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Selection for High Gamete Encounter Rates Explains the Success of Male and Female Mating Types

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Sexual reproduction occurs in many small eukaryotes by fusion of similar gametes (isogamy). In the absence of distinguishable sperm and eggs, male and female mating types are missing. However, species with distinct males and females have so prospered that almost all familiar plants and animals have these mating types. Why has sexual reproduction involving sperm and eggs been so successful? An answer is obtained by considering physical limitations on encounter rates between gametes. A biophysical model based on well-established relationships produces fitness landscapes for the evolution of gamete size and energy allocation between motility and pheromone production. These landscapes demonstrate that selection for high gamete encounter rates favors large, pheromone-producing eggs and small, motile sperm. Thus, broadcast-spawning populations with males and females can reproduce at lower population densities and survive under conditions where populations lacking males and females go extinct. It appears that physical constraints on gamete encounter rates are sufficient to explain the first two steps in the isogamy → anisogamy → oogamy → internal fertilization evolutionary sequence observed in several lineages of the eukaryotes. Unlike previous models, assumptions concerning zygote fitness or decreasing speed of swimming with increasing gamete size are not required.

Introduction

In biology, males are defined by their production of many small motile gametes (sperm), while females produce fewer, larger, immobile gametes (eggs). However, in a variety of small eukaryotes, sexual reproduction involves identical gametes (isogamy), other species produce gametes with various degrees of distinction (anisogamy), and only some species produce eggs and sperm (oogamy) for either broadcast spawning or internal fertilization. The evolutionary record indicates that the isogamy → anisogamy → oogamy → internal fertilization sequence has occurred many times, in many different lineages of the eukaryotes (Baccetti, 1985; Margulis & Sagan, 1986), suggesting that there are general selective pressures for evolution in this direction. But what are these pressures? Why have the lineages that developed male and female mating types been so successful that almost all the familiar large organisms have males and females?

The most common explanation is based on assumptions that gametes have a difficult time finding partners to fuse with and, in addition, that large zygotes have a great advantage over smaller zygotes after fertilization (Bell, 1997; Hoekstra, 1987; Smith & Szathmáry, 1995). Thus, numerous, small, motile sperm solve the gamete

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encounter problem, and the large eggs provide a size that facilitates success of the zygote.

However, in quantitative models assuming size does not affect gamete encounter rates (Charlesworth, 1978; Hoekstra, 1980; Parker, 1984; Parker *et al.*, 1972; Smith, 1978), the second assumption requires that (over some size range) the fitness of zygotes be more than proportional to their volume. This assumption seems unlikely, and there is no evidence for such an extreme relationship (Madsen & Waller, 1983). A model making the more reasonable assumption that zygote fitness is proportional to volume (Cox & Sethian, 1985) makes the assumption that larger gametes swim slower (speed inversely proportional to gamete radius). And a model making no assumptions about zygote size assumes that swimming speed is inversely proportional to the *square* of gamete radius (Hoekstra, 1984; Hoekstra *et al.*, 1984).

Taken together, these studies suggest that there is a tradeoff between the strength of fitness dependence on zygote volume and swimming speed dependence on radius. As the exponent of the contribution of zygote volume to fitness has decreased, the exponent of gamete radius in swimming speed has become more negative. But available data reveal no significant correlation between size and speed of gametes (see the Methods section), and basic biophysical considerations lead to the expectation that larger cells generally swim faster (Dusenbery & Snell, 1995). Furthermore, none of these models recognize that gametes must carry a cargo (of chromosomes), and chromatin often occupies a significant part of gamete volume.

A way out of these problems is suggested by a recent biophysical model demonstrating a minimum size for effective pheromone use in mate attraction (Dusenbery & Snell, 1995). Large eggs can increase their target size to sperm by producing attractant pheromones. The Dusenbery–Snell model indicates that for equal-size gametes, with one type immobile and producing pheromone, the encounter rate per gamete is proportional to the seventh power of gamete radius (or volume to the $2\frac{1}{3}$ power). This result suggested that physical limitations on the encounter process itself can explain the success of male and female types, without any assumptions about zygote fitness. The effect of size on pheromone production is even sufficient to overcome a plausible direct proportionality between speed of swimming and size.

Methods

CALCULATIONS

The calculations start with the rate of collision in the hard-sphere model of gases [eqn (1)] [e.g. Kauzmann, 1966, eqn (5–15)]. For density, I assume that the total volume of each type of gamete produced by the population is some fraction V_T of the environment. Then $n = 3V_T/(4\pi r_s^3)$, where r_s is the radius of the gamete surface. For the speed, I use a previous model [Dusenbery & Snell, 1995, eqn (1)] modified for the volume occupied by chromosomes. This gives $u^2 = (2P_V E/9\eta)\ (r_s^3 - r_c^3)/r_s$, where P_V is the power per unit volume of cytoplasm available from general metabolism for locomotion (or pheromone production), E is the efficiency with which this power is effectively applied to locomotion, r_c is the radius of a sphere equal in volume to the chromosomes, and η is the viscosity of the water through which the gametes swim. Substituting these relations into eqn (1) and using the dimensionless sizes, $r_A = r_{sA}/r_c$ and $r_B = r_{sB}/r_c$, yields eqn (2), where $H = (3/\pi)(V_T/4)^2\ (2P_V E/\eta)^{1/2}\ r_c^{-3}$ with units of inverse time and volume. When one gamete has the minimum size ($r_B = 1$), the other has an optimum size of

$$r_A = (1/2)\left[(7 + 4\sqrt{3})^{1/3} + (7 + 4\sqrt{3})^{-1/3}\right] \cong 1.411.$$

For oogamy, I start with the same model, assuming sperm are mating type A, and eggs are type B. Then $u_B = u_E = 0$, and, in the term for target size of the egg, r_B is replaced by the larger of the egg relative radius (r_E) or the relative radius (r_P) of the active space of the pheromone released by the egg. Assuming that the pheromone is released uniformly over the egg surface and that diffusion is the only mechanism of pheromone transport, the radius of the active space is estimated using Fick's law of diffusion [eqn (5) of Dusenbery and Snell, 1995] modified for the volume occupied by the chromosomes. The pheromone detection radius is then

$r_d = (KP_V/3DC_{Th}) \quad (r_s^3 - r_c^3) = (r_c^3 \quad KP_V/3DC_{Th})$ $(r_E^3 - 1)$, where P_V is the specific power available for pheromone production at the level of general metabolism, K is the efficiency of converting metabolic energy into released pheromone, D is the diffusion coefficient of the pheromone through the environment, and C_{Th} is the threshold concentration for detection of the pheromone by sperm. For convenience, the relative active space size ($r_P = r_d/r_c$) can be expressed as $r_P = P(r_E^3 - 1)$, where $P = r_c^2 KP_V/(3DC_{Th})$, a dimensionless number. The rate of gamete contact is then given by eqn (3). Large eggs means $r_E \gg 1$ and $r_E \gg P^{-1/2}$. With standard values, $P^{-1/2} = 10$.

The curvature of a gamete's path can be characterized by the length (L) over which on average it changes by some angle $\langle\theta\rangle$, and $L = ut$, where t is the time in which rotational diffusion changes the orientation by $\langle\theta\rangle$. Both u and t depend on size; u is described above, and Brownian motion results in $t = \langle\theta^2\rangle 2\pi\eta r^3/kT$ (Berg, 1993, p. 84). Algebra then reveals that $L = \langle\theta^2\rangle \ (2\pi\eta/kT) \ (2P_V E/9\eta)^{1/2} \ r_c^4 \ (r^8 - r^5)^{1/2}$, where r is a relative gamete radius ($= r_A$, r_B, or r_S). Using the standard values, the paths of optimal isogametes, $r = (3/2)^{1/3}$, change direction by one radian on average over a distance $L \cong 180$ μm, while the paths of optimal sperm targeting large eggs, $r = (7/4)^{1/3}$, have $L \cong 250$ μm and optimal sperm targeting minimal eggs, $r \cong 1.411$, have $L \cong 570$ μm.

NUMERICAL VALUES

The volume of the nucleus in the sperm of 12 species of aquatic invertebrates was estimated from published electron micrographs (Afzelius, 1955; Austin, 1968; Baccetti, 1985; Chia *et al.*, 1975; Dan, 1967) to fall in the range 0.6–14 (median 1.2) μm^3. The radii of the equal-volume spheres range from 0.5 to 1.5 (median 0.65) μm. Two species of *Chlamydomonas* have nuclear volumes of 1 and 4.4 μm^3 (Harris, 1989; Tsubo, 1961), with equivalent radii of 0.6 and 1.0 μm. Gametes of an aquatic fungus (Pommerville & Fuller, 1976) have nuclear volumes of 4 and 14 μm, with equivalent radii of 1.0 and 1.5 μm. Considering all these values, it was assumed that the radius (r_c) of the sphere equal to the volume occupied by the chromosomes, was 1 μm, which is within 50% of all these observed values.

Data on gamete size and speed were found for two species of isogamous green algae (Haxo & Clendenning, 1953; Racey *et al.*, 1981; Rüffer & Nultsch, 1985), one anisogamous green alga (Togashi *et al.*, 1997), one anisogamous aquatic fungus (Pommerville, 1978), sperm of a brown seaweed (Maier & Müller, 1986), and sperm of four sea urchin species (Chia *et al.*, 1975; Gray, 1955; Levitan, 1993; Levitan *et al.*, 1991). The rank correlation between gamete speed and volume was not significant by either the Spearman or Kendall methods (StatView). The relative speeds fell in the range 6–95 (median = 23) lengths s^{-1}. Approximating gamete shapes as equal-volume spheres, the relative speeds were in the range 6–120 (median = 33) diameters s^{-1}.

The standard values assumed here for the parameters are generally the same as previously assumed (Dusenbery, 1997a, b; Dusenbery & Snell, 1995): viscosity, $\eta = 0.01$ poise; efficiency of propulsion, $E = 0.005$; efficiency of pheromone production, $K = 10^{-14}$ mol erg^{-1}; diffusion coefficient of the pheromone, $D = 10^{-5}$ cm^2 s^{-1}. Additional assumptions are: the threshold concentration for detection of pheromone, $C_{Th} = 10^{-11}$ mol cm^{-3} ($= 10^{-8}$ M); the total volume of the gametes, $V_T = 10^{-9}$ the volume of the environment; and the genome radius, $r_c = 1$ μm. In comparison with previous assumptions that organisms allocate 10% of their energy budget to locomotion or pheromone production, it was assumed here that the more specialized gametes allocate 50% of their energy to locomotion or pheromone production, since they have fewer other demands for energy; consequently, the available power density is $P_V = 3 \times 10^4$ erg s^{-1} cm^{-3}. With these assumptions, $H = 1.03 \times 10^{-5}$ s^{-1} cm^{-3} and $P = 0.01$, which gives an active space radius of $r_p = 1$ mm for $r_E = 46$ and $r_p = 10$ mm for $r_E = 100$. Thus, the egg sizes of interest produce a range of sperm attraction of several millimeters, as found in many brown algae (Maier & Müller, 1986). The speed of swimming in the model with standard parameter values is 29 diameters s^{-1}, which is typical of reported data (see above).

The Models and Results

For simplicity, assume that a population consists of individuals that reproduce once after reaching a certain age, and these individuals are randomly distributed in a three-dimensional aquatic environment at a density n_R. Large numbers of gametes of two types are produced in equal total volume but may vary in size and occur at densities of n_A and n_B. Equal total volumes of cytoplasm for each gamete type is reasonable considering arguments that there should be equal investment by both sexes (Smith, 1978, p. 157). Such variations in size and numbers occur among closely related green algae (Cox & Sethian, 1985; Togashi *et al.*, 1997).

I follow Scudo (1967) in starting with the hard-sphere model of gases. But, whereas he concentrates on the effects of high gamete density, I focus on mechanisms that increase encounter rates in the limit of low population density, which is the condition in which extinction can be caused by insufficient gamete encounter rates.

In order to sustain the population when it is at low population densities, we must have $Z_{AB}tf \geqslant n_R$, where Z_{AB} is the rate (per unit volume) at which gametes of types A and B encounter one another, t is the time period over which gametes are functional (a few minutes or hours in most cases), and f is the fraction of gamete encounters that lead to the formation of zygotes that survive and reproduce.

Here, I focus on variations in Z_{AB} and take t and f as constant. If it is assumed that the gametes swim sufficiently straight and get randomly distributed through the environment, Z_{AB} can be estimated from the formula derived for the hard-sphere model of gases [e.g. Kauzmann, 1966, eqn (5–15)]:

$$Z_{AB} = n_A n_B \pi d^2((3u_A^2 + u_B^2)/(3u_A)), \qquad (1)$$

where d is the distance separating the centers of the gametes at encounter, and $u_A \geqslant u_B$ are the speeds of the two types of gametes. This kind of model has worked well in laboratory studies of sea urchin fertilization (Levitan *et al.*, 1991).

Since the defining difference between males and females is the size and speed of the gametes produced, we need a relationship between size and speed. There are no clear empirical relationships (see the Methods section), and so I employ a model based on a biological generalization and a physical "law". The specific metabolic rates of active organisms and tissues are confined to a relatively narrow range. Since the specific rates (per volume) do not correlate with size (Dusenbery, 1997, 1998b; Dusenbery & Snell, 1995), it is appropriate to assume a typical value. Stoke's law predicts the power required to move spheres through a viscous fluid at low Reynolds number. This condition is satisfied for speeds as high as 100 diameters s^{-1}, for sizes below 70 μm diameter (Dusenbery, 1997), and thus applies to the motile gametes of interest here.

Consequently, all gametes are approximated as spherical shapes, with a surface radius of r_s. In nature, eggs are usually spherical (Austin, 1965), and sperm functioning in external fertilization are usually close to spherical (Baccetti, 1985). The gametes are also assumed to be neutrally buoyant, as are many fish eggs (Sundby, 1997).

The energy available for gametes to devote to locomotion or pheromone production is assumed proportional to their volume (Dusenbery, 1997, 1998b; Dusenbery & Snell, 1995). However, to be effective, gametes must carry a cargo of genetic material, and the volume occupied by the chromosomes is assumed to be unavailable for energy storage and metabolism. This volume is characterized by the radius (r_c) of a sphere with the same volume (but the actual shape of the volume occupied by the genome is of no consequence to the model as long as the genome can fit within the spherical boundaries of the gamete).

The search process is assumed to end when a motile gamete comes within detection distance (d) of a gamete of the opposite mating type (Dusenbery, 1992, pp. 388–391) (Fig. 1). If a diffusable pheromone is not functional, the surfaces of the two gametes must come into contact, and the detection distance is the sum of the radii of the two gametes, $d = r_s + r_s$. If pheromone is functional, one of the two gametes expands its effective target size to a radius of r_p, and the detection distance is $d = r_s + r_p$.

Combining these assumptions, the initial rate at which gametes of type A contact slower gametes of type B, in the absence of pheromone,

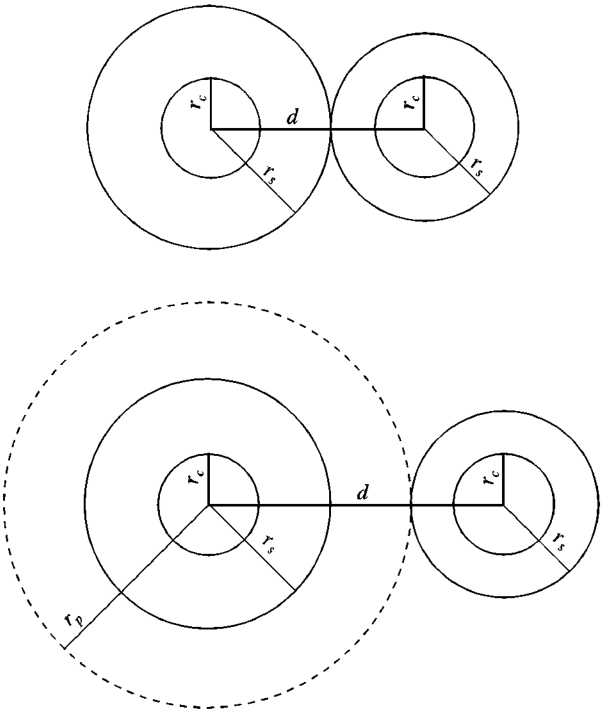

FIG. 1. Geometry of gamete model. The inner circle represents the volume occupied by chromosomes and unavailable for producing metabolic energy; it is assumed to be equal to a sphere of radius r_c. The heavy circles of radius r_s represent the surface of the gametes. The large dashed circle represents the surface at which pheromone concentration falls to the threshold level for detection by the other gamete; its radius is r_p. Detection of a mate occurs when the centers of gametes come within a distance d of one another. Two cases are shown. Above, encounter occurs when the surfaces of the two gametes come into contact with one another; no pheromone is functional and $d = r_s + r_s$. Below, the gamete on the left produces sufficient pheromone to be detected beyond the surface of the gamete; in this case $d = r_s + r_p$.

is given by (see the Methods section)

$$Z_{AB} = H(r_A r_B)^{-3}(r_A + r_B)^2 \times \frac{3(r_A^2 - r_A^{-1}) + r_B^2 - r_B^{-1}}{(r_A^2 - r_A^{-1})^{1/2}}, \qquad (2)$$

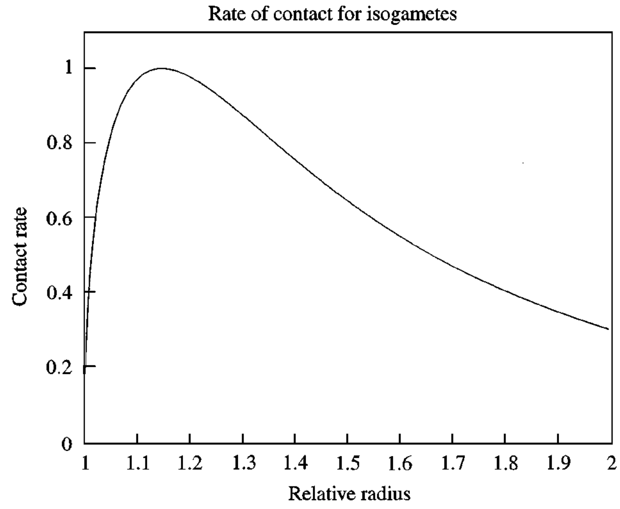

FIG. 2. Contact rate of isogametes. Equation (2), with relative radius $= r_A = r_B$. A well-defined maximum rate of $32 \times 3^{-3/2}$ $H \cong 6.16H$ occurs at a relative radius of $(3/2)^{1/3} \cong 1.145$. The rate here and in other plots is normalized to this maximum isogamous value.

where H is the inherent rate of gamete contact (number of contacts per unit time per unit volume of the environment) that reflects the total gamete volume in the environment, the volume occupied by the chromosomes, the energy density available from cytoplasm applied to locomotion, and the viscosity of the environment. The parameter H is independent of gamete size, and the effect of size is expressed in the rest of the equation, where r_A and r_B are the dimensionless radii of the two types of gametes relative to the radius of the chromosome volume: $r_A = r_{sA}/r_c$ and $r_B = r_{sB}/r_c$. If the gametes do not swim at the same speed, r_A refers to the faster gamete, and thus $r_A \geqslant r_B$ because speed is proportional to r_s in this model (Dusenbery & Snell, 1995). The second term contains the effect of gamete size on the density of gametes in the environment, the third their target size and the ratio on the right measures their relative speeds.

For isogamous reproduction ($r_A = r_B$), there is a size yielding a maximum rate of contact (Fig. 2). This maximum rate is $Z_{AB} = 32 \times 3^{-3/2}H \cong 6.16H$, and it occurs at $r_A = r_B = (3/2)^{1/3} \cong 1.145$, where the chromosomes occupy 2/3 the volume of the gamete. [Little relevant data was found for isogametes, but among ten invertebrate species the chromosomes appeared to occupy 0.25–0.8 (median 0.42) of the sperm volume.] In subsequent plots, Z_{AB} has been normalized to this optimum isogamous value so that it is easier to see how the rates compare to it.

Allowing r_A and r_B to vary independently, generates the landscape of the gamete-contact component of fitness, shown in Fig. 3. We see that the optimum isogamous condition sits on a saddle, and the rate of contact can be increased by 14%, if one gamete type shrinks to its minimum size (where it will be immobile because it has no cytoplasm to provide energy for motility), and the other gamete type grows toward an optimal size of $r \cong 1.411$. This model provides a mechanism to break the symmetry of isogamy. Although few if any species are known in which the non-motile gamete is smaller than the motile gamete, this mechanism might provide an important pathway for starting down the path of anisogamy. If this does occur, the lack of observation of such gametes suggests that they are easily replaced by more effective gamete types.

Next I model the oogamous condition in which females produce eggs, which are immobile and expend their energy releasing pheromone to attract sperm. Pheromone attraction appears to be the rule among anisogamous and oogamous aquatic species (Hoekstra, 1987). The initial rate at which sperm (S) find eggs (E) is given by (see the Methods section)

$$Z_{SE} = 3H(r_S r_E)^{-3} (r_S + R_E)^2 (r_S^2 - r_S^{-1})^{1/2}, \quad (3)$$

where R_E is the larger of r_E and the radius of the active space of the pheromone, $r_P = P\ (r_E^3 - 1)$, with P a dimensionless parameter characterizing the effectiveness of pheromone production and reception. In the limit of large eggs, the rate of gamete encounters is proportional to $HP^2 r_E^3$ and increases in proportion to egg volume and the square of pheromone effectiveness.

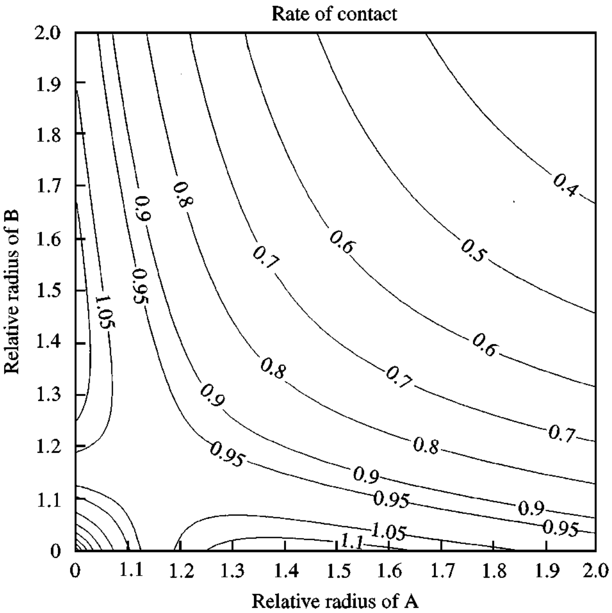

FIG. 3. Contact rate of ansiogametes. Equation (2), where A and B refer to two different mating types. The contours are the rate of contact relative to the optimum isogamete. Isogametes occur along the diagonal of symmetry, and the maximum isogametic rate occurs in the saddle in the lower left corner. The contact rate can increase above the optimal isogamous value if one type increases in size and the other decreases. The maximum rate ($\cong 7.03H$) occurs with a mobile gamete relative radius of $r = (1/2)\,[(7 + 4\sqrt{3})^{1/3} + (7 + 4\sqrt{3})^{-1/3}] \cong 1.41$. The smaller gamete ($r = 1$) has no cytoplasm devoted to locomotor energy production.

Assuming standard values for the parameters (see the Methods section), the fitness landscape for oogamy is presented in Fig. 4. Here we see a peak of high fitness at the bottom, corresponding to the peaks in Fig. 3, where one gamete has minimal size. But a much higher rate of contact occurs with large eggs. If the egg radius is more than 38 times the genome radius (or 37 times the sperm radius), the rate can be greater than any rate obtained by gametes without pheromone (Fig. 4; see the Discussion section).

This pattern is primarily due to the strong size dependence of pheromone effectiveness. A calculation that assumes swimming speed is inversely proportional to gamete radius, as assumed by Cox and Sethian (1985), produces a pattern similar to Fig. 4, except for the decline in encounter rate as sperm size approaches the limit imposed by chromosome volume.

In this model, increased egg size increases encounter rates without limit, but in nature other factors will eventually limit the practical size of an egg. However, some aquatic eggs are as large as several millimeters diameter and nearly a thousand times the diameter of corresponding sperm (Jaeckle, 1995; Jaffe, 1985).

Discussion

How reasonable are the assumptions in this model? Is the assumption of spherical shapes reasonable? Aquatic eggs are almost always spherical (Austin, 1965). Although sperm are rarely spherical, they only depart radically from the compact shapes to which spheres are good

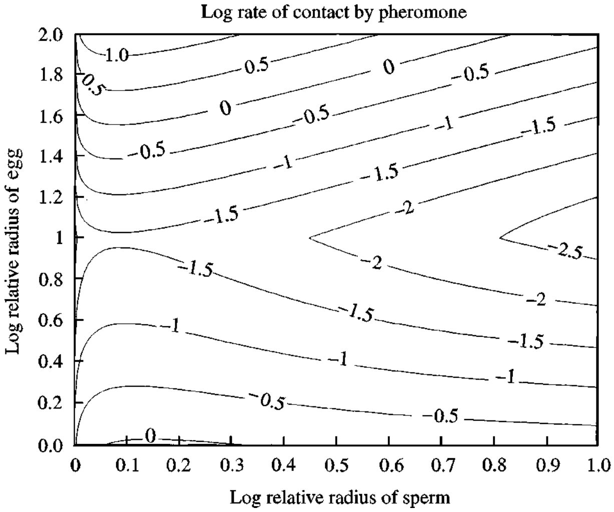

FIG. 4. Encounter rates for sperm and pheromone-producing eggs [equation (3)]. The contours are the log of the rate relative to that of the optimum isogamete. Two peaks are present. At the bottom left, the peak rate occurs for a minimum size egg that has no cytoplasm to support pheromone production; it corresponds to the peaks in Fig. 3, and the optimal sperm size is the same ($r_S \cong 1.41$ at $\log r_S \cong 0.15$). At the top left, very high encounter rates are achieved for small sperm and large eggs producing significant amounts of pheromone. In the limit of large eggs, the optimal sperm has the smaller size $r_S = (7/4)^{1/3} \cong 1.205$ at $\log r_S \cong 0.081$. The location of the valley extending horizontally across the landscape is influenced by the assumed values for the pheromone parameters. The standard values were assumed here.

approximations in cases of internal fertilization (Baccetti, 1985). Furthermore, shape primarily impacts the model through hydrodynamic drag, and at the low Reynolds numbers relevant here, shape has relatively little impact on drag (Berg, 1993, p. 57; Vogel, 1981, p. 247).

SENSITIVITY

It is important to consider how sensitive the advantage of oogamy is to the values of the parameters in the model. What are the conditions required for $Z_{SE} > 7.03H \geqslant Z_{AB}$? Using eqn (3) for Z_{SE}, and recognizing that for standard conditions $P = 0.01 < 1 < r_S$, the condition is met if $P^2 (r_E/r_S)^3 (r_S^2 - r_S^{-1})^{1/2} > 7/3$. Rearranging this, we require $r_E/r_S > (7/3)^{1/3} P^{-2/3} (r_S^2 - r_S^{-1})^{-1/6}$. The factor $(r_S^2 - r_S^{-1})^{-1/6}$ has the value 1.08 for optimal size sperm ($r_S = 1.205$). For observed sperm, the volume fraction occupied by chromosomes ranges over 0.25–0.8, $r_S = 1.08$–1.6, and the corresponding values of the factor range only over 0.9–1.3 because of the 1/6 power. Taking the less advantageous end of this range (1.3), it is concluded that oogamy is advantageous when

$$\frac{r_E}{r_S} > 1.7P^{-2/3}. \tag{4}$$

For the standard values assumed, $P = 0.01$, and oogamy is advantageous when $r_E/r_S > 37$. More effective pheromone function ($P > 0.01$) could reduce the required egg size and less effective function ($P < 0.01$) would increase it. However, the effect is less than proportional to P because of the 2/3 power. For example, a ten-fold change in P causes only a 4.6-fold change in the gamete size ratio.

The pheromone effectiveness factor is defined as (see the Methods section)

$$P \equiv \frac{r_c^2 K P_V}{3DC_{Th}}. \tag{5}$$

Among these factors, the diffusion coefficient, D, varies little for any molecule smaller than a protein. The specific metabolic rate P_V, is relatively well known and varies only an order of magnitude above and below median values for ordinary cells. The threshold concentration for detecting pheromone, C_{Th}, varies over several orders of magnitude among different kinds of cells, and is a major source of uncertainty. But the biggest source of uncertainty is the metabolic cost of pheromone production, K; there is little data available, and its value was based on the minimum required by thermodynamics with a guess as to the level of inefficiencies. The radius of the equivalent chromosome volume, r_c, is potentially more influential because it appears as the square; however, all observed chromosome volumes (see the Methods section) have radii within 50% of the assumed value of 1 μm. This range of r_c would cause P to change by factors of only 0.25–2.25.

Thus, likely variations in the values of these parameters have modest effects on the minimum egg-to-sperm size ratio, but none of them eliminate the advantage of oogamy.

TURBULENCE

The model assumes that the pheromone is transported only by diffusion, and consequently the active space is spherical in shape. This will hold for sufficiently small r_P but will not hold when r_P approaches the size of eddies in turbulent currents. With the standard values assumed here, oogamous reproduction can be superior to isogamous if $r_E > 38$ (Fig. 4). In this situation, $r_P > 520$. Measurements from electron micrographs of a variety of motile gametes from aquatic organisms (see the Methods section) led to the estimate that typically $r_c = 1$ μm. Thus, the radius of the active space can be as small as 520 μm or half a millimeter and pheromone production is still effective.

Unfortunately, the effects of turbulence at small scales are complicated, and there are few experimental investigations (Karp-Boss *et al.*, 1996). It is estimated that the smallest eddies in the open ocean are of the order of 4–20 mm (Grant *et al.*, 1962; Mann & Lazier, 1991, p. 19; Tolmazin, 1985). However, chemical concentrations vary at smaller scales because the diffusion coefficient for molecules in water is smaller than the diffusion coefficient for momentum, and the smallest fluctuations are roughly estimated to be 0.2–2 mm, depending on the energy of turbulence in the environment (Bowen *et al.*, 1993; Mann & Lazier, 1991, p. 19). Another estimate (Bowen *et al.*, 1993) suggests that, in the open ocean, the active space is unaffected at radii of 45–450 μm, depending on depth. Beyond these distances, the active space becomes distorted from a spherical shape towards prolate or oblate ellipsoids, but in simulations of chemotaxis these distortions had little effect on chemotaxis to the source. In view of these estimates, the best that can be concluded at this time is that pheromones can probably be effective in calm environments and this is probably not a serious problem for the model. It is known that brown algae have a sperm attraction system that functions over distances of several millimeters in the laboratory (Maier & Müller, 1986), and presumably this ability would not exist if it were not functional in nature.

Another important consideration is that the pheromone gradient is established in less than a minute for distances up to a millimeter (Dusenbery, 1992, Figs 4–6).

SWIMMING PATH

Can the gametes swim straight compared to the detection distance, as assumed? Motile objects that do not have reference to external stimuli can maintain straight paths over only limited distances (Dusenbery, 1992, pp. 396–397). For small cells, Brownian motion causes random rotations and is the most significant source of unavoidable constraint on straight swimming (Berg, 1975). For a cell of radius 1 μm, the time in which the average orientation changes on average by 1 rad is about a second, and this time increases with the third power of the radius (Berg, 1993, pp. 83, 84). Since speed increases in proportion to radius (Dusenbery & Snell, 1995), the distance a cell can swim before its orientation is changed by a given amount increases as the fourth power of the radius. With the assumptions used here, the optimal isogamete swims along a path that on average changes direction by 1 rad in a distance of 180 μm (see the Methods section) compared to its diameter of 2.3 μm, and so this effect is of little consequence for contact by isogametes.

However, when small sperm search for a large egg, loss of direction might reduce the rate of egg-finding, although the significance of the effect is unclear because the path length over which gamete swimming direction wanders by 1 rad (see the Methods section) is comparable to the target size (see above). Since this path length varies as the fourth power of gamete size, a small increase in motile gamete size can eliminate the problem. Also, elongation of the cell can sharply reduce the rate of loss of orientation (Dusenbery, 1998a). Alternatively, a collimating stimulus can be used to maintain a constant orientation (Dusenbery, 1992, p. 397; Pline & Dusenbery, 1987). The gametes of many marine algae are known to be phototactic (Haxo & Clendenning, 1953; Togashi *et al.*, 1997), and they may be using light as a collimating stimulus, which allows them to maintain a straight path over very large distances. So failure to swim straight paths is not a problem for the model, because gametes can avoid the effect if necessary.

EVOLUTION

The fitness landscape produced by this model (Fig. 4) contains a valley between isogamous and oogamous peaks which must be crossed, if initially isogamous populations are to become oogamous. Large isogametes do not face the problem. With the standard values, isogametes with relative radii greater than 10, are not separated from the oogamous peak. Thus, any other selective force that led to large gametes could overcome the gulf.

For smaller isogametes, the valley might be jumped by random mutation or recombination in individuals, leading to genetic drift of the population. Although this may seem improbable, we have little knowledge of what the probabilities actually are. For example, large changes in size can occur by simply changing the number of cell divisions in gametogenesis, as occurs in some algae (Callow *et al.*, 1985; Togashi *et al.*, 1997). Variations in other selective pressures, such as postzygotic selection or predation on gametes, might temporarily change the fitness landscape in ways that eliminate the valley. In any case, once the gap is crossed (and we know it has been crossed several times), this model demonstrates that species with male and female types have a clear superiority in gamete encounter rates, and broadcast spawners can reproduce at lower population densities, giving them a distinct selective advantage in the long run.

Reproduction at even lower population densities can be accomplished by coordinating spawning in time and/or space to increase local gamete densities. Selection for internal fertilization may be based on other factors, such as mate choice or avoiding predation on gametes.

Hoekstra has proposed abstract models that are similar to the one proposed here in that they do not assume postzygotic selection (Hoekstra, 1984; Hoekstra *et al.*, 1984). However, his models are based on several assumptions that conflict with established physical and chemical knowledge: (1) that a gamete can both produce a pheromone and detect the same pheromone produced by another gamete, which may be possible but is much more complicated than assumed, (2) that gametes travel along straight paths with respect to their targets, which is never true when the target gamete is moving, as is assumed, and (3), most importantly, that swimming speed is inversely proportional to cross-sectional area ($v \propto r^{-2}$), which might be valid for a fixed power of propulsion at large Reynolds numbers, but gametes swim at low Reynolds numbers and constant power per unit volume is a more appropriate assumption, which implies $v \propto r$. The latter problem is major and would probably cause his model to fail if this assumption were changed to the more plausible relationship. The assumption made here ($v \propto r$) is more conservative in that it favors isogamy by placing small sperm at a disadvantage. A major point is that the size dependence of pheromone production is so strong that it overcomes the effect of larger gametes swimming faster.

In contrast to the abstract and arbitrary assumptions of previous models, the model proposed here is based on fundamental biophysical knowledge and can be related quantitatively to anatomical and physiological parameters. It satisfies Occum's razor by connecting the explanation of male and female mating types to several well-established relationships from physics, chemistry, and biology. In addition, it makes quantitative predictions that can be tested by obtaining more detailed observations.

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