COMPARATIVE SURVIVORSHIP AND FECUNDITY OF
MICRIC AND AMICIC FEMALE ROTIFERS

CHARLES E. KING
Department of Biology, Yale University, New Haven, Connecticut 06520

INTRODUCTION
A striking life-history feature of monogononot rotifers is the alternation of their parthenogenetic and bisexually reproducing generations. Amictic females reproduce by diploid parthenogenesis and their ovarial cells do not undergo meiotic divisions. In contrast, the mictic females meiotically produce haploid eggs which, if unfertilized, hatch into haploid male rotifers. If fertilized, the mictic females produce thick-shelled resting eggs that hatch into amictic females.

A series of studies in the early part of this century produced comparative data on the mean survivorship and fecundity of amictic, unfertilized mictic, and fertilized mictic females. It was frequently found that the three types of females had different reproductive rates. Moreover, the relative fecundities of the different females were found to vary among species of rotifers. For some species, the unfertilized mictic female produced fewer eggs than the amictic female. For other species, the fecundities were about equal, and for a third group of species, the unfertilized mictic females had higher fecundity rates than the amictic females. It will be demonstrated that these conflicting results may be arti-

MATERIAL AND METHODS
The experimental data on which this paper is based were obtained for six different clones of the rotifer *Euchlanis dilatata*. The stem individuals used to initiate these clones were collected from the littoral region of a small man-made lake in Allerton Park, 30 miles southwest of Urbana, Illinois. Clones A and B were started from a collection made on May 1, 1968 (surface water temperature = 23°C), clone C from a collection made on June 5, 1968 (28°C), and clones D, E, and F from a collection made on June 12, 1968 (28°C).

Individuals from each collection were brought back to the laboratory and isolated at 25°C for 1 week. The descendants of each stem female were then split into two groups, one group being maintained at 19°C and the other at 27°C. Each group was kept under these conditions for a minimum of 10 generations prior to being used in experiments.

Both stock and experimental cultures were maintained in Pourriot-Gilbert medium (Gilbert 1968), at pH 8.0 with Sorensen's buffer (Clark 1928, p. 210). *Chlamydomonas reinhardtii* (Indiana University culture collection no. 89) grown on *Euglena* medium (Starr 1960) was used as food for the
rotifers in all experiments at an initial density of 500,000 cells per milliliter (≈16.4 μg per milliliter).

Experiments were performed with isolated individuals in 0.5 ml of the food suspension. These cultures were changed daily, at which time the egg counts and survivorship data were taken.

The experimental design employed in this study was determined by methods needed for a study on clonal variation of amictic females which will be described elsewhere. Fecundity and survivorship data were taken for each kind of female (amictic, unfertilized mictic, and fertilized mictic) at two different temperatures, 19°C and 27°C. Three groups of 15 animals each were followed for the different clones, female types, and temperatures.

RESULTS

Net reproduction (eggs per female lifetime) values for the described experiments are presented in table 1. It is apparent that the different types of females differ in the number of eggs produced and, also, in their response to an increase in acclimation temperature from 19°C to 27°C. The overall temperature responses may best be seen from the $Q_{10}$ values calculated by the van't Hoff equation. These values indicate that the rate of fecundity increase with increasing temperature is much greater for the unfertilized mictic female than for either of the other two types of female.

A very different response to temperature is obtained for the mean life-spans (table 2). Differences in mean life-span among the female types are much less apparent than was the case for fecundity. Moreover, the $Q_{10}$ values are approximately the same for each kind of female, in each case being close to zero.

DISCUSSION

An organism's phenotype is determined by the separate and interacting effects of its genotype and environment. Thus, in a constant environment the phenotypic variance among members of an isogenic clone is expected to be zero. Changes in the phenotype as the result of altered physiological states are seldom considered to be environmentally induced, at least in the ecological sense of the word "environment." For this reason a convenient distinction is often drawn by physiol-

### TABLE 1

<table>
<thead>
<tr>
<th>Female Type</th>
<th>19°C</th>
<th>27°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amictic</td>
<td>4.6 ± 0.2</td>
<td>6.4 ± 0.3</td>
</tr>
<tr>
<td>Unfertilized Mictic</td>
<td>3.0 ± 0.2</td>
<td>11.1 ± 0.5</td>
</tr>
<tr>
<td>Fertilized Mictic</td>
<td>3.5 ± 0.1</td>
<td>10.7 ± 0.3</td>
</tr>
</tbody>
</table>

**Note:** Each value is the mean ± SE of three groups of 15 animals each.
TABLE 2
MEAN LIFE-SPAN OF AMICTIC, UNFERTILIZED MICTIC, AND FERTILIZED MICTIC
"EUCHLANIS DILATATA" FEMALES AT 19°C AND 27°C

<table>
<thead>
<tr>
<th>Clone</th>
<th>19°C</th>
<th>27°C</th>
<th>19°C</th>
<th>27°C</th>
<th>19°C</th>
<th>27°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3.1±0.2</td>
<td>2.4±0.3</td>
<td>3.6±0.1</td>
<td>2.5±0.2</td>
<td>3.3±0.1</td>
<td>2.6±0.2</td>
</tr>
<tr>
<td>B</td>
<td>3.5±0.3</td>
<td>2.5±0.2</td>
<td>3.7±0.2</td>
<td>2.7±0.2</td>
<td>3.4±0.2</td>
<td>2.8±0.2</td>
</tr>
<tr>
<td>C</td>
<td>3.3±0.0</td>
<td>2.2±0.3</td>
<td>3.5±0.1</td>
<td>2.6±0.3</td>
<td>3.3±0.0</td>
<td>2.5±0.2</td>
</tr>
<tr>
<td>D</td>
<td>3.3±0.0</td>
<td>2.7±0.2</td>
<td>3.5±0.4</td>
<td>2.5±0.3</td>
<td>3.3±0.0</td>
<td>2.6±0.2</td>
</tr>
<tr>
<td>E</td>
<td>3.4±0.4</td>
<td>4.3±0.3</td>
<td>3.8±0.1</td>
<td>4.6±0.2</td>
<td>3.4±0.0</td>
<td>3.5±0.3</td>
</tr>
<tr>
<td>F</td>
<td>4.1±0.4</td>
<td>3.7±0.3</td>
<td>3.7±0.2</td>
<td>4.4±0.2</td>
<td>3.9±0.2</td>
<td>4.0±0.2</td>
</tr>
<tr>
<td>X ± SE</td>
<td>3.4±0.1</td>
<td>3.1±0.3</td>
<td>3.8±0.1</td>
<td>3.5±0.3</td>
<td>4.1±0.3</td>
<td>4.0±0.3</td>
</tr>
<tr>
<td>Q₁₀</td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Note.—Each value is the mean ± SE of three groups of 15 animals each.

ogists and geneticists between the “external” and “internal” environments.

Two major types of changes can be related to alterations in the internal environment. First, qualitative changes may occur as different genes are activated or deactivated, and second, quantitative changes occur as the activities of different genes are increased or decreased. These two types of changes are commonly studied as functions of time, because in most organisms the major effects of an altered internal environment are displayed in the phenotypic changes that occur from early development to the latter stages of senescence. However, the existence of different female types within rotifer clones permits an investigator to study phenotypic changes that are independent of both age and the external environment. In the present study, the different females were obtained for each clone in the same environment, thus the reported intraindividual differences in fecundity and survivorship may be directly attributed to differences in the internal environments of the three kinds of females.

As pointed out in the introduction, different relative net reproduction values (R₀) of amictic and unfertilized mictic females have been reported for various rotifers. The species which have been studied can be classified in three groups:

Group I. Amictic ? R₀ > unfertilized mictic ? R₀
1. Asplanchna intermedia (Tauson 1925)
2. Leane inermis (Miller 1931)

Group II. Amictic ? R₀ ≈ unfertilized mictic ? R₀
1. Epiphanes senta (Ferris 1932)
2. Euchlanis triquetra (Lehmanckick 1926)

Group III. Amictic ? R₀ < unfertilized mictic ? R₀
1. Asplanchna sieboldi (Wesenberg-Lund 1930)
2. Testudinella elliptica (Luntz 1926)

The grand means of the data presented in table 1 bear on the putative value of this classification as Euchlanis dilatata at 19°C would be placed in Group II and at 27°C would fall into Group III. This classification becomes still more questionable if the individual clones are examined. These comparisons are made in figure 1 by plotting
the fecundity ratios of the unfertilized mictic to the amictic females so that a
Group I pattern is indicated by a ratio of less than unity, a Group II pattern
by a ratio of about unity, and a Group
III pattern by a ratio greater than
unity. Assuming a linear relationship
as plotted, clones C, D, E, and F clearly
belong to Group III. Clones A and B,
however, fall into Group I at or below
19°C, into Group II in the area of
21°C, and into Group III at higher tem-
peratures. Thus the relative fecundities
are related to both the genetic con-
titution of the specific clone and the
experimental temperature.

Different temperature-specific fecun-
dity ratios of the type reported here
had been observed in one of the first
quantitative laboratory investigations
of rotifers. Whitney (1907), studying
Epiphanes sena, found the relative
fecundity ratio of unfertilized mictic
females to amictic females to be about
1:1 at 20–22°C, 2:1 at 24–25°C, and
4:1 at 26–29°C. Although this paper
was cited in some of the studies men-
tioned earlier, cognizance was not taken
of Whitney’s results, probably because
he did not use clones, based his mea-
sures on a very small number of ani-
mals (2–12), and observed a striking
decrease in total number of eggs laid
as the temperature increased.

The three types of eggs differ in their
size, density, and structure. For in-
stance, unfertilized mictic eggs are
usually significantly smaller than either
amictic or resting eggs and resting eggs
have more yolk and a much thicker shell
than either of the other egg types. The
average size of each type of egg for
Euchlanis dilatata is presented in table
3. Ten eggs of each type were measured
for each clone and the standard error
for each type and dimension was less
than 1.54. It should be noted that while there is generally little variation within species, the relative size and morphology of the different eggs vary widely among rotifers. Thus the relations found for *Euchlanis dilatata* may not hold for other species.

Volumes presented in Table 3 were calculated by assuming the eggs to be prolate spheroids. These values may be used to compare the response of fecundity to a change in temperature on a basis that is more closely related to metabolic expenditure than are the egg numbers. Much of the variation in net reproduction observed between the amictic and unfertilized mictic females when egg numbers are considered (Fig. 2A) disappears when fecundity is expressed in terms of egg volume (Fig. 2B). The parallel slopes of the two curves in figure 2B may be taken to indicate a similar pattern of energy allocation for both amictic and unfertilized mictic eggs. However, the slope of the resting egg curve in figure 2B is clearly lower than that of the other two curves. At 19°C, the volumes of eggs produced in a lifetime by each type of female are more nearly alike than 27°C. This observation implies that, at the higher temperature, less energy is effectively allocated for resting egg production than at the lower temperature. It may be that the relative amount of energy devoted to resting egg production is lower at 27°C than at 19°C. If this is true, either the feeding rate at 27°C is not increased in proportion to the increased maintenance energy requirements, or the energy ingested is processed with a lower efficiency at 27°C than at 19°C. Alternatively, if the same relative amount of energy is expended in production of all three types of eggs, it is reasonable to suppose that the efficiency of expenditure is lower for resting eggs than for either amictic or unfertilized mictic eggs. In this case, direct caloric measures of the energy expended in egg formation would be expected to remove the differences in slope so that all three curves would be parallel.

### SUMMARY

Net reproduction and mean lifespan were measured at both 19°C and 27°C for amictic, unfertilized mictic, and fertilized mictic females in each of six clones of the monogonont rotifer *Euchlanis dilatata*. A comparison of the survivorship data indicated that temperature has little effect on mean life-span; the temperature coefficients for all three kinds of females were close to zero. However, large effects were noted for the action of temperature on fecundity rates. The average temperature coefficients were, for amictic females, 2.8; for unfertilized mictic females, 3.6; and for fertilized mictic females, 2.4. Differences among the female types within clones may be attributed to differences in their internal environments and not to either

### TABLE 3

**LINEAR DIMENSIONS (WIDTH X LENGTH) AND CALCULATED VOLUMES OF "Euchlanis dilatata" EGGS**

<table>
<thead>
<tr>
<th>Egg Type</th>
<th>Dimensions (a)</th>
<th>Vol./Egg (X 10^11)</th>
<th>Egg Vol./V Lifetime</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amictic</td>
<td>90 X 140</td>
<td>5.9 X 10^11</td>
<td>23.6</td>
</tr>
<tr>
<td>Unfertilized mictic</td>
<td>75 X 98</td>
<td>2.9 X 10^11</td>
<td>18.3</td>
</tr>
<tr>
<td>Resting</td>
<td>86 X 125</td>
<td>4.8 X 10^11</td>
<td>14.9</td>
</tr>
</tbody>
</table>

*Note: Dimensions in micrometers (μm).*
SURVIVORSHIP AND FECUNDITY OF FEMALE ROTIFIERS

Fig. 2.—Mean fecundity per female lifetime over all clones of the different types of *Euchlanis dilata* females. A, In terms of egg numbers. B, In terms of egg volumes.

...age or the external environment. Some of the fecundity differences between females may be removed by considering egg production in terms of the volume rather than the number of eggs produced. This observation probably holds because energy expenditures in egg formation are more accurately estimated by egg volume than by egg number.

LITERATURE CITED

Clark, W. M. 1928. The determination of hydrogen ion concentration. 3d ed. Williams & Wilkins, Baltimore. 717 p.


