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## “Grandfather Effects” on Offspring Size in the Eastern Mosquitofish, *Gambusia holbrooki*

STEPHEN C. WEEKS AND GARY K. MEFFE

Offspring size at birth can be an important determinant of initial offspring success (see reviews in Roff, 1992): larger offspring may have advantages in predator avoidance (Reznick and Endler, 1982; Weeks and Gaggiotti, 1993), growth (Kaplan, 1980), and starvation resistance (Bagenal, 1969; Marsh, 1986). However, the production of larger offspring has a significant energetic cost to the parent (Blaxter, 1969; Sinervo, 1990), and it is commonly assumed that producing larger offspring necessitates the production of fewer overall offspring, resulting in a trade-off between offspring size at birth (hereafter “offspring size”) and offspring number (Smith and Fretwell, 1974; McGinley et al., 1987; Winkler and Wallin, 1987).

Several authors have suggested that, within any habitat and specific to any particular species, there will be natural selection for an “optimal” offspring size (Smith and Fretwell, 1974; Morris, 1987; Winkler and Wallin, 1987). This optimum is the size at which the increase in offspring fitness with increased offspring size begins to plateau (Smith and Fretwell, 1974). Producing offspring of this size should balance the benefits to the parent by producing as many offspring as possible, while allocating enough energy to each offspring to provide them a good probability of survival (Morris, 1987). Thus, it is predicted that there should be an identifiable optimal offspring size for an organism living in a particular habitat and that natural populations should be at or near this optimal size because of directional or balancing selection toward this optimum.

The above statement implies that natural selection has the appropriate genetic variation with which to work. For natural selection to be effective at modifying a phenotype, there must exist some level of additive genetic variation for the phenotypic trait being selected (Fisher, 1930; Falconer, 1985). Nonadditive genetic variation is considered unimportant for shaping phenotypic variation by natural selection (Falconer, 1985). Yet, variation in offspring size at birth in lecithotrophic fish (fish that package all energy in the form of yolk before fertilization occurs) appears to be primarily under maternal control (Reznick, 1981, 1982). Thus, differences among individuals within a clutch are due to nongenetic “maternal” effects rather than to

genetic differences among siblings. Such maternal effects can have great influences on the response to natural selection (Kirkpatrick and Lande, 1989). However, differences in average size of offspring among female parents could be partially determined by genetic effects (Reznick, 1981, 1982), and thus modification of the trait within a population could be affected by natural selection acting among parents. To detect such an effect, one would need to perform controlled matings of the offspring’s grandparents before genetic effects on offspring size could be detected. To detect additive genetic variation in offspring size thus requires assessing genetic differences among “grandfathers,” hence the term “grandfather effects” (Reznick, 1981, 1982).

In his attempt to identify grandfather effects in mosquitofish, Reznick (1981) hybridized individuals from populations that differed in average offspring size. He noted that in the crossings, the first filial generation offspring would resemble their maternal parent, rather than resembling a mixture of the maternal and paternal phenotypes (Reznick, 1981). It was not until the second filial generation that mixed phenotypes began to appear. This experiment clearly showed a maternal effect on offspring size and underscored the genetic nature of differences in offspring size among populations operating through the filter of maternal effects. However, the hybridization design used by Reznick did not allow quantification of the levels of additive genetic variation within populations.

To determine the level of additive genetic variation for offspring size in poeciliid fishes, we require data on within-population genetic variation. In this paper, we present data from a full-sib/half-sib mating design followed for two filial generations, using individuals from a single population of the poeciliid, *Gambusia holbrooki*. This breeding design allows us to determine the level of additive genetic variation within a population by comparing similarities in offspring size among related individuals. These data can be used to estimate the levels of additive genetic variation for offspring size and thus to examine the importance of grandfather effects within populations of mosquitofish.

*Materials and methods.*—Thirty pregnant *G. holbrooki* were collected from Pond C (located on

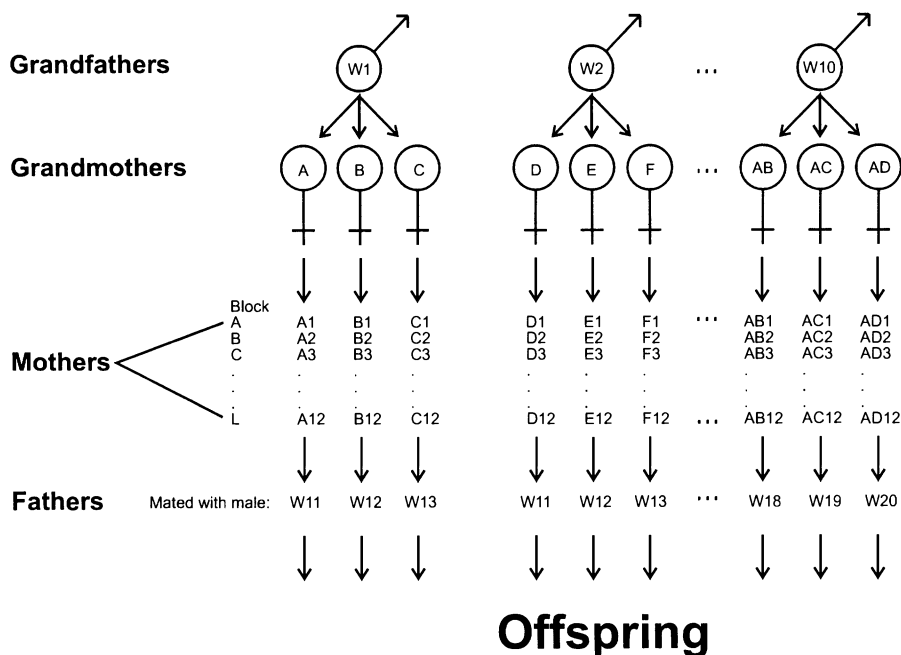


Fig. 1. First- and second-generation mating designs. First-generation matings were 10 grandfathers (W1–W10) mated with 30 grandmothers (A,B,C,...,AD). Female offspring from these pairings (A1–AD12) were then mated to 10 wild-caught fathers (W11–W20). Third-generation offspring were then collected from these matings and were used for calculating offspring size at birth.

the US Department of Energy's Savannah River Site near Aiken, South Carolina) and transported to the laboratory, where they were placed in individual 3.7-liter plastic jugs (one fish per jug), contained within a 220-liter aquarium (30 jugs/aquarium) with under-gravel filters (see Weeks and Meffe, 1996). Each jug had 4 × 8 cm, mesh-covered holes cut in each wall to allow continuous water exchange. Up to 10 offspring from a single brood were collected from each female (P generation), and these offspring (hereafter "grandmothers") were reared in family groups in 30 18.5-liter aquaria until mature. Nearing the age of maturity (at approximately four weeks), the 30 family groups were monitored daily to remove any developing males, thereby eliminating the possibility of brother-sister mating within families. When the grandmothers matured, they were individually placed in the 3.7-liter jugs. Only one grandmother per family group (30 total) was chosen for mating. Grandmothers were allowed to grow an additional 40–60 d after maturity to allow them to reach sizes from which we could collect a minimum of 12 offspring per brood for a concurrent experiment (Weeks and Meffe, 1996). Each grandmother was then mated with an unrelated, wild-caught male (hereafter "grandfathers"), with each grandfather (10 total) mating

with grandmothers from three different families (Fig. 1).

After mating, the grandmothers were again placed in individual jugs with artificial grass. The first brood from most of the grandmothers had a large number of "premature" births, a phenomenon not observed in subsequent broods. Offspring from the second brood were used in a concurrent study (Weeks and Meffe, 1996). Therefore, offspring (hereafter "mothers") from the third brood were chosen from each grandmother for the current experiment (Fig. 1).

The mothers from the third brood were again raised in family groups, as described for the grandmothers above, and the 30 family groups were monitored daily to remove developing males. From three to 12 mothers were used per grandmother, for a total of 224 mothers (Fig. 1). Upon maturation, the mothers were mated with a second collection of wild-caught males (hereafter "fathers"; Fig. 1) and then individually isolated in the 3.7-liter jugs. The mating design was similar to the grandparental generation, except that the fathers were specifically paired with groups of mothers that did not share a similar grandfather (Fig. 1). In this way, the effects of the fathers could be separately assessed from the effects of the grandfathers.

Each father was mated with all mothers from three grandmother lineages and, thus, were mated with from nine to 36 mothers. Each of the 10 fathers was housed in a 27-liter aquarium, and the mothers were cycled through for mating on a 3-d cycle (i.e., were left in the aquarium with the father for three days each).

Each mated mother from each grandmother was placed in a 3.7-liter jug in a separate large aquarium, was fed ad libitum quantities of frozen brine shrimp daily, and was checked each morning for offspring. When a mother had a brood, the offspring were removed and preserved in 5% buffered formalin, and the mother was measured (SL) by capturing a dorsal image of the fish on a computer image analysis system, with MorphoSys® software. Standard length was measured on three separate images of each fish, and the average was used as the estimate of standard length.

From one to 11 broods were collected from each mother, for a total of 9719 measured offspring. The preserved offspring were measured for SL, as described above, three to four weeks after being preserved; SL was then used in all analyses of offspring.

Variation in offspring size at birth was quantified using a nested ANOVA. The independent factors were grandfathers, grandmothers, mothers, fathers, and broods. Because of imbalance in the design (one of 30 grandmothers was not represented, and not all blocks were represented for each grandmother by grandfather mating; Fig. 1), Type IV sums of squares were used to calculate F-ratios (SAS/STAT, vers. 6. 4th ed., Statistical Analysis Systems Institute, Inc., Cary, NC, 1990, unpubl.). The nested ANOVA's were calculated in two separate analyses in a sequential order. First, an ANOVA was calculated using a design that grouped full-sib mothers into three groups of grandmother lineages, grouped by which lineages were mated with each of the fathers (Fig. 1). In this analysis, the independent factors were fathers, grandmother lineages nested within fathers, mothers nested within grandmothers, and broods nested within mothers. Although grandmothers, per se, did not mate with the fathers, each of the mothers within a grandmother lineage (e.g., A1–A12) were mated to the same father, and thus grouping by grandmother lineages was appropriate for this analysis. An insignificant father effect in this analysis would indicate that the fathers did not contribute to the birth size of their offspring, which meant that the second analysis could be pursued, testing for a grandfather effect. In this second analysis, the only difference was that the grandmother lineages would be regrouped ac-

cording to initial matings with the 10 grandfathers. For example, full-sib family group A would be paired with D and G for the first analysis (fathers analysis), and A would be paired with B and C for the second analysis (grandfathers analysis; Fig. 1). A significant grandfather effect would indicate a significant additive genetic contribution by the males in the grandparental generation to offspring size at birth of their grand-offspring.

In both ANOVAs, standard length of the mothers and brood size were found to be independently, positively associated with offspring standard length. Therefore, residuals of a multiple regression of standard length of the mothers (measured at each brood) and number of offspring in a brood on offspring size were used as the dependent variables in the ANOVAs (Kelly, 1993). Because only one mother from each grandmother lineage was in a separate 220-liter aquarium, variation among mothers was confounded with variation among aquaria.

Partitioning of the variance components was conducted with the restricted maximum likelihood procedure in PROC VARCOMP (SAS/STAT, vers. 6, 4th ed., Statistical Analysis Systems Institute, Inc., Cary, NC, 1990, unpubl.), which constrained all components to nonnegative values. Estimations of heritability followed Falconer (1985). The power calculations were computed using the JMP statistical package for the PC (vers. 3.1, Statistical Analysis Systems, Inc., Cary, NC, 1995, unpubl.).

**Results.**—Grouping the offspring according to their fathers revealed no significant contribution of fathers to offspring size (Tables 1–2). Indeed, the variance components analysis estimated that none of the total variance was explained by grouping according to fathers (Table 1). This zero variance component translated into an estimate of zero heritability for offspring size when grouping by fathers, as predicted by consideration of poeciliid reproductive biology (Reznick, 1981, 1982). Most of the variation among offspring was due to nonadditive affects (Table 1), with the largest of these variance components (63%) being due to differences among broods.

A greater proportion of the variation in offspring size was explained when offspring were regrouped according to grandfathers (Tables 2–3). The variance component analysis indicated that approximately 2% of the variation among offspring size at birth was due to differences among grandfathers (Table 3). Because the variance component attributable to fathers (or sires) estimates one-quarter of the additive ge-

TABLE 1. FATHERS ANALYSIS: ANOVA RESULTS FOR MODEL WITH FATHER MATED TO MOTHERS IN GRANDMOTHER LINEAGES. In the column labeled Source, terms in parentheses are those within which the factor is nested (F = Fathers, Gm = Grandmothers, M = Mothers). Column labeled Test refers to which source of variation was used as the denominator in the F-ratio tests.

Source	df	Sum of squares	Test	F-ratio	Pvalue	Variance component (%)
(a) Fathers	9	30.9	(b)	1.16	0.3699	0.0
(b) Grandmothers (F)	19	56.0	(c)	1.14	0.3182	2.5
(c) Mothers (Gm)	195	505.6	(d)	1.22	0.0434	11.9
(d) Broods (M)	590	1259.4	(e)	28.89	0.0001	62.6
(e) Error	8905	658.1				23.0
Total	9718	2937.1				

netic variation (Falconer, 1985), this variance component translated into an estimated heritability of approximately 7% for offspring size at birth. A large nonadditive affect was again noted by the large contribution of variance com-

ponents among broods and among mothers (Table 3).

TABLE 2. AVERAGE AND STANDARD ERROR OF OFFSPRING SIZE WITHIN PARENTAL LINEAGES (Gf = GRANDFATHERS, Gm = GRANDMOTHERS, AND F = FATHERS).

Parent	Average length (SE)	N	Parent	Average length (SE)	N
Gf			Gf		
1	6.45 (0.02)	1279	6	6.37 (0.02)	829
2	6.60 (0.02)	969	7	6.50 (0.02)	1517
3	6.28 (0.02)	697	8	6.50 (0.01)	1061
4	6.70 (0.02)	769	9	6.49 (0.02)	638
5	6.36 (0.02)	1208	10	6.36 (0.02)	772
Gm			Gm		
1	6.77 (0.02)	333	16	6.29 (0.03)	366
2	6.22 (0.05)	97	17	6.30 (0.02)	950
3	6.57 (0.04)	295	18	6.38 (0.03)	224
4	6.47 (0.03)	264	19	6.19 (0.03)	526
5	6.48 (0.03)	235	20	6.34 (0.04)	315
6	6.44 (0.02)	380	21	6.66 (0.04)	197
7	6.65 (0.03)	462	22	6.64 (0.02)	563
8	6.57 (0.02)	533	23	6.22 (0.03)	333
9	6.39 (0.04)	290	24	6.50 (0.02)	581
10	6.41 (0.03)	228	25	6.22 (0.03)	263
11	6.67 (0.05)	154	26	6.79 (0.04)	161
12	6.62 (0.07)	76	27	6.51 (0.03)	334
13	6.51 (0.03)	353	28	6.55 (0.03)	171
14	6.51 (0.02)	672	29	6.27 (0.04)	144
15	6.65 (0.04)	239	30		
F			F		
1	6.49 (0.02)	820	6	6.61 (0.02)	989
2	6.54 (0.02)	827	7	6.54 (0.02)	1362
3	6.45 (0.03)	631	8	6.34 (0.02)	1204
4	6.51 (0.02)	868	9	6.38 (0.02)	768
5	6.35 (0.03)	757	10	6.42 (0.01)	1513

Discussion.—For a phenotype to be shaped by natural selection, there must be sufficient additive genetic variation for that trait (Fisher, 1930). For traits that have large maternal effects, detection of significant levels of additive genetic variation will be at least one generation removed (Falconer, 1985; Kirkpatrick and Lande, 1989), and response to selection for such traits will often be greatly influenced by the strength and directionality of these maternal effects (Kirkpatrick and Lande, 1989). Offspring size is one such trait that has been found to be greatly influenced by maternal effects (Berven, 1982; Semlitsch, 1985; Bernardo, 1996). In particular, offspring size appears to be overwhelmingly influenced by maternal effects in lecithotrophic fish such as *Gambusia* (Reznick, 1981). In essence, initial offspring size in lecithotrophic fish is determined by the maternal investment in each egg and, therefore, can be thought of as an extension of the maternal phenotype. To detect any level of heritable variation for offspring size in these fish requires following specific crosses through two generations (Reznick, 1981, 1982).

However, to estimate additive variation within a population, one cannot merely follow the typical full-sib/half-sib nested breeding design for two successive generations, because this design will confound grandfather effects with father effects. For instance, in the current experimental design, if grandfather W1 was mated with grandmothers A, B, and C, and father W11 was mated with mothers A1–A12, B1–B12, and C1–C12, then one could not separate a genetic effect of W1 from W11. To avoid this confounding, either each mother must be mated to a separate father (necessitating hundreds of males) or a smaller number of males would need to be mat-

TABLE 3. GRANDFATHERS ANALYSIS: ANOVA RESULTS FOR MODEL WITH GRANDFATHERS MATED TO GRANDMOTHERS AS OUTLINED IN FIGURE 1. In the column labeled Source, terms in parentheses are those within which the factor is nested (Gf = Grandfathers, Gm = Grandmothers, M = Mothers). Column labeled Test refers to which source of variation was used as the denominator in the F-ratio tests.

Source	df	Sum of squares	Test	F-ratio	P-value	Variance component (%)
(a) Grandfathers	9	40.5	(b)	2.13	0.0791	1.6
(b) Grandmothers (Gf)	19	40.2	(c)	0.82	0.6875	1.1
(c) Mothers (Gm)	195	505.6	(d)	1.22	0.0434	12.1
(d) Broods (M)	590	1259.4	(e)	28.89	0.0001	62.2
(e) Error	8905	658.1				23.0
Total	9718	2937.1				

ed to whole grandmother lineages in a separate pattern to that of the original full-sib/half-sib mating design. For instance, W11 must be mated to only one of the lineages mated by W1 to avoid confounding a father with a grandfather effect (Fig. 1). This second design also allows the detection of either a father or a grandfather effect, if either exists, and was the option chosen for the current experiment.

Estimation of father and grandfather effects had to be tested in sequential order. The design was constructed such that grandmother lineages would all be sired from a single father and a single grandfather. By constructing the crosses outlined in Figure 1, these grandmother lineages could then be rearranged in two separate nested analyses of variance to detect either a father or a grandfather effect. If a significant father effect was detected in the first test, detection of a grandfather effect would be problematic, because father effects could swamp the weaker grandfather effects. However, we did not expect to find a father effect, because previous experiments and poeciliid biology suggested father effects were minimal (Reznick, 1981). In fact, we found no detectable father effects, which was consistent with previous work on mosquitofish (Reznick, 1981).

Because variation in offspring size appears to be entirely maternally inherited, we could then move on to the second analysis, which regrouped grandmother lineages into nested groups within grandfathers. The second analysis revealed a 92% likelihood of there being a grandfather effect on the offspring size of their grand-offspring, even though the numbers of grandfather “sires” was relatively low (10). The variance component analysis suggested that heritability was on the order of 7%, which is in the typical range for life-history traits (Mousseau and Roff, 1987). The power to detect heritable variation in offspring size of this magnitude

(~7%) using the current experimental design (10 sires and 3 dams/sire) with a Type I error rate of 0.05 was low (~0.65). The power to detect heritable variation in the current breeding design with a Type I error rate of 0.05 was estimated to be greater than 0.9 only when the magnitude of variation explained by the sire component was approximately twice the observed level (i.e., heritability in the 15% range). The power of the current breeding design to detect a level of heritability of 7% was 0.77 if the Type I error rate was increased to 0.10. Thus, the current results suggest that *Pond C Gambusia* do have sufficient levels of additive genetic variation for natural selection to modify offspring size at birth, as originally suggested by Reznick (1981).

These results have two significant ramifications for tests of life-history evolution in poeciliid fishes. First, the observation that offspring size at birth in mosquitofish appears to be entirely maternally inherited suggests that selection acting on this important trait can have non-intuitive results. Such maternal affects can either increase or decrease the rate of response to selection and in some cases can cause evolution in an opposite direction from that being selected (Kirkpatrick and Lande, 1989). Additionally, maternal effects can create inertial responses to selection, creating evolution in an affected character long after selection has ceased (Kirkpatrick and Lande, 1989). Thus, the combined results of the current study and those of Reznick (1981, 1982) indicate that the evolution of “optimal offspring size” in mosquitofish will be complicated by strong maternal effects.

Second, although offspring size within *Gambusia* populations appears to be entirely maternally controlled, additive differences among females for offspring size can allow for natural selection to shape offspring size (Kirkpatrick and Lande, 1989). Reznick's studies indicated

this with hybridizations among populations, but his data were insufficient to detect levels of additive genetic variation within populations, which is necessary for local adaptation (Falconer, 1985; Kirkpatrick and Lande, 1989). If the levels of additive variation for offspring size suggested in the current study generally hold for other mosquitofish populations, then this important life-history trait should be responsive to natural selection (Falconer, 1985), assuming no additional pleiotropic or linkage constraints exist (Lande, 1982). However, as suggested above, even with genetic variation for this trait, the filter of maternal effects may cause nonintuitive responses to selection (Kirkpatrick and Lande, 1989). Since initial offspring size appears to be important in many fish populations (Reznick and Endler, 1982; Hutchings, 1991; Weeks and Gaggiotti, 1993), identifying significant levels of within-population additive variation for this trait allows the potential for the evolution of optimal offspring size.

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