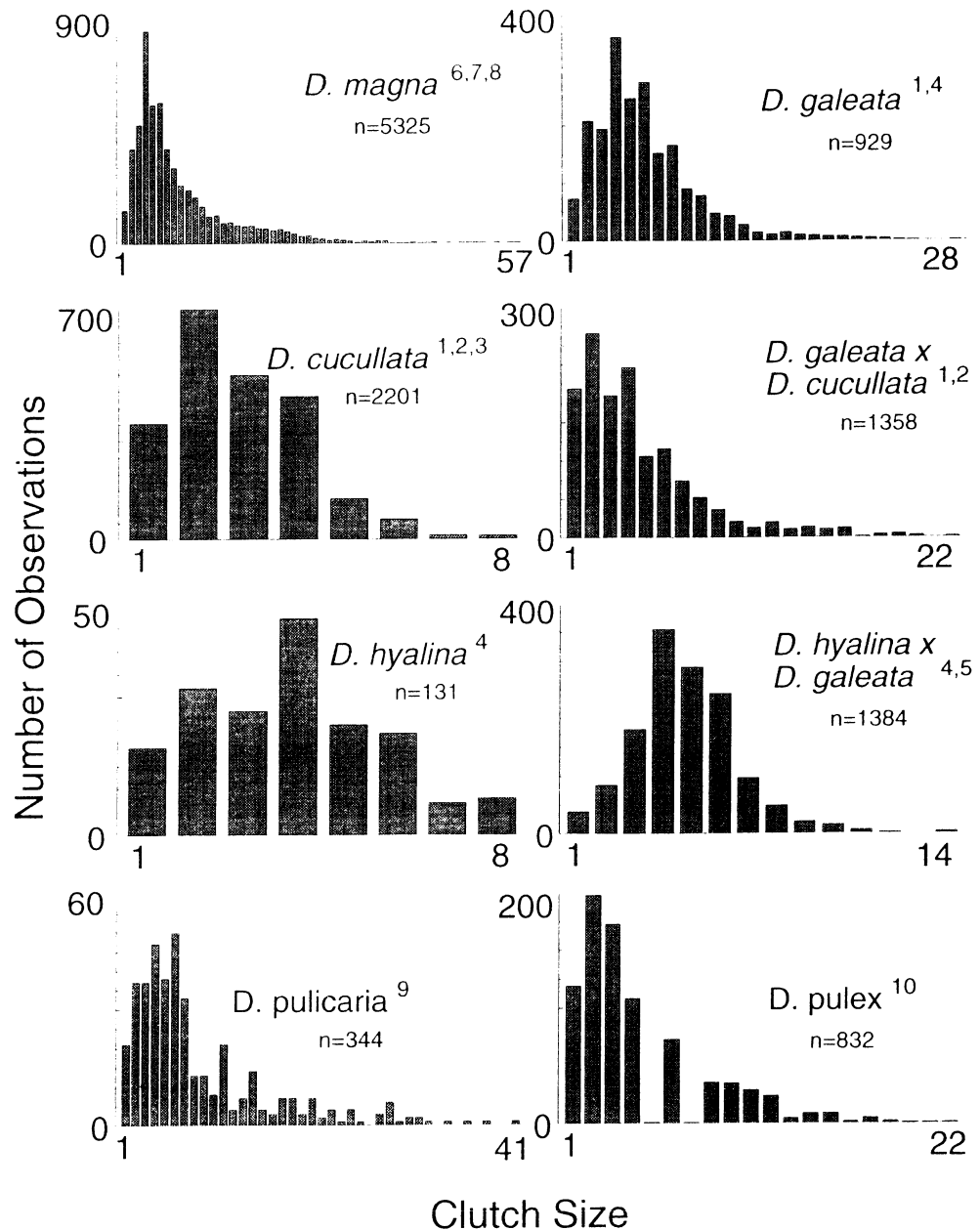
When FD's had been obtained for all clutch-size classes across all data sets, we calculated overall mean FD values for even and odd-sized clutches (the means were weighted according to the number of clutches in each data set). This procedure was performed twice: firstly, for all clutch sizes; and secondly, for small clutch sizes (arbitrarily defined as clutches with less than 8 eggs). T-tests were then used to establish whether there were statistically significant differences between these overall mean FD values (i.e. whether there were differences in the occurrence of even-sized versus odd-sized clutches).

Our method of data analysis assumes that the values in the observed clutch-size frequency distribution, on either side of the value to be predicted, can be used to calculate this predicted value (i.e. we assume a uniform distribution). This is clearly an oversimplification, and can generate error. In particular, when an observed distribution is strongly peaked, our method will underestimate the predicted value for the peak. However, if we further assume that peaks are randomly odd or even in nature (i.e. have an equal chance of consisting of odd-sized or even-sized clutches) then, on average, the FD's will tend towards zero. What we are interested in, and what the method can highlight, are systematic deviations from this randomly generated average FD of zero.

A fully rigorous method of data analysis would require that the exact distribution of the clutch sizes be known. In this case, the difference between the expected (as obtained from the distribution) and the observed frequencies could be used to calculate the FDs. However, several problems forced us to use the mean of the two adjacent clutch-size categories to calculate the expected frequency. Firstly, we had no good idea of the real underlying distribution. Preliminary tests showed that different standard distribution types (e.g. normal, Poisson) fitted the data equally well. This problem was particularly influenced by the fact that we had no reliable estimates of the frequency of zero egg clutch sizes. Secondly, in many cases we had too few data points to fit a distribution at all. For example, in some of the small *Daphnia* species/hybrids, clutch sizes in poor feeding conditions may vary from 1 to 5. Fitting distributions with only 5 categories, half of them being supposed to have too high, and the other half having too low frequencies is not possible. Our method of obtaining expected frequencies was the next best feasible solution to the problem. We tried several different modifications to the method (e.g. Log or square-root transformation of the frequencies before calculating the FDs) but we found the same patterns as described below.

## Results and discussion

Fig. 1 shows the overall clutch-size frequency distributions for each species/hybrid. Table 1 shows the mean FD values and t-test results. In *D. cucullata*, *D. galeata* × *D. cucullata*, *D. hyalina*, and *D. magna* even-sized clutches were significantly more frequent than odd-sized clutches; in *D. galeata*, *D. galeata* × *D. hyalina*, and *D. pulex* there were no significant differences in the occurrence of even or odd-sized clutches; and in *D. pulicaria* even-sized clutches were more common when clutches were small, but not when the data was considered as a whole. Thus, our results do not strongly support the hypothesis



**Fig. 1.** Clutch size distributions for each *Daphnia* species/hybrid. The number of clutches making up each distribution (n) is shown. The superscripted numbers indicate the studies from which the data were obtained: **1**, SPAAK & HOEKSTRA (1995); **2**, BOERSMA & VIJVERBERG (1994); **3**, EBERT & JACOBS (1991); **4**, WEIDER (1993); **5**, VON ELERT (unpublished); **6**, MCKEE & EBERT (1996); **7**, WEIDER & PIJANOWSKA (1993); **8**, EBERT (unpublished); **9**, MCKEE (unpublished); **10**, EBERT & YAMPOLSKY (1993).

that even clutch sizes are more frequent than odd. On the other hand, the hypothesis is not completely contradicted either.

Little is specifically known about cladoceran reproductive physiology, and about energy allocation in the ovaries in particular. If the resources available

**Table 1.** Overall mean frequency difference (FD) values, for each data set as a whole (All) and for small clutches only (Small). Each mean is followed in parentheses by its standard error, and then by the number of FD's used to calculate the mean. T-tests were used to ascertain differences between the means (test statistic *t*, and significance level *p* are shown). Note, that for *D. cucullata* and *D. hyalina* the sets of data for All and Small are the same, because the observed clutch-size range was of 8 or less.

		All	<i>t</i>	<i>p</i>	Small	<i>t</i>	<i>p</i>
<i>D. cucullata</i>	even	0.090 (0.01,63)			0.090 (0.01,63)		
	odd	-0.039 (0.01,47)	7.21	0.001	-0.039 (0.01,47)	7.21	0.001
<i>D. galeata</i>	even	0.002 (0.01,28)			-0.0004 (0.02,14)		
	odd	0.007 (0.01,25)	-0.30	0.762	0.012 (0.02,16)	-0.50	0.622
<i>D. galeata</i> ×	even	0.031 (0.01,22)			0.057 (0.02,11)		
<i>D. cucullata</i>	odd	-0.025 (0.01,21)	3.73	0.001	-0.041 (0.01,11)	3.74	0.001
<i>D. galeata</i> ×	even	0.028 (0.02,16)			0.033 (0.02,14)		
<i>D. hyalina</i>	odd	-0.013 (0.02,16)	1.60	0.121	-0.014 (0.02,14)	1.59	0.123
<i>D. hyalina</i>	even	0.055 (0.03,11)			0.055 (0.03,11)		
	odd	-0.057 (0.03,9)	2.87	0.010	-0.057 (0.03,9)	2.87	0.010
<i>D. magna</i>	even	0.014 (0.003,151)			0.037 (0.01,55)		
	odd	-0.012 (0.002,139)	6.42	0.001	-0.025 (0.01,55)	7.10	0.001
<i>D. pulicaria</i>	even	0.003 (0.004,15)			0.016 (0.004,3)		
	odd	-0.002 (0.004,14)	0.85	0.403	-0.006 (0.01,3)	3.18	0.034
<i>D. pulex</i>	even	0.007 (0.02,25)			0.011 (0.02,20)		
	odd	0.019 (0.01,20)	-0.62	0.538	0.021 (0.02,16)	-0.43	0.671

for reproduction tend to be divided equally between the two ovaries (and therefore eggs produced in pairs), a constraint would be placed on the production of odd-sized clutches. Realisable clutch size, and consequently offspring size, could then be quite different from the optimum size predicted by theory. This effect would be particularly pronounced for small clutches. For example, in a clutch of only two eggs, it may be difficult to produce one egg less, and producing two eggs less means that the animal does not reproduce at all. Conversely, increasing a clutch of two eggs to three involves a one third decrease in energy investment per egg, whereas increasing from two eggs to four eggs means that energy investment per egg would drop by half.

The even/odd clutch size hypothesis would be of evolutionary significance when its effect on clutch size distribution is strong. However, the effect as found in this study was weak. Even in the strongest case of support (*D. cucullata*, Table 1) even sized clutches were only 9% more common than expected. For the other species/hybrids, the effect was generally weaker (less than 6%). Thus, there is evidence that in some *Daphnia* taxa even-sized clutches are more common than odd-sized clutches, but this effect does not appear to be overwhelming.

Care must be taken when interpreting the results of studies where a number of pooled data sets of different sizes are analysed. Depending on the exact size and specific peculiarities of each data set we might or we might not find significant results. Moreover, very large data sets may generate statistically significant results which in reality have little effect on life histories. Therefore, without the presence of strong patterns in our data, we must conclude that trends towards the production of even numbers of eggs per clutch are weak, and unlikely to be of major significance in affecting optimal clutch and egg sizes.

### Acknowledgements

Many thanks to MAARTEN BOERSMA, PIET SPAAK, ERIC VON ELERT and LARRY WEIDER for kindly letting us use their data, and for helpful comments and suggestions during manuscript preparation.

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Submitted: 15 August 1996; accepted: 9 October 1996.