Helical Nature of Sperm Swimming Affects the Fit of Fertilization-Kinetics Models to Empirical Data

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Abstract Models of fertilization kinetics rely upon estimates of the swimming velocity of sperm to predict collision rates between egg and sperm. Most investigators measure sperm swimming velocity without accounting for the helical motion of sperm, thereby obtaining an inflated estimate of the velocity with which sperm approach eggs. In turn, models of fertilization predict inflated rates of sperm/egg collision. I observed sea urchin sperm colliding with eggs, quantified the rate of sperm/egg collision, and measured sperm velocity as a component of the helix through which they swim. I also adjusted the “target size” of eggs to reflect the diameter of the helix. My estimate of sperm swimming velocity is an order of magnitude lower than other estimates for the same species. By using helical parameters in fertilization kinetics models and accounting for dead sperm in laboratory trials, I was able to accurately predict lower rates of sperm/egg collision. Moreover, making these adjustments in the model increased the estimated proportion of sperm that initiate fertilization by 6- to 7-fold, suggesting that a better understanding of sperm swimming might lead to a more complete understanding of fertilization biology and natural selection on gamete traits.

Introduction

Broadcast-spawning marine invertebrates release both eggs and sperm into the water column, where fertilization and development consequently take place. Variation in the proportion of eggs fertilized in nature has long been postulated (Lillie, 1915; Mortensen, 1938; Thorson, 1950), and variability in fertilization success has been empirically quantified in the laboratory (Pennington, 1985; Havenhand, 1991; Levitan et al., 1991; Oliver and Babcock, 1992; Levitan, 1993, 1996a, 2000; Benzie and Dixon, 1994), in field experiments (Pennington, 1985; Levitan et al., 1992; Babcock et al., 1992, 1994; Levitan and Young, 1995; Levitan, 1996a, 1998), and in situ surveys of spawning events (Babcock and Mundy, 1992; Babcock et al., 1992, 1994; Brazeau and Lasker, 1992; Oliver and Babcock, 1992; Sewell and Levitan, 1992; Lasker et al., 1996; Coma and Lasker, 1997). Much of this empirical work has confirmed that fertilization success rarely approaches 100% in nature, where factors such as water-flow velocity (Pennington, 1985; Levitan et al., 1992; Benzie et al., 1994; Levitan, 1996a, 1998), turbulence (Benzie et al., 1994), the distance among spawning animals (Pennington, 1985; Grosberg, 1987; Levitan, 1991, 1998; Yund, 1990; Babcock et al., 1992, 1994; Benzie et al., 1994), and synchrony of spawning (Oliver and Babcock, 1992; Babcock et al., 1992, 1994) all affect the mixing of male and female gametes.

Variation in fertilization success can contribute to selection on gamete characteristics (Levitan, 1993, 1996b), and efforts to understand the evolution of gamete phenotype have relied in part upon models of fertilization kinetics. There have been three principal attempts to model the proportion of eggs fertilized in still water in the laboratory (Rothschild and Swann, 1951; Hultin, 1956; Vogel et al., 1982). The Rothschild and Swann (1951) and Vogel et al. (1982) models are at least partially derived from models of molecular kinetics, which assume random motion of all particles involved and estimate reaction rates based upon the rates at which molecules collide. Hultin (1956) predicted laboratory fertilization based upon the proximity of sperm to virgin eggs, although he did not address the manner by which sperm approach eggs.

Of these three attempts to model fertilization, the model of Vogel et al. (1982) has received the most attention. Vogel and colleagues recognized three possible sperm-egg interactions: (1) permanent adhesion of a sperm to the first egg found (“Don Ottavio”); (2) adhesion to the first egg for a...
negligible time, followed by resumed swimming ("Don Giovanni"); and (3) adhesion for some "longer-than-negligible" period, after which nonfertilizing sperm detach and resume searching ("Masetto"). They state that, during their observations, sperm behavior closely matched the first alternative (collision with, and permanent adhesion to, the first available egg), and subsequent authors have used their "Don Ottavio" model (hereafter VCCW) almost exclusively. The model has been modified by several authors (Denny, 1988; Denny and Shibata, 1989; Denny et al., 1992; Babcock et al., 1994; Benzie et al., 1994; Levitan and Young, 1995) to predict fertilization success under turbulent flow conditions in nature. Styan (1998) also adapted the VCCW model to incorporate the negative effects of polyspermy on fertilization success at high sperm concentrations; however, his model uses the framework of the VCCW model to predict sperm-egg collision rates prior to fertilization.

The VCCW model predicts the proportion of eggs fertilized in a sample (\(\phi\)) by first predicting the number of sperm colliding with a single egg:

\[
\text{# of sperm colliding} = S_0(1 - \exp(-\beta_0 E_0 \tau))
\]

(1, VCCW Eq. 10)

where \(S_0\) is the initial sperm concentration (sperm/\(\mu\)l), \(E_0\) is the initial concentration of virgin eggs (eggs/\(\mu\)l), \(\tau\) is sperm half-life (seconds), and \(\beta_0\) is a rate constant for sperm-egg collisions (\(\text{mm}^3\)/s). \(\beta_0\) is estimated by multiplying sperm swimming speed (\(v\), \(\text{mm} / \text{second}\)) and the area of the egg cross-section (\(\sigma\), \(\text{mm}^2\)):

\[
\beta_0 = v \sigma
\]

(2, VCCW Eq. 7)

where \(\sigma = \pi (\text{egg radius})^2\). The time of sperm-egg exposure, \(t\), can be substituted for sperm half-life (\(\tau\)) when \(t\) is less than \(\tau\). This substitution probably reflects natural conditions, where sperm longevity may exceed contact time due to rapid dilution of gametes.

The proportion of eggs fertilized is then a function of the number of sperm-egg collisions and a rate constant describing fertilization (\(\beta\), \(\text{mm}^3\)/s):

\[
\phi = 1 - \exp[(-\beta S_0 E_0)(1 - \exp(-\beta_0 E_0 \tau))]
\]

(3, VCCW Eq. 14)

Again, \(t\) can be substituted for \(\tau\) when \(t\) is less than \(\tau\). The value of the fertilization rate constant (\(\beta\)) is estimated by iterating the model, using empirical estimates for the proportion of eggs fertilized in a sample (\(\phi\)), the initial sperm concentration (\(S_0\)), the initial egg concentration (\(E_0\)), the time of sperm-egg exposure (\(t\)), and the rate constant describing collisions (\(\beta_0\), \(\text{mm}^3\)/s).

Estimates of \(\beta_0\) are likely to be inflated because the VCCW model, like the models of chemical reaction kinetics upon which it is based, assumes that the motion of eggs and sperm is Brownian—that is, completely random. However, sperm swimming is far from random; rather, sperm (and other microbiota) both translate and simultaneously rotate about their long axis, and so describe a helix as they swim (Jennings, 1901; Bullington, 1925; Gray, 1955; Gray and Hancock, 1955; Crenshaw, 1993a, b, 1996; Crenshaw and Edelstein-Keshet, 1993). The velocity of sperm swimming through helices can therefore be estimated in two ways. The absolute velocity of a swimming sperm describes the velocity with which a sperm passes through a helical trajectory. However, the velocity of a sperm relative to a target such as an egg is better estimated as the rate of advance of the helix (analogous to the "pitch" of a screw) through which the sperm swims. Investigators measuring sperm swimming velocity typically measure the former quantity, which may inflate estimates of the collision rate constant \(\beta_0\).

In contrast to any inflation caused by considerations of sperm velocity, estimates of \(\beta_0\) can also be deflated when the helical swimming of sperm is not considered. As sperm pass through a helix, they sweep out a cylindrical volume of water; the diameter of that cylinder is equal to the diameter of the helix through which they swim. If the diameter of the helix is less than or equal to the diameter of the egg, then the additional volume of water searched by sperm might increase the likelihood that sperm will collide with eggs. In the VCCW model, this quantity should be added to the area of the egg cross-section (\(\sigma\)), such that

\[
\sigma = \pi (\text{egg radius})^2 + \pi (\text{helix radius})^2
\]

(4)

This will increase the estimate of the collision rate constant \(\beta_0\) relative to estimates that do not incorporate the helical nature of sperm swimming.

Changes to the estimated value of \(\beta_0\) also affect estimates of the fertilization rate constant, \(\beta\), in the VCCW model, as well as the value of the ratio between the two rate constants (\(\beta/\beta_0\)). This ratio is important, because investigators ascribe biological importance to \(\beta/\beta_0\). The ratio \(\beta/\beta_0\) describes the proportion of sperm that are capable of initiating fertilization, or the fraction of the egg surface area available for fertilization (Vogel et al., 1982). Estimates of \(\beta/\beta_0\) range from 0.01 (Vogel et al., 1982) to 0.17 (Levitan, 1993), but these estimates are very sensitive to estimates of the collision rate constant \(\beta_0\) (Vogel et al., 1982; Styan and Butler, 2000).

Although the ability of the VCCW model to predict fertilization has been comprehensively tested in the laboratory by varying sperm age, sperm concentration, egg concentration, and sperm-egg contact time (Vogel et al., 1982; Levitan et al., 1991), the ability of the model to predict the quantity underlying fertilization—collisions between sperm and eggs—has never been tested. In this study, I measure the rate at which helically swimming sperm approach eggs,
estimate sperm-egg collision rate by observing gametes of the sea urchin *Lytechinus variegatus*, and test the ability of the VCCW model to predict sperm-egg collision rates by comparing predictions with empirical estimates. I then re-estimate fertilization efficiency ($\beta/\beta_0$) to compensate for reducing sperm swimming velocity in the VCCW model.

**Methods and Materials**

*Gamete manipulation*

Using modified syringes, I injected 90 single *Lytechinus variegatus* eggs into 1-ml pools of sperm on the stage of a trinocular microscope (Farley and Levitan, 2001). The microscope was fitted with a low-light-level video camera, which was in turn connected to a video monitor and a videocassette recorder. I videotaped eggs until fertilization had occurred (marked by the complete expansion of the fertilization membrane); among eggs that were not fertilized, I terminated the videotape after 20 min. The ability of *L. variegatus* sperm to fertilize eggs declines after 20 min (Levitan, 2000); the same is true for many other species (Vogel et al., 1982; Levitan et al., 1991; Benzie and Dixon, 1994). Using a hemacytometer, I quantified the sperm concentration for each trial.

From a frame-by-frame analysis of the videotapes, I quantified the number of sperm colliding with each egg or egg jelly coat (Farley and Levitan, 2001) and estimated the radius and rate of forward advance of the helix through which *L. variegatus* sperm swim. Because I removed the jelly coats from one-half of the eggs tested, and because eggs that were not fertilized were exposed to sperm for longer than eggs that were fertilized, I compensated for variation in the sizes of egg targets and in the time of exposure to sperm: collisions were standardized by the time of sperm-egg exposure and by the area of egg cross-section, yielding a final unit of collisions/s/mm$^2$. Because the data showed a skewed distribution, I used a 4th-root transformation to de-emphasize non-normality (Downing, 1981), then regressed transformed standardized collisions on 4th-root transformed sperm concentration using a least-squares regression to ascertain relationships between the two variables. I performed two such regressions—first regressing standardized collisions on the sperm concentrations that I quantified, and then regressing standardized collisions on 60% of the quantified sperm concentration. The second method was based on the observation (Levitan, 2000) that about 40% of *L. variegatus* sperm are inactive on microscope slides in the laboratory.

*Fertilization assays*

I assayed fertilization across a gradient of sperm concentration represented by seven serial dilutions (Farley and Levitan, 2001). I collected eggs from dissected *L. variegatus* gonads, adjusted egg concentration to about 200 eggs/ml, and exposed eggs from each female to seven serial dilutions of sperm from a single male. Ten seconds after adding sperm to each vial, I added 5 ml of 0.55 M KCl and swirled vials to ensure thorough mixing. Potassium chloride immobilizes sperm without interrupting the development of fertilized eggs (Schuel, 1984), and it does not induce fertilization in unfertilized eggs.

After incubating the vials in running seawater in a wet table for 2 h following the introduction of KCl, I counted at least 200 eggs from each vial, scoring each egg as fertilized or unfertilized. The 2-h wait allowed embryos to develop to the two- or four-cell stage, making fertilized/developed eggs distinct from unfertilized eggs. I collected data from 17 male-female urchin pairs, using urchins whose gametes were not used in videotaped observations of sperm-egg interactions.

*Predictions of sperm-egg collisions*

I predicted collisions of sperm to eggs using the portion of the VCCW model designed for this purpose (Eq. 1, above). I generated two sets of predictions. In the first set, the collision rate constant ($\beta_c$ estimated as $\sigma v$) was estimated using absolute sperm swimming speed ($v = 0.2$ mm/s, Levitan, unpubl. data) and the diameter of eggs without jelly coats (0.0994 mm, Farley and Levitan, 2001). This yielded $\beta_0 = 0.00155 \text{mm}^2/\text{s}$. In the second set of predictions, the rate of forward advance of the helix ($v = 0.027$ mm/s) was used in place of absolute sperm velocity, and the area of helical cross-section (0.00190 mm$^2$) was added to the egg target size (Eq. 4 above). This yielded $\beta_0 = 0.000261$. In both cases, $t$ was set equal to 10 s and $E_0$ to 0.001 eggs/μl. Predicted collisions were standardized by time of exposure and egg target size, and the predictions were 4th-root-transformed to make them comparable to the empirical data. I then plotted both predictions and empirical data as a function of sperm concentration and used analyses of covariance to search for congruence between the two.

*Estimation of fertilization efficiency*

I fitted fertilization assay data to the Styan (1998) model using SAS (1996; proc nlin) to estimate the fertilization rate constant $\beta$ for *L. variegatus* eggs with intact jelly coats. Sperm velocity was set equal to the rate of forward helical advance ($v = 0.027$ mm/s). To estimate $\sigma$, the diameter of eggs with intact jelly coats (193.6 μm; Farley and Levitan, 2001) was used and the area of helical cross-section (0.00190 mm$^2$) was added. This yielded $\sigma = 0.0313$ and $\beta_0 = 0.000846$. Empirical estimates of $E_0$ were used (0.1–0.28 eggs/μl), and $t$ was set equal to 10 s to reflect laboratory conditions.

I also fitted fertilization assay data to the Styan (1998) model and estimated the fertilization rate constant $\beta$ for *L.
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variegatus eggs without jelly coats. Values for sperm velocity and \( \sigma \) were as specified above except that the diameter of eggs without jelly coats (99.4 \( \mu m \); Farley and Levitan, 2001) was substituted in estimating \( \sigma \), which yielded \( \sigma = 0.00966 \) and \( \beta_0 = 0.000261 \). Again, empirical estimates of \( E_0 \) were used (0.1–0.272 eggs/\( \mu l \)), and \( t \) was set equal to 10 s to reflect laboratory conditions.

Iterating the Styan (1998) model in SAS provided estimates of \( \beta \) for eggs with and without jelly coats, and also generated 95% confidence intervals about mean assayed fertilization success for both egg types. I used the estimates of \( \beta_0 \) above and the iterated estimates of \( \beta \) to generate predictions of fertilization success using the Styan (1998) model, and plotted predictions and 95% confidence intervals together to compare model predictions to the data.

**Results**

**Predictions of sperm-egg collision rates**

Sperm concentration was a good predictor of the number of collisions (standardized for time and size differences between targets) between sperm and eggs; increasing sperm concentration yielded increased sperm-egg collision rates in my trials. When standardized collision rates were plotted as a function of sperm concentration, variation in sperm concentration explained 27% of the variation in collision rates (Fig. 1A; \( y = 0.279x + 0.127; r^2 = 0.270; P < 0.0001 \)). However, the empirical collision rate was significantly lower than that predicted by the VCCW model [ANCOVA; \( r^2 = 0.859 \); \( P(\text{interaction term}) < 0.0001 \)].

Because I estimated sperm concentration by counting killed sperm on a hemacytometer, I may have overestimated the proportion of active spermatozoa in my samples. About 40% of Lytechinus variegatus sperm on microscope slides are inactive (Levitan, 2000). To determine whether variation in sperm concentration could be driving differences between empirical and predicted sperm-egg collision rates, I plotted the predicted and empirical numbers of collisions (adjusted by target size and area) as a function of 60% of the estimated sperm concentration (Fig. 1B). This also yielded a significant positive relationship (\( y = 0.317x + 0.127; r^2 = 0.270; P < 0.0001 \)), which was greater in slope but similar in intercept than the relationship in Figure 1A. By accounting for dead sperm, I reduced the disparity between the slope predicted by the model and the slope of empirical data, but the empirically estimated collision rate was still significantly lower than the VCCW model predicted [ANCOVA; \( r^2 = 0.859 \); \( P(\text{interaction term}) < 0.0001 \)].

The power of the VCCW model to predict sperm-egg collisions (Eq. (1) above) improved when I substituted the helical rate of advance for the absolute sperm swimming velocity and added the helical cross-section to the egg target size. I plotted standardized sperm-egg collision rate as a function of 60% sperm concentration (Fig. 2), and used the parameters of the helix to generate a predicted collision rate. Empirical collision rate was similar to model predictions [ANCOVA, \( r^2 = 0.585 \); \( P(\text{sperm concentration}) < 0.0001 \); \( P(\text{data type: empirical or predicted}) = 0.692 \); \( P(\text{sperm concentration \times data type}) = 0.261 \)], indicating that the VCCW model accurately predicted rates of encounter between sperm and eggs when helical sperm swimming was considered.

**Estimation of fertilization efficiency**

I fitted empirical data to Styan’s (1998) model to estimate fertilization efficiency in L. variegatus eggs with intact jelly coats. Using \( \beta_0 = 0.000846 \) to reflect helix parameters resulted in a value of 0.0000070 for \( \beta \), making \( \beta/\beta_0 = 0.0827 \). Predictions using \( \beta/\beta_0 = 0.0827 \) fell within the 95% confidence interval about empirical fertilization rates.

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**Figure 1.** Sperm-egg collision rates as a function of sperm concentration. Predicted rates (dashed line) are compared to empirical data (solid line). The collision rates predicted by the VCCW model (Eq. 1 in text) using absolute sperm swimming velocity were significantly greater than the observed rates, whether the latter were based on counts of killed sperm on a hemacytometer (A: closed circles) or calculated by plotting the empirical data against 60% of the empirical sperm concentration to account for dead sperm in laboratory trials (B: open circles).
for *Lytechinum variegatus* eggs with intact jelly coats in the laboratory (Fig. 3A).

To estimate $\beta$ for eggs without jelly coats, I fitted an estimate of $\beta_0 = 0.000261$ and empirical fertilization data to Styan’s (1998) model. This yielded an estimate of $\beta = 0.000044$, and $\beta/\beta_0 = 0.169$. Again, predictions of fertilization success fell within the 95% confidence interval about empirical fertilization rates for *L. variegatus* eggs without jelly coats in the laboratory (Fig. 3B).

**Discussion**

Consideration of the helical nature of sperm swimming significantly improves the ability of the VCCW model (and the Styan (1998) model, which is derived from the VCCW model) to predict sperm-egg collisions. Adjusting sperm velocity in fertilization-kinetics models to reflect the rate of helical advance, rather than the absolute speed of sperm in the water, adjusting egg “target size” ($\sigma$) to reflect the diameter of the helix, and adjusting sperm concentration to reflect dead sperm in laboratory conditions, all contribute to significant improvements in the accuracy with which sperm-egg collision rates are predicted.

An improved understanding of sperm swimming may affect our understanding of sperm viability. In fertilization kinetics models (Vogel et al., 1982; Styan, 1998), the quantity $\beta/\beta_0$ is interpreted as the quantity of viable sperm, or as the proportion of colliding sperm that initiate fertilization (“fertilization efficiency”; Styan, 1998; Styan and Butler, 2000). Typical estimates of $\beta/\beta_0$ from laboratory data range from 0.01 to 0.1, indicating that 1%–10% of sperm are thought to be viable (see, e.g., Vogel et al., 1982; Levitan, 1993; Styan and Butler, 2000; Farley and Levitan, 2001). The highest recorded value of $\beta/\beta_0$ for eggs with intact jelly coats is 0.17 (the sea urchin *Strongylocentrotus droebachiensis*, Levitan, 1993).

In this study, incorporating helical swimming characteristics into estimates of sperm-egg collision rates increases $\beta/\beta_0$. For *Lytechinum variegatus* eggs with intact jelly coats, the previous estimate of $\beta/\beta_0$ was 0.0119 (Farley and Levitan, 2001). Incorporating helical parameters into the Styan (1998) fertilization-kinetics model increased $\beta/\beta_0$ to 0.0827, a 7-fold increase in the estimate of fertilization efficiency for this species. Among *L. variegatus* eggs without jelly coats, the increase is similar: $\beta/\beta_0$ is increased from 0.0284 (Farley and Levitan, 2001) to 0.169. This constitutes a 6-fold increase in fertilization efficiency.

When sperm swim through a helix, their rate of forward progress is much less than their absolute swimming speed: in *L. variegatus*, the rate of forward progress (0.027 mm/s) is an order of magnitude less than the absolute swimming velocity to reflect helical swimming prompts a reappraisal of fertilization efficiency in this species.

![Figure 2](image2.png)

**Figure 2.** As in Figure 1, with empirical data (open circles, solid line) plotted against 60% of empirical sperm concentration. Dashed line: Collision rate predicted by the VCCW model (Eq. 1 in the text), using the rate of forward progression of sperm swimming through a helix. The model predictions are similar to the data.

![Figure 3](image3.png)

**Figure 3.** Fertilization success in *Lytechinum variegatus* eggs, plotted as a function of sperm concentration, for eggs with intact jelly coats (A), and for eggs without jelly coats (B). Dashed lines: upper and lower 95% confidence intervals about mean fertilization in laboratory assays. Heavy solid lines: predicted fertilization using helical sperm velocity and a newly fitted value for fertilization efficiency ($\beta/\beta_0 = 0.368$). Reducing sperm swimming velocity to reflect helical swimming prompts a reappraisal of fertilization efficiency in this species.
speed (0.2 mm/s). The fact that the lower, helical-advance velocity results in a higher...  

The movement of sperm in nature is probably more strongly affected by turbulent mixing of the water column than by sperm swimming (Denny, 1988; Denny and Shibata, 1989). Here, I have measured the helical parameters of sperm swimming in still water, a condition that is probably rare in nature. This raises the possibility that helical swimming is a hydrodynamic constraint imposed on small swimming bodies. However, if turbulent motion were sufficient for fertilization, then we would expect little variation in the swimming characteristics of sperm. Inverse relationships between egg size and absolute sperm swimming speed in congenic urchins (Levitan, 1993) suggest that sperm swimming is important, even if only at very small spatial scales, and that it might be shaped by natural selection.

If sperm swimming is adaptive (Levitan, 2000), selection may act on sperm swimming to maximize the probability of fertilization. Variation in flagellar motion can affect the characteristics of the helix through which sperm swim (Brockaw, 1962; Crenshaw, 1993a, b). Flagellar motion depends on the number and placement of proteins (dynein) on the microtubules that make up flagellae (Alberts et al., 1989), so genetic mutation may affect helix characteristics, and such quantities as the rate of forward progress and the diameter of the helix may be subject to variation and selection. Moreover, unlike variation in egg size and number, there is no a priori reason to suspect trade-offs between helix characteristics and other characteristics of sperm, such as abundance or longevity. Investigators interested in selection on gamete traits should consider the helical nature of sperm swimming and variations in helix characteristics, as well as variation in egg size and number.

Acknowledgments

I thank the two anonymous reviewers who thoughtfully critiqued the manuscript. This research was supported by an NSF grant to D.R. Levitan, who also provided the SAS model for estimating $\beta$. The FSU Marine Laboratory donated space and materials to the project.

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