Egg Reaction to Sperm: A Proposed Mechanism

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Received 26 January 1988, 27 June 1988

Abstract. Female selection of males and gametic selection (in the form of sperm competition theory) are well documented. A conceptual analysis of the literature supports the proposal that eggs are dynamically involved during fertilization.

Positive Assortative mating for morphological and chromosomal traits has been reported in invertebrate and vertebrate species (reviewed in Thiesson and Gregg, 1980). In addition, Bateson (1978, 1980, 1982, 1983) and Shields (1982) proposed the existence of a mate selection mechanism that would (1) result in the production and maintenance of co-adapted gene complexes specific for local conditions and would also (2) avoid inbreeding/outbreeding depression (hereafter termed "inbreeding theory"). Such a mating system would require the ability to discriminate between individuals (Bateson, 1980; Shields, 1982). Such individual recognition has been reported in a number of invertebrate and vertebrate species (e.g. Falls, 1982; Holmes and Sherman, 1983; Clark, 1984; Glinski and Krekorian, 1985; Ryan, 1985; Davis, 1986). In regards to mate selection, females exhibit male selection in many invertebrate and vertebrate species (e.g. Searcy, 1982; Halliday, 1983; Ryan, 1985; Kelves, 1986; Watt et al., 1986); one result of female selection of males is that it could confer the selective advantages discussed in inbreeding theory. Here, I propose that female "selection" of males also occurs at the gametic level. (There are many hypotheses regarding the function of mate choice. Here, I am emphasizing female choice for one reason: Male competition for access to females at the organism level implied (and led to) sperm competition theory; logically, female choice of males at the organism level allows the possibility of egg "selection" of sperm. Gametic selection in itself has already been proposed in Beatty [1970].) This mechanism would confer the selective advantages discussed above as well as those conferred according to sperm competition theory (see Smith, 1984).

Bernstein et al. (1985) discussed the evolution of sexual reproduction as a means to compensate for genetic damage (repair of genetic damage through fertilization has been shown experimentally, e.g. Generoso [1980]; Mason et al., [1986]), but they did not suggest an egg reacts to a specific sperm. Devine (1984) suggested some female reptiles may be able to "choose" between sets of sperm following copulation with multiple males, but he did not elaborate further. However, there is a species-specific reaction between egg(s) and sperm in some invertebrate and vertebrate species (reviewed in Wasserman, 1987) that can serve as a model for the same

Evolutionary Theory 8: 397-401 (April, 1989)
The editors thank L. Seisler and G.F.B. Schumacher for help in evaluating this

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reaction within a subdivision of a subspecies (i.e. the "extended family deme" in Cade, 1983). This mechanism is primarily mediated by sperm receptors (in mice, oligosaccharides and polypeptides) in the eggs' zona pelucida. The ability of an egg's sperm receptors to activate a sperm's acrosome is dependent on the polypeptide chains present in the sperm receptor. Thus, considering that oligosaccharides can exist in a "...staggering number of combinational possibilities" and "The great diversity of known oligosaccharide structures is compatible with the generation of species specificity for mammalian sperm receptors (Wasserman, 1987), and also considering the potential diversity in polypeptide structure, it is not unreasonable to suggest the above speciesspecific reaction between egg and sperm functions at the subpopulational level (i.e. at the level of an extended family deme). This proposal is also allowable within inbreeding theory. Similar to female selection at the level of adult organism (for which West-Eberhard [1979] suggested a female selection mechanism that would choose genetic components of fitness as they appeared) an egg would not neccessarily react to a sperm with a specific trait, but would react to the best "choice" among those present. (No conscious choice is implied or neccessary; the mechanism would be the same [i.e. electrochemical] as that implied in Paterson's [1982] specific mate recognition system.) This is possible given the present knowledge of biochemistry: many cells generate chemical and/or electrical messages for intercellular communication (e.g. Stryer, 1981), some plant species have a genetic pollen selection mechanism (e.g. Clegg and Brown [1983]) that may be under strong maternal control (Mazer, 1987), and some invertebrates have a cellular or gametic compatibility mechanism (e.g. Hepper, 1986; Grosberg, 1987, respectively).

Such a mechanism would confer one additional selective advantage besides those listed above: the saving of the energy lost when parental DNA is rearranged or rejected. This phenomenon is well described (e.g. Tunner, 1973, 1974; Abraham, 1985; Cavalier-Smith, 1985abc; Reik et al., 1987; Sapienza et al. 1987; Woodruff et al., 1987), is referred to by various terms (e.g. "hybrid dysgenesis", "transposable elements", "hybridogenesis", "eliminitable DNA", "selfish DNA", "intragenomic selection"), and has various proposed functions. However, by taking these terms and treating them as manifestations of molecular selection and molecular drift (as defined in Van Valen [1983]), and also applying inbreeding theory at the gametic level, it is possible to view some rearrangement or rejection of parental DNA as a post-fertilization isolating mechanism that would reduce outbreeding depression. There is also evidence that suggests this phenomenon is under maternal (i.e. female) control. Hybrid dysgenesis in Drosophila is related to interactions between unknown parental factors present at multiple locations in the parental genome and maternally donated "cytotype", the physical nature of which is unknown (see review in MacLean et al., 1984.) methylation of parental transgenes in mice is dependent on parental contribution (Reik et al., 1987; Sapienza et al., 1987), and the direction and rate of chromosome segregation in interspecies crosses indicated the direction of loss may be determined by the presence of a specific chromosome from one of the parental lines (Pravtcheva and Ruddle, 1983; cited in Worton and Grant, 1985).

While the concept that egg(s) react to specific sperm may appear radical at first glance, the development of sperm competition theory

allows the proposal that eggs are also dynamically involved during fertilization. The literature supports this proposal, and further experimentation that applies inbreeding theory at the gametic level may show the above concept is an extant mechanism in some biological systems.

ACKNOWLEDGMENTS

I thank the following for their valuable comments: H. Byerly, D. Jameson, M. Niklasson, G. Schuett, B. Scott, H. Quinn, and particulary S. Mays.

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