Bateman’s Principle and Simultaneous Hermaphrodites: A Paradox

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SYNOPSIS. Bateman’s principle states that reproductive success is limited a) in females by the resources available for egg production; and b) in males, only by access to females and/or eggs. The principle has been used to generate predictions for two aspects of hermaphroditism: a) the advantage of hermaphroditism and b) sexual conflict. Comparing these predictions to the empirical data offers tests of Bateman’s principle. Charnov’s prediction that hermaphroditism would occur under circumstances where Bateman’s principle does not apply is found to be largely correct. However, the prediction as to the association of hermaphroditism and low fixed costs is inconsistent with the data. Alternative explanations that predict that hermaphroditism is a strategy for reducing variance in reproductive success may better explain the data. Probability theory demonstrates that where two strategies have equal mean fitness, which must be the case for male and female function, the strategy with the lower variance in reproductive success must have higher fitness (Gillespie’s principle). Bateman’s principle predicts that this will be the female role in hermaphrodites. However, Charnov, assuming Bateman’s principle, predicted that sexual conflict stemming from a preference for the male role would be important in hermaphroditic mating systems, creating a paradox. Many hermaphroditic mating systems are based on conditional reciprocity with a preferred sexual role indicating sexual conflict. The data demonstrate that the preferred role varies among taxa, contrary to the predictions of Bateman’s principle. It has been suggested that Bateman’s principle can explain cases in which the female role is preferred (sperm-trading) as involving energy rather than gamete trading. However, energetic considerations suggest that energy trading would only be adaptive if Bateman’s principle does not apply, paradoxically. The gamete trading model, based on the prediction that the role that offers control of fertilization will be preferred, is more consistent with the data. Application of Bateman’s principle to hermaphrodites leads to contradictory predictions and does not offer the basis for a coherent theory of sexual selection, as Bateman proposed.

INTRODUCTION

Although the sexual behavior and reproductive biology of hermaphroditic organisms have been of interest for as long as biology can be traced, interest in sexual selection and such allied topics as mating systems, mate choice and sexual conflict, in hermaphrodites, is relatively recent. In “The Descent of Man, and Selection in Relation to Sex” Darwin (1871) explicitly excluded such hermaphrodites as snails and earthworms from the influence of sexual selection, arguing that their intellectual powers were insufficiently developed to allow for mate choice. A. J. Bateman laid the foundation for a more modern understanding of sexual selection in a seminal paper based on experiments on reproductive success in Drosophila melanogaster using genetic markers to estimate paternity (Bateman, 1948). Bateman started with the generally accepted assumptions that “intra-sexual selection almost invariably involves competition between males, the females exercising choice, and not the reverse” (Bateman, 1948, p. 350), and that “a sex difference in variance of fertility is therefore a measure of the sex difference in intensity of selection” (ibid, p. 353). His stated goal was to “search for a fundamental cause of intra-masculine selection . . . this same cause should show us why it is a general law that the male is eager for any female, without any discrimination whereas the female chooses the male.” The results of his experiments demonstrated that variance in both offspring number and mate number were higher in males than in females (but see Sutherland, 1987 and Fig. 1A) and the correlation between number of mates and number of offspring was stronger in males than in females (Fig. 1). Bateman proposed that the fundamental cause of sexual selection is that, because “…the fertility of the female is limited by egg production . . . (ibid, p. 364),” female reproductive success is, in general, restricted by the availability of energy to produce eggs, whereas male reproductive success is usually limited only by access to mates, or their eggs. This statement is what is referred to as Bateman’s principle by Charnov (1979) and in the current review (see Table 1). (The definition of Bateman’s principle has varied among authors [see other papers in this volume]. For example, Arnold [1994] identified three Bateman’s principles: 1) “males show greater variance in number of offspring than do females” (ibid, p. S126); 2) males have higher variance in number of mates than do females; and 3) there is a direct correlation between number of mates and fecundity in males, but in females fecundity increases little after the first mating [for tests of Arnold’s version of Bateman’s principles see Jones, 2005; Jones et al., 2000, 2002]. Here Arnold’s three Bateman’s principles are considered assumptions contributing to Bateman’s principle.) Bateman concluded that, “The primary cause of intra-mas-
culine selection would thus seem to be that females produce much fewer gametes than males. Consequently there is competition between male gametes for the fertilization of the female gametes” (ibid, p. 365). Bateman (1948) explicitly predicted that, if true, this principle would extend to all anisogamous organisms, including plants and hermaphrodites, saying, “If . . . differentiation into . . . gametes is the basis . . . there should be signs of this selection in plants . . . . Since plants are usually hermaphroditic . . . such selection would only be expected to show in the pollen, (ibid, p. 367).”

Although the range of phenomena associated with hermaphroditism came under consideration by biologists focusing on selection acting on selfish individuals very early on (Ghiselin, 1969, 1974; Williams, 1975), the first author to follow up on Bateman’s prediction explicitly was Eric Charnov. In a seminal paper, Charnov (1979) began to explore the predictions that Bateman’s principle makes for hermaphrodites, saying “I propose here that ‘Bateman’s principle’ is also valid for these organisms [simultaneous hermaphrodites]—that fertilized egg production by an individual is limited not by the ability to get sperm, but by resources

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<th>Table 1. Definitions of Terms.</th>
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<td>A. Bateman’s Principle: (as used here, see discussion in text): “. . . egg production is limited by a female’s ability to garner resources to make eggs, not by a lack of sperm to fertilize them. Reproductive success for males is thus limited by access to females (and their eggs).” (Charnov, 1979, p. 2480)</td>
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<td>B. Gillespie’s Principle: “natural selection can work on variances in offspring number and it works in such a way that increasing the variance in offspring number . . . will decrease its fitness” (Gillespie, 1977, p. 1013).</td>
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<td>C. Egg-trading: hypothesized mating system in which hermaphrodites provide eggs (or access to eggs) to a partner in return for access to the partner’s sperm for fertilization. Egg-trading is accompanied by egg parceling (i.e., not all eggs are made available at once). The male role is assumed (Fischer, 1980) or hypothesized (Leonard and Lukowiak, 1984) to be preferred because of potential fitness advantages. First proposed for the serranine fish Hypoplectrus nigricans by Fischer (1980). May apply to either internally- or externally-fertilizing taxa (Leonard and Lukowiak, 1984; Leonard, 1991).</td>
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<td>D. Sperm-trading: hypothesized mating system in which hermaphrodites provide sperm (or theoretically, access to sperm) to a partner in return for access to the partner’s sperm for use in fertilization. Sperm-trading predicts that male-acting individuals will limit the amount of sperm given to the partner. The female role is hypothesized to be preferred because of potential fitness advantages. First proposed for the opisthobranch, Navanax inermis by Leonard and Lukowiak (1984). May apply to either internally- or externally-fertilizing taxa.</td>
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<td>E. Control of fertilization: the sex (or sexual role in a hermaphrodite) whose release of gametes leads more immediately to fertilization is said to control fertilization (Leonard and Lukowiak, 1984; see also Alexander and Borgia, 1979). For example, in an internally-fertilizing species with allo sperm storage copulation is not tied to ovulation and the male runs a risk of wasting the sperm contributed by a copulation if those sperm are not ultimately used to fertilize eggs. This risk comes from such factors as a) sperm competition if the female mates with multiple individuals before laying eggs, b) sperm digestion in species with a gametolytic gland; or c) simple failure of the female to live to egg laying in species where there is (or may be) a long latency between copulation and egg-laying. Conversely, one could have male control of fertilization in an internally-fertilizing species where hypodermic insemination leads to fertilization of the eggs directly in the ovary, or with conventional copulation where there is no sperm storage or sperm digestion and egg laying is tightly coupled in time to copulation (see Leonard, 1991). In externally-fertilizing species, if eggs are spawned first and then covered with sperm by the partner, the male should control fertilization. Conversely, if individuals were to spawn eggs in response to the presence of sperm in the environment, then the female would control fertilization. The sex that retains the greater control over the fate of its gametes (Alexander and Borgia, 1979) is said to control fertilization and is predicted to be the preferred sexual role in hermaphrodites according to the gamete-trading model (Leonard and Lukowiak, 1984; Table 2).</td>
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allocated to eggs. This is a strong assumption . . . . If it is approximately true, then the theory . . . has several important implications for reproductive biology" (ibid, p. 2480). Charnov then went on to explore the implications of Bateman’s principle for two major aspects of hermaphroditism; a) the circumstances under which there is an advantage to hermaphroditism over dioecy; and b) the potential for male-female conflict in mating hermaphrodites. A comparison of Charnov’s predictions with the data that have accumulated from simultaneous hermaphrodites over the last 25 years offers an opportunity to test Bateman’s principle. In the process of testing these predictions, it is useful to compare the performance of Bateman’s principle with that of alternative explanations.

Bateman’s principle, Gillespie’s principle and a paradox

Bateman’s principle (Table 1) is a hypothesis founded on data from *D. melanogaster*. It assumes that males are eager and females “choosy” or “coy” and predicts that reproductive success is limited a) in females by the resources available for egg production; and b) in males, only by access to females and/or eggs. Therefore, variance in reproductive success should be higher in males than in females and the eagerness of males in mating encounters can be explained by the greater “upside potential” (to use a term from economics) available to males. For simultaneous hermaphrodites, Bateman’s principle also predicts that the male role will be preferred (Charnov, 1979). However, this creates a clear paradox. It is an axiom of probability and gambling theory that where two games or investments have equal mean return, the game or investment with the lower variance will be a better investment, if capital and/or the length of the game are finite (Epstein, 1977). This is true because choice of the high variance investment will be more likely to lead to bankruptcy (or extinction, in biological terms). Applied to biology this axiom is termed Gillespie’s principle (Table 1), which states that where two strategies (or alleles, etc.) have equal mean reproductive success, which must be the case for male and female function across a finite population, the strategy with the lower variance in reproductive success will have higher fitness (Gillespie, 1974, 1977; Leonard, 1999). The sexual role with greater variance will in general have greater “upside potential” (has the greatest potential success) but, also greater “downside potential” (has the greatest potential for failure): the higher the variance, the greater the probability of zero success, and therefore, the higher the probability of zero fitness. Bateman’s principle predicts that, all else being equal, that will be the male role. This would not be a problem in an infinite, panmictic population but there is no such thing as an infinite population and the larger a population is, the less likely it is to be panmictic. Application of Gillespie’s principle predicts that a hermaphrodite, faced with two strategies with equal mean success should behave prudently and try to avoid the role with the greater “downside potential” (see Leonard, 1999 for discussion) due to the higher probability of reproductive failure. Therefore, from a mathematical point of view, Charnov’s prediction from Bateman’s principle is paradoxical in that it predicts that hermaphrodites should prefer the sexual strategy that has greater “upside potential” although, it will yield lower fitness for most individuals due to the greater variance. Application of Gillespie’s principle to mating hermaphrodites predicts that hermaphrodites will prefer the role with lower variance in reproductive success (Leonard and Lukowiak, 1991; Leonard, 1999), contrary to the expectation from Bateman’s principle. Both Bateman’s principle and Gillespie’s principle predict that mating hermaphrodites will have a consistently preferred sexual role, creating sexual conflict (see below). Moreover, the two principles suggest alternative explanations of the advantages of hermaphroditism relative to dioecy.

**Bateman’s Principle and Hermaphroditism vs. Dioecy**

The adaptive significance of the ecological and taxonomic distribution of separate sexes (here, dioecy) relative to hermaphroditism has been a recurrent question in evolutionary biology (Table 2; Muller, 1932; Altenburg, 1934; Ghiselin, 1969, 1974; Williams, 1975; Maynard Smith, 1978; Charnov, 1982; Leonard, 1990, 1999; Crowley et al., 1998; Wilson and Harder, 2003; etc.). As H. J. Muller (1932) phrased it “the existence of the two sexes in separate individuals, is of advantage in the same way as any other division of labor. . . . But in cases where conditions are such that these functions in the same individual would not greatly interfere with one another . . . the efficiency may not be increased . . . enough to compensate for . . . halving the number of individuals giving each type of gamete and in reducing the proportion of contacts which would be of service in fertilization, and so these organisms may have retained or developed hermaphroditism” (ibid, p. 124) (but see Crowley et al., 1998). The problem was formulated graphically by Charnov, et al. (1976; see also Charnov, 1979; Maynard Smith, 1978). These authors pointed out that where fitness through each sexual role increases proportionately to investment in that sexual role, a “concave” fitness curve in Figure 2, separate sexes will be favored, whereas hermaphrodites will have higher fitness when investment in one sexual role does not interfere with fitness in the other sexual role, a “convex” fitness curve (Fig. 2). The question, then, becomes one of determining which factors will produce a convex vs. a concave fitness curve.

It had long been known that low mobility and low population density would provide an advantage to hermaphroditism (e.g., Muller, 1932; Tomlinsob, 1966; Ghiselin, 1969; see Table 2). Leonard (1999) suggested, based on the Modern Portfolio Theory from economics (first applied to biology by Real, 1980), that by partitioning reproduction between eggs and sperm
I. Bateman’s Principle and Predictions from Charnov’s Model (Charnov, 1979)

A. An advantage to simultaneous hermaphroditism over dioecy is predicted:
1. When fixed costs are low and the male gain curve saturates, in violation of Bateman’s Principle, due to such factors as Local Mate Competition (Charnov, 1982) or sexual conflict.
2. When male and female function use different resources (currency) or are temporally separated.
3. When the female gain curve saturates (due to space limitation associated with brooding, sib-sib competition, etc.) at a point below that would be predicted by Bateman’s principle (limit due to resources available to make eggs).

B. For simultaneous hermaphrodites Bateman’s principle predicts:
1. that “... individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another’s eggs).” (Charnov, 1979, p. 2482)
2. “There must often be a conflict of interest between mating partners—as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give its sperm away. As a donor, one should be selected to induce one’s partner to use the new sperm in fertilization.” (ibid)

II. Variance Reduction Models

A. Arguments based on Modern Portfolio Theory (Real, 1980; Leonard, 1999) suggest that hermaphroditism may offer an advantage over dioecy if individuals who partition their reproductive success between eggs and sperm experience increased fitness through decreased variance in offspring number as a result of reduced covariance between offspring (Leonard, 1999). These arguments are consistent with Gillespie’s Principle (see text; Table 1).

B. Wilson and Harder’s (2003) formal theoretical model, derived independently, showed that dioecy would tend to increase variance in fitness, thereby reducing fitness relative to hermaphrodites. This result is consistent with Gillespie’s Principle (see text; Table 1).

III. Other Models

A. The Low Density Model (see text): it has long been argued (formal model by Tomlinson, 1966) that where encounter probabilities are low, hermaphrodites have twice the probability of encountering a suitable mate as dioecious individuals.

B. Crowley et al.’s (1998) theoretical model found that simultaneous hermaphroditism would be favored where expensive eggs are produced serially.

...
the male gain curve could arise if males have access to only a very limited number of females (and their eggs), due to low mobility, small population size, or lack of pollinators, etc. A convex fitness curve could also be produced if male and female function drew on separate pools of resources (Charnov et al., 1976; Maynard Smith, 1978; Charnov, 1979, 1982) and there is some evidence, from attempts to measure sex allocation, that the resources important for male vs. female reproductive success do differ (see review in Klinkhamer and de Jong, 2002).

The unique insight of Charnov’s (1979) analysis was to identify sexual conflict as a factor that could limit male reproductive success in such a way as to make hermaphrodites violate Bateman’s principle. That is, if the recipient of sperm does not use all of the sperm to fertilize eggs, perhaps digesting the sperm, male fitness will not be proportional to investment, and hermaphroditism would be adaptive because individuals can increase fitness by reallocating resources from sperm to eggs. Bateman’s principle predicts, therefore, that simultaneous hermaphroditism will, in general, occur in regions of fitness space where Bateman’s principle does not apply either because female reproductive success is limited by factors other than energy available for egg production or because male reproductive success reaches a plateau due to lack of access to mates or their eggs. If reproduction in each sexual role requires “fixed costs” in the form of the development and maintenance of structures dedicated to each sexual role (Heath, 1977; Charnov, 1979) then even more stringent conditions must apply in order to give hermaphroditism an advantage over dioecy. Charnov summarized the results of the analysis by saying, “Under Bateman’s principle, SH {simultaneous hermaphroditism} will be favored by a combination of low fixed costs and limited opportunities for an individual to reproduce through male function” (1979, p. 2481). However, many hermaphroditic taxa, such as stylommatophoran gastropods and turbellarians are characterized by very elaborate reproductive anatomy and the ability of the recipient to digest sperm and/or mobility and population densities similar to those of related dioecious taxa (see Leonard, 1990 for discussion).

Comparison of these predictions to the distribution of hermaphroditism among metazoans (Leonard, 1990) suggests that while the formal mathematical analysis provided by Charnov and colleagues (Charnov et al., 1976; Charnov, 1979, 1982) has contributed to a much deeper understanding of the relative fitness advantages of hermaphroditism vs. dioecy, it has not resolved “Williams’s paradox,” i.e., that these predictions as to the conditions that favor hermaphroditism do not explain the taxonomic or ecological distribution of hermaphroditism today (Williams, 1975; Leonard, 1990, 1999). For example, while gastropods are slow-moving in general, opisthobranchs and pulmonates are simultaneously hermaphroditic whereas the other gastropod subclasses, the so-called, “prosobranchs” are predominantly dioecious. Moreover, the opisthobranchs and pulmonates are characterized by rather elaborate reproductive tracts that should represent high “fixed costs” whereas dioecious prosobranchs show a range from taxa with internal fertilization and elaborate internal genitalia in both sexes, to simple broadcast spawners with low fixed costs, contrary to Charnov’s prediction (see Williams, 1975; Leonard, 1990). The available data suggest that both dioecy and hermaphroditism are stable under a wider range of ecological conditions than would be predicted by theory. The models based on variance in reproductive success (Table 2), do not seem to address Williams’s paradox, either.

Further progress in theory will require attention to factors that may stabilize either hermaphroditism or dioecy. Mate choice and/or sexual conflict may be such a factor. Eric Fischer (1980) pointed out (see also Axelrod and Hamilton, 1981; Leonard, 1990), that once hermaphroditism has evolved, conditionally reciprocal mating among hermaphrodites (as a result of sexual conflict, see below) would produce a convex fitness set by linking fitness in the male and female roles. Leonard (1990) argued that sexual conflict would act to produce conditionally reciprocal mating systems among pair mating hermaphrodites. Berglund (1991) has shown that mate choice may stabilize hermaphroditism in the polychaete Ophryotrocha puerilis, since, in this pantropical species, hermaphrodites prefer small males as mates. Although larger males are more successful in male-male competition, they are rejected by hermaphrodites with eggs to be fertilized, and therefore individuals that become hermaphrodites at a small size have higher fitness. One might expect that in dioecious species, sexual selection would act to put hermaphrodites at a disadvantage, stabilizing dioecy even when ecological conditions might otherwise favor hermaphroditism. The most important predictions of Charnov’s (1979) analysis, therefore, are that a) Bateman’s principle will seldom apply to hermaphrodites; b) sexual conflict in hermaphrodites will produce a flattening of the male gain curve, creating a violation of Bateman’s principle; and c) sexual conflict will be important in shaping mating systems in hermaphrodites.

SEXUAL CONFLICT AND THE SIMULTANEOUS HERMAPHRODITE

Including male-female (sexual) conflict as an arena of selection on reproductive parameters (Trivers, 1972; reviews in Andersson, 1994; Eberhard, 1985, 1996; Birkhead and Möller, 1998; Simmons, 2001; Shuster and Wade, 2003; etc.) has been one of the major advances of sexual selection theory over the last few decades. Since Bateman’s 1948 paper, the ultimate source of differences between the sexes in sexual behavior has come to be seen as differential variance in reproductive success. Bateman’s principle assumes that the two sexes (or sexual roles) differ in variance in fitness and predicts that this difference plays a major
role in shaping mating systems. That is, females are expected to have a narrow variance in reproductive success because they are limited by the energy available to produce eggs or offspring, whereas males are expected to have a high variance because their reproductive success is more open-ended due to the low cost of sperm production and they also are expected to experience high rates of reproductive failure due to failure to compete with other males or to attract females. For simultaneous hermaphrodites, the potential fitness gains from the two sexual roles may differ (Bateman, 1948; Charnov, 1979; Fischer, 1980 1987; Axelrod and Hamilton, 1981; Leonard and Lukowiak, 1984; Sella, 1985; Leonard, 1990, 1999; Arnold, 1994; Morgan, 1994, Michiels, 1998; Baur, 1998, etc.). Both the mean and the total fitness through male function across the population must be exactly equal to the mean and total fitness through female function. However, if the variance in fitness for the two sexual roles differs, the potential, or the probable, pay-off to an individual may be greater through mating in one sexual role than in the other (Bateman, 1948; Charnov, 1979; Leonard, 1990, 1999). An individual that specializes in the more profitable sexual role, should have greater likelihood of positive fitness than an individual that does not. Therefore, it ought to be the case that there will be a preferred sexual role in a simultaneously hermaphroditic species that is the same for all individuals in a species, all else being equal.

Charnov (1979) predicted that sexual conflict would be important in pair-mating simultaneous hermaphrodites, saying, “Bateman’s principle suggests that individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another’s eggs). . . . There must often be a conflict of interest between mating partners—as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give sperm away” (1979, p. 2482). The predictions from Bateman’s principle (Table 2) are therefore that a) sexual conflict will be important in pair-mating hermaphrodites; b) the male role should be preferred; c) the variance in fitness through male function should be greater than that through female function; and d) female reproductive success should be limited by the energy available to produce eggs rather than sperm availability.

The identification of sexual conflict as an important aspect of sexual selection in hermaphrodites has major implications for understanding not only hermaphrodites but sexual selection in general. The question of whether sex differences in variance in fitness play the decisive role in shaping mating systems remains an important one (see review in Shuster and Wade, 2003) and the prediction of sexual conflict in simultaneous hermaphrodites (Charnov, 1979) is an important test of sexual conflict theory (see above). It is often difficult to establish whether sexual conflict exists in species with separate sexes since, on the level of fitness in each generation, males compete with males and females with females (but see Rice, 1996 etc.; review in Simmons, 2001). In outcrossing simultaneous hermaphrodites, on the other hand, the fitness of an individual will depend on its allocation of reproductive effort between male and female function (Charnov, 1982, etc.). In simultaneous hermaphrodites, therefore, sexual conflict is expected to be direct, suggesting that such species will provide good models for testing theories based on sexual conflict (Leonard, 1990, 1999; Leonard and Lukowiak, 1991).

Evidence for sexual conflict in simultaneous hermaphrodites

The first evidence for sexual conflict in pair-mating hermaphrodites came from Eric Fischer’s descriptions (Fischer, 1980, 1981) of egg-trading in the black hamlet, Hypoplectrus nigricans, a serrane fish. In H. nigricans, fertilization is external and unilateral with one individual releasing eggs and the other, sperm, while in a spawning clasp. The same two individuals will then reverse roles repeatedly in a bout of spawnings. The behavior was called “egg-trading” because the egg clutch of each individual is parcelled out over the series of spawnings. In egg-trading, “individuals give up eggs to be fertilized in exchange for the opportunity to fertilize the eggs of a partner.” (Fischer, 1988, p. 119). Fischer (1980) assumed, on the basis of theory (Charnov, 1979) that the male role would be preferred and concluded from his observations that the reciprocity was conditional; i.e., that individuals would abandon a partner that failed to reciprocate by offering its own eggs. Axelrod and Hamilton (1981) were the first to relate the egg-trading mating system of H. nigricans directly to sexual conflict. Similar mating systems in which a pair of hermaphrodites actively alternate sexual roles in a bout of matings (Fig. 3) have now been described for several taxa with both internal and external fertilization (e.g., opisthobranchs, Navanax inermis [Fig. 3], Leonard and Lukowiak, 1984, 1985, 1991; Bursatella, Ramos et al., 1995; two species of polychaete Ophryotrocha, Sella, 1985, 1991; Premoli and Sella, 1995; Sella et al., 1997; and other serranines, see reviews in Fischer and Petersen, 1987; Leonard, 1993). In the stylommatophoran slug Ariolimax californicus, typical mating encounters involve bouts of unilateral copulations which may involve alternation of sexual roles, although it is not clear that that is the rule (Leonard et al., 2002). As Axelrod and Hamilton (1981) pointed out, mating systems based on serial alternation of sexual roles during a bout of matings represent a potentially equitable resolution of such conflicts. These authors suggested that such mating systems represent a cooperative (Tit-for-Tat) solution to a Prisoner’s Dilemma problem created by sexual conflict (see also Fischer, 1987, 1988). A more detailed analysis suggests that, while Prisoner’s Dilemma is a first approximation, the situation created by a sexual role preference in mating hermaphrodites is somewhat more complex (Leonard, 1990; see also Connor, 1992; Landolfa, 2002).
The Hermaphrodite's Dilemma

The Hermaphrodite's Dilemma model (Table 3; Fig. 4; Leonard, 1990) describes the situation faced by a pair of hermaphrodites which both prefer the same sexual role. It is a conditional, iterated, non-zero-sum game of strategy which includes both Prisoner’s Dilemma (Rapoport, 1966) and Game of Chicken (Riechert and Hammerstein, 1983) as special cases (see Table 3). Game theorists have long recognized that Prisoner’s Dilemma and Game of Chicken shared a motivational structure (Rapoport and Dale, 1966). Both games present two selfish players with two choices; to cooperate or to defect. In each case the highest payoff is to the player that chooses to defect when the other player chooses to cooperate. For a pair of mating hermaphrodites with a preference for one sexual role (Hermaphrodite’s Dilemma) the choices are to defect (insist on mating only in the preferred role) or to cooperate (offer to mate in both roles) (Leonard, 1990). The reasoning is that mating in the non-preferred role, while it may yield fitness gains, will also involve costs that decrease the player’s reproductive value to a greater extent than mating in only the preferred role. The payoff matrix that defines Hermaphrodite’s Dilemma is $T > R > S; R > P$. The fame of Prisoner’s Dilemma and Game of Chicken, stems from the fact that both have stable solutions involving cooperation between selfish players (see Table 3). A major difference between Prisoner’s Dilemma and Hermaphrodite’s Dilemma is that while an all-defector strategy (never reciprocate, insist on the preferred role) is an evolutionarily stable solution to Prisoner’s Dilemma, a population of defectors would not mate at all and all individuals would have zero fitness in Hermaphrodite’s Dilemma. The Hermaphrodite’s Dilemma is more complex than either Prisoner’s Dilemma or Game of Chicken because Hermaphrodite’s Dilemma is a conditional game in which the payoff matrix can change over the course of the game (see also Gardner et al., 1987; Dugatkin et al., 1992) whereas Prisoner’s Dilemma and Game of Chicken are static, symmetrical games. The payoff matrix for Hermaphrodite’s Dilemma is conditional since for example, if an individual may expect many mating encounters in its lifetime, and mating in the
A. The Eager Male Model: An informal, verbal model of mating systems in hermaphrodites that predicts, derived from Charnov’s (1979) argument that “... individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs)” (Charnov, 1979, p. 2482), based on Bateman’s principle (see text and Table 1). The model predicts that hermaphrodites will consistently prefer the male role due to its “upside potential”. This model can predict reciprocal mating behavior as the result of a symmetrical eagerness of both parties to donate sperm (unconditional reciprocity) (see text and Pongratz and Michiels, 2003) if individuals are assumed to be willing to behave as females, or if it can predict egg-trading (Charnov, 1979; Fischer, 1980). This model is inconsistent with Gillespie’s principle (see text; Table 1) which predicts that hermaphrodites will prefer the sexual role with lower variance in reproductive success.

B. Gamete Trading: An informal, verbal model of mating systems in hermaphrodites that predicts the preferred sexual role by consideration of control of fertilization (Leonard and Lukowiak, 1984). The gamete-trading model may predict either egg-trading or sperm-trading (defined in Table 1) for a species, depending on the control of fertilization (Table 1). Gamete trading assumes that control of fertilization and therefore the relative risk of mating in the two sexual roles does not differ among individuals. The model argues that in hermaphrodites the two sexual roles although offering equal mean fitness across a population, may differ in their potential fitness to an individual due to differential risk of loss of investment in gametes due to control of fertilization (defined in Table 1). That is, where fertilization is controlled by female-acting individuals, i.e., where allosperm are stored and released by the female for fertilization at a later time, sperm donors run a risk of wasting all or most of the ejaculate they have donated, as well as the time and effort involved in mating. In this situation, individuals acting as females, on the other hand, are assured of obtaining sperm when copulating but may not have made any investment in eggs. The sex that retains the greater control over the fate of its gametes (Alexander and Borgia, 1979) (controls fertilization, Table 1) is the preferred sexual role.

C. The Prisoner’s Dilemma (PD): A symmetrical, non-zero sum, two person game of strategy (Rapoport, 1966). The matrix is defined as \( T > R > P > S \) where \( T \) is the pay-off to an individual which defects when the partner cooperates, \( R \) is the pay-off to an individual when both choose to cooperate, \( P \) is the pay-off to an individual which defects when the partner cooperates, and \( S \) is the pay-off to an individual who cooperates when its partner chooses to defect. In a Prisoner’s Dilemma situation it is preferable not to mate at all in a given encounter than to mate only in the non-preferred role. Axelrod and Hamilton (1981) first suggested that egg trading (see Table 1) in \( H. m. nigricans \) represented a Tit-for-Tat solution to a PD problem (see also Fieser, 1999, but see Connor, 1992), PD is the best known to biologists of all games of strategy due to its stable, cooperative solutions. For Prisoner’s Dilemma, if \( \omega \), the probability of encountering an individual again is high enough. Tit-for-Tat (cooperate on the first move and do what the opponent did on subsequent moves; Rapoport and Dale, 1966) is a collectively stable (sensa Boyd and Lorberbaum, 1987; Lorberbaum, 1994) although not an evolutionarily stable strategy. An all-defector strategy (never reciprocate, insist on the preferred role) is also an evolutionarily stable solution to Prisoner’s Dilemma.

D. The Game of Chicken: The Game of Chicken is a symmetrical, non-zero sum, two person game of strategy (Riechert and Hammerstein, 1983) whose matrix is defined as \( T > R > P > S \) where \( T \) is the pay-off to an individual which defects when the partner cooperates, \( R \) is the pay-off to an individual when both choose to cooperate, \( P \) is the pay-off to an individual which defects when the partner chooses to defect, and \( S \) is the pay-off to an individual who cooperates when its partner chooses to defect. The Game of Chicken assumes that individuals will not change their behavior over the course of multiple mating encounters, and that individuals will not mate if they have already done so. In this situation, individuals acting as females, on the other hand, are assured of obtaining sperm when copulating but may not have made any investment in eggs. The sex that retains the greater control over the fate of its gametes (Alexander and Borgia, 1979) (controls fertilization, Table 1) is the preferred sexual role.

E. The Hermaphrodite’s Dilemma: The Hermaphrodite’s Dilemma model (HD) (Fig. 4; Leonard, 1990) is a conditional, iterated, non-zero-sum game of strategy which includes both Prisoner’s Dilemma (PD) (Rapoport, 1966) and Game of Chicken (GC) (Riechert and Hammerstein, 1983) as special cases (see text). The payoff matrix that defines HD is \( T > R > S > P \) where \( T \) is the pay-off to an individual which defects when the partner cooperates, \( R \) is the pay-off to an individual when both choose to cooperate, \( P \) is the pay-off to an individual which defects when the partner chooses to defect, and \( S \) is the pay-off to an individual who cooperates when its partner chooses to defect. The Hermaphrodite’s Dilemma model is more complex than either PD or GC because HD is a conditional game in which the pay-off matrix can change over the course of the game (see also Gardner, et al., 1987; Dugatkin et al., 1992). Like both PD and GC, HD has both start and end effects. On the last mating encounter, a hermaphrodite has nothing to lose from mating in both roles since its reproductive value becomes zero. Although HD is a conditional game that allows the relative value of the different pay-offs to change over the course of the game, it assumes that the preferred sexual role will not change over the course of the game and that it will be the same for all individuals of a species. It predicts the behavior of individuals over the course of mating encounters or (in a possible iterated form) their lives but does not predict which role will be preferred. In the HD model, an individual will benefit, under most circumstances, from choosing to cooperate (hermaphrodites offer to mate in both sexual roles), but there will be circumstances under which it will pay an individual to defect (insist on mating only in the preferred role) (see Leonard, 1990; Table 3). Like both Prisoner’s Dilemma and Game of Chicken, Hermaphrodite’s Dilemma has both start and end effects. On the last mating encounter, a hermaphrodite has nothing to lose from mating in both roles since its reproductive value becomes zero in any case. Therefore, for hermaphrodites meeting for the last (or only) mating encounter of their lives, there is no conflict of interests and they should mate reciprocally. If Prisoner’s Dilemma conditions prevail (that is, mating encounters are sufficiently frequent that it pays to sit out
an encounter rather than mate only in the non-preferred role) then an individual should defect frequently near the start of the game (early in its reproductive life) and cooperate more frequently toward the end of its life since its reproductive value is approaching zero in any case. The juvenile protandric phase found in *Ophryotrocha* spp. (Premoli and Sella, 1995) may represent such a start effect. Prisoner’s Dilemma may in fact obtain in cases, such as *H. nigricans* (Fischer, 1980; Axelrod and Hamilton, 1981; but see Connor, 1992) or those in which self-fertilization is an option. Under Game of Chicken conditions however, any mating is better than no mating at all and an individual should always cooperate near the start of the game and choose to defect more frequently toward the close of the game. Similarly if Tit-for Tat is a stable solution, it will pay an individual to defect near the end of the game since opportunities for retaliation are limited. Two egg-trading hermaphrodite species of the polychaete genus *Ophryotrocha* may illustrate the two types of game within Hermaphrodite’s Dilemma. Game of Chicken conditions may prevail for *O. diadema*; fertile partners are rare and defection occurs at a low frequency regardless of the partner’s behavior (Sella and Lorenzi, 2000). In *O. gracilis*, on the other hand, a higher proportion of individuals carry eggs at any given time and pair bonds are more labile; desertion occurs at a higher rate (Sella et al., 1997), as predicted for Prisoner’s Dilemma parameters under Hermaphrodite’s Dilemma. Similarly, in the serranine *S. psittacinus* (= *S. fasciatus*; C. W. Petersen, personal communication) Petersen (1990) reported that the tendency for individuals to specialize in male behavior, defending harems of hermaphrodites and/or losing ovarian function to become pure males, increased with increasing population density as predicted by Hermaphrodite’s Dilemma. Isolated pairs reciprocated in a monogamous relationship, suggesting that they are experiencing Game of Chicken conditions.

**Sexual conflict, reciprocity and cheating: testing Hermaphrodite’s Dilemma**

From the assumption that sexual conflict exists, that is, that one sexual role is potentially more profitable than the other for all individuals of a species, the Hermaphrodite’s Dilemma (Leonard, 1990) predicted that 1) mating systems in hermaphrodites will be based on reciprocity; and 2) cheating (defection) will exist in a consistent sexual role. A further prediction is that selection will favor mechanisms to prevent cheating and/or retaliate against cheaters, except perhaps under Game of Chicken conditions (Table 3). The predictions made by the Hermaphrodite’s Dilemma were strong predictions since at that time little was known about the mating systems of simultaneous hermaphrodites. However, it had long been known that many hermaphroditic organisms have simultaneous reciprocal intromission, such as earthworms, leeches, many land snails, many opisthobranchs, planarians (Jenkins and Brown, 1964; Michiels and Streng, 1998; reviews in Michiels and Streng, 1998; Baur, 1998; etc.). Reciprocity in mating may also involve reciprocal transfer of external spermatophores (*e.g.*, the nudibranch, *Aeolidiella*, Karlsson and Haase, 2002). *De facto* reciprocity might be expected to occur among members of a group of sessile invertebrates or plants in a local mating group. The question then becomes whether such familiar systems involve conditional reciprocity as would be predicted if sexual conflict is important. Normal mating behavior involving a single alternation of sexual roles, inconsistent with expectations from a Prisoner’s Dilemma model, has been described for the freshwater pulmonates, *Lymnaea stagnalis* (van Duivenboden and ter Maat, 1985), and * Biomphalaria glabrata* (Webster, 2002), for the opisthobranch, *Chelidonura sandrana* (Anthes and Michiels, 2004) and for stylommatophoran slugs of the genus *Deroceras* (Reise, 1996).

**Is reciprocity conditional?**

Pongratz and Michiels (2003) argued that the many reciprocal mating systems in hermaphrodites might not represent cooperative solutions to sexual conflict but simply be a direct consequence of Bateman’s principle, saying “one would expect hermaphrodites to attempt to inseminate as many mates as possible, in accordance with Bateman’s principle . . . leading to ‘unconditional reciprocity’” (ibid, p. 1426). These authors apparently assume that hermaphrodites will always be willing to accept sperm, but perhaps, as has been previously suggested (Charnov, 1979; Leonard and Lukowiak, 1984, 1985, 1991), not for use in fertilization. Review of the few hermaphrodite mating systems that have been ex-

![Fig. 4. Pay-off matrix for the Hermaphrodite’s Dilemma (Table 3; Leonard, 1990), the game of strategy that represents the situation faced by two hermaphrodites in a mating encounter if sexual conflict exists. Hermaphrodite’s Dilemma is a two-player, conditional, non-zero-sum game of strategy. The pay-off matrix of Hermaphrodite’s Dilemma is \( T > R > S ; R > P \) where \( T \) is the pay-off to an individual which defects when its partner cooperates, \( R \) is the pay-off to an individual when both choose to cooperate, \( P \) is the pay-off to an individual when both choose to defect, and \( S \) is the pay-off to an individual who cooperates when its partner chooses to defect. It includes those of the classic games, Prisoner’s Dilemma and Game of Chicken as subsets (see text, Table 3). (Reproduced from [Leonard, 1990]).](http://icb.oxfordjournals.org/)

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*[Hermaphrodite’s Dilemma](http://icb.oxfordjournals.org/)*
amined for conditional reciprocity, suggests that it is common. Although behavioral observations suggested that the alternation of sexual roles was conditional in both H. nigricans (Fischer, 1980; see discussion in Maynard Smith, 1982) and the opisthobranch Navaanax inermis (Leonard and Lukowiak, 1985, 1991), the first direct evidence for conditional reciprocity came from the polychaete, Ophryotrocha diadema.

In O. diadema, observations from laboratory culture using genetic strains that produce yellow or white eggs, show that pairs of simultaneous hermaphrodites form long-lasting associations that may persist as long as both individuals have oocytes and that members of the pair lay alternate clutches of eggs (Sella, 1985). This species shows protandry in that young individuals of 5–11 body segments produce sperm only (Sella, 1985). Gabriella Sella (1988) demonstrated that this egg-trading mating system was based on conditional reciprocity in experiments that showed that a) hermaphrodites prefer other hermaphrodites as partners and will reject young males; and b) hermaphrodites paired with young males spawn fewer eggs and at longer intervals than hermaphrodites paired with other hermaphrodites. In flatworms, conditional reciprocity has been demonstrated in the form of exchange of equal volumes of sperm during simultaneously reciprocal copulation in the planarian Dugesia gonocephala (Vreys and Michiels, 1997; Michiels, 1998). Vreys and Michiels (1997) demonstrated both size assortative mating in this species and that the volumes of sperm exchanged between mating partners were more similar than expected on the basis of autosperm stores. In Schmidtea polychroa, another flatworm with simultaneously reciprocal intromission, unilateral sperm transfer was less common than expected by chance, whereas both non-transfer and reciprocal transfer were more common than expected, suggesting that individuals were reluctant to give sperm to a partner that did not reciprocate (Michiels and Bakovski, 2000). In a very interesting case in the basommatophoran gastropod Biomphalaria glabrata, Webster et al. (2003) gave free-moving snails, which either were or were not infected with the parasite, Schistosoma mansoni, a choice between two tethered potential mates, one from a genetic strain selected for resistance to the parasite and one from a susceptible strain. The results show that reciprocation was common with both types of tethered mates when the free-moving snail was uninfected. When the free-moving snail was infected, resistant tethered snails refused to reciprocate with it. The resistant tethered snails would mate as males, but not as females, with infected free-moving individuals. Susceptible tethered individuals, on the other hand, did reciprocate with infected free-moving individuals (Webster et al., 2003). Spermatophore exchange in the stylommatophoran Arianta arbustorum has also been reported to be conditionally reciprocal (Baur et al., 1998) and in the nudibranch gastropod, Aeolidiella glauca, individuals are less likely to retain a spermatophore received from a partner if there was not reciprocal exchange of spermatophores (Karlsson and Haase, 2002). In another stylommatophoran, Reise (1996) reported that if intromission was not reciprocal the male-acting individual would chase and bite the partner (see below). In contrast, Anthes and Michiels (2004) argued, based on a lack of evidence for retaliation against vasectomized individuals, for unconditional reciprocity in the opisthobranch, Chelidonura sandrina which has a mating system involving a single alternation of sexual roles. This mating system, a single alternation of sexual roles, is a relatively poorly understood one from a theoretical standpoint. Under a Prisoner’s Dilemma pay-off matrix (Table 3) such a mating system could not evolve since the stable solution for this game is to defect on the last turn; an unknown length of the game is a requirement for cooperative solutions to Prisoner’s Dilemma (Rapoport and Dale, 1966). One would not expect Tit-for-Tat behavior therefore, in C. sandrina. Such single exchanges of sexual role have been observed in other hermaphrodites (see above; Leonard, 1991) and the Hermaphrodite’s Dilemma model predicts that they represent responses to Game of Chicken situations, for which always reciprocate, or reciprocate most of the time with occasional defections are stable solutions (see Table 3).

The examples cited above show that most of the studies that have examined hermaphrodite mating systems, in pair-mating animals, specifically with a view to identifying conditional reciprocity, have found it. Unconditional reciprocity, which Michiels (1998) cited as a prediction of Bateman’s principle, although it may occur, does not appear to be the rule. In conclusion, therefore, reciprocal mating systems appear to be common in hermaphrodites, as predicted from the Hermaphrodite’s Dilemma model, and the reciprocity appears to be conditional where studied. This is strong evidence that sexual conflict is common in pair-mating hermaphrodites, as Charnov (1979) predicted from Bateman’s principle. However, other models also predict sexual conflict over a preferred role in pair-mating hermaphrodites (see below). In contrast, Connor’s (1992) has argued that reciprocal systems such as egg-trading may evolve without an advantage to defection or punishing cheating if parceling is used as a mechanism to keep T < R. From a practical standpoint, this would suggest that parceling is in fact a mechanism to prevent or punish cheating, as Fischer (1980) predicted. While Connor’s (1992) distinctions may be important from a purely game theoretical standpoint, it is unclear that they predict differences in behavior or represent mating systems without sexual conflict.

It is important to remember that, in reality, few, if any, encounters between pair-mating hermaphrodites will meet the conditions of formal game theory models. For example, a key element of Prisoner’s Dilemma is the requirement that there is no interaction or communication between the participants. This is clearly violated by the hermaphrodites discussed here. It may be more appropriate in situations of broadcast spawn-
ing or pollinator-mediated fertilization. The interest in models such as Prisoner’s Dilemma and Hermaphrodite’s Dilemma is that they make clear, falsifiable predictions from a few basic assumptions and the general validity of the predictions offers a test of fundamental assumptions of sexual selection theory, such as sexual conflict. More recently, Landolfa (2002) has argued that egg trading in *H. nigricans* should be viewed as an exchange of sexual signals rather than as a game involving sexual conflict. He regards interpretation of mating systems in terms of games involving sexual conflict as peculiar to the hermaphrodite literature as opposed to the emphasis on exchange of sexual signals in the literature on dioecious species. Viewing sexual behavior in terms of games of strategy involving sexual conflict and interpreting individual behaviors as sexual signals are in no way mutually exclusive. A conflict of interests between the sexes has been seen as fundamental to understanding the evolution of mating systems in animals with separate sexes for 30 years (see above and reviews in Andersson, 1994; Gowaty, 2004). The relationship between signal evolution and conflicts of interests between sender and receiver has been discussed by Zahavi (1977, 1987; Zahavi and Zahavi, 1997). The question of how hermaphrodites should behave under conditions of continuous mutual assessment is an important one, however, and will require a new generation of models.

Another open question is to what extent the reciprocal mating behaviors that have been studied represent reciprocal fertilization. In the cases of the externally fertilizing hamlets, paternity is clearly reciprocal. Similarly in monogamous pairs of *Ophytrochoa*, the members of a pair fertilize each others eggs (Sella and Lorenzi, 2000). However in the case of internally-fertilizing hermaphrodites with sperm storage, pair-mating hermaphrodites may have little certainty of paternity when transferring sperm to a partner (Charnov, 1979; Leonard and Lukowiak, 1984; reviews in Michiels, 1998; Baur, 1998). In fact, a key aspect of the gamete-trading (Table 3; below) model of mating systems is that the preferred sexual role is the one that offers greater control over the fate of gametes. Reciprocity in sexual behavior can evolve without complete reciprocity in paternity as long as hermaphrodites that reciprocate produce more offspring than hermaphrodites that do not; that is, certainty of paternity does not need to be 100% to select for reciprocity in mating behavior.

In the first study to use microsatellites to look at reciprocal paternity in pair-mating hermaphrodites, Pongratz and Michiels (2003) collected *Schmidtea polychroa* (planarian flatworms) from the field and held them in groups of ten individuals for four weeks. Their results show very high levels of multiple paternity with more than 80% of cocoons (3–5 eggs/cocoon) having more than two sires and more than 28% of offspring sired by unknown individuals, suggesting that sperm can be stored more than a month and that they persist in the sperm storage organ in spite of many subsequent matings by the recipient. Overall, reciprocal paternity was found in only 41/110 “registered mate combinations” and these authors estimated that at best an individual giving sperm to a mate could expect only 25% immediate paternity. The individuals used in this study were not known to be virgins so the role of the sexual history of individuals could not be assessed. It is difficult to say whether 25% represents a high or low certainty of paternity without other data for comparison. One of the assumptions made by Charnov (1979) in predicting a preference for the male role in pair-mating hermaphrodites was that there would be a strong last male advantage in paternity, which is clearly not the case in these planarians. Pongratz and Michiel’s (2003) data showed a strong correlation between the number of female partners and male reproductive success as predicted by Bateman’s principle but also a strong correlation between the number of male partners and female reproductive success, contrary to Bateman’s principle. No correlation was found between either the number of female partners and male reproductive success or the number of male partners and male reproductive success in these planarians (Pongratz and Michiels, 2003) as might be expected if success through male and female function positively associated as required for a convex fitness curve (Fig. 2; Charnov, 1979). In this pioneering study it was not possible to relate variations in mating behavior to variations in reciprocity or to success through either sexual role.

It is clear that although sexual conflict is probably common in pair-mating hermaphrodites, the behavioral reciprocity that has been considered a resolution of this conflict (Axelrod and Hamilton, 1981; Leonard and Lukowiak, 1984; Leonard, 1990) does not necessarily lead to exactly reciprocal paternity. Moreover, there are many apparent exceptions to even behavioral reciprocity, in which internally fertilizing simultaneous hermaphrodites have been described as having unilateral copulation such as the freshwater pulmonate *Phyllis* (DeWitt, 1991, 1996; Wethington and Dillon, 1991, 1997); hypodermic insemination by multiple individuals (Rivest, 1984) or chain copulation in species such as *Aplysia* (Pennings, 1991; Angeloni and Bradbury, 1999; see reviews in Leonard, 1991; Michiels, 1998; Baur, 1998). These exceptions offer very interesting tests of the Hermaphrodite’s Dilemma model and the role of sexual conflict in hermaphrodites.

**Is there a “preferred” sexual role?**

Charnov (1979) argued, on the basis of Bateman’s principle, that hermaphrodites would be more eager to donate sperm than to receive it; i.e., they would prefer to mate as males (the Eager Male Model, Table 3). This formed the basis of his prediction of sexual conflict in hermaphrodites. The empirical data reviewed above demonstrates that pair-mating simultaneous hermaphrodites behave as predicted if sexual conflict were important in their mating system. The next question is whether the sexual conflict is in fact over a
preferred sexual role. That is, when hermaphrodites meet to mate is there a temptation to “cheat” by mating only in the preferred role as predicted by the Hermaphrodite’s Dilemma model. The best evidence for cheating on a reciprocal mating system in a preferred sexual role comes from a comparison of mating systems in the simultaneously hermaphroditic serranine fishes (review in Leonard, 1993). Comparison of the variety of mating systems in that have been described for serranines (Fischer, 1980, Fischer, 1984b; Pressley, 1981; Hastings and Petersen, 1986; Petersen and Fischer, 1986; Fischer and Petersen, 1987) suggests that the basic mating system is a form of conditional reciprocity called egg-trading (see above) and deviations from egg-trading consist of attempts by individuals to get extra spawnings in the male role. For example, in Serranus tigrinus, a monogamous serranine, the members of a pair defend a joint territory and at sunset fertilize each others’ eggs. At other times both members of a pair compete with each other to mate as males with neighboring solitary individuals. Solitary individuals spawned only in the female role until they were joined by another solitary individual to form a new pair (Pressley, 1981). In S. tortugarum and S. tabacarius, pairs form for egg-trading as in H. nigricans, but in these two Serranus species, which lack the tight spawning clasp found in H. nigricans, additional individuals may be attracted to the mating pair (Fischer, 1984b; Petersen, 1990). These “streakers” attempt to dart in and probably release sperm, apparently trying to “cheat” on a reciprocal mating system by getting extra matings in the male role. Specialization in the male role is associated with social dominance in two territorial species, S. baldwini and S. psittacinus (previously S. fasciatus). These two species apparently have an androdioecious sexual system with individuals starting life as hermaphrodites and some large individuals losing ovarian tissue and becoming pure males. In both species, the common social system is for large males to defend territories which contain the home ranges of a harem of smaller simultaneous hermaphrodites (Hastings and Petersen, 1986; Petersen and Fischer, 1986). The hermaphrodites spawn eggs with the harem holder but otherwise attempt to sneak spawnings as males when the harem holder spawns with other hermaphrodites (Hastings and Petersen, 1986; Petersen and Fischer, 1986, etc.). In S. psittacinus, the social system varies with population density (Petersen, 1990). Under low density conditions, monogamous pairs of hermaphrodites may form which alternate spawns each evening as in S. tortugarum. Harem polygamy is the common pattern under moderate density conditions and under high density conditions, a complex system of harem polygamy whereby large individuals become pure males and defend harems of simultaneous hermaphrodites, some of whom may have subharems of smaller simultaneous hermaphrodites, is found. Comparison of these systems indicates that social dominance is associated with the ability to monopolize the male role in spawning and that deviations from the pair mating system occur in the form of attempts by individuals to obtain extra spawnings in the male role. There is, therefore, strong evidence from serranines for a preference for the male role as predicted by Bateman’s principle (Charnov, 1979; Leonard, 1993). Other evidence for a male role preference comes from the observations that 1) O. diadema give fewer eggs to a male than to a hermaphrodite partner (see above; [Sella, 1988]), although apparently the protandrous males may be unable to fertilize a full clutch, and 2) parasite-resistant B. glabrata will mate as males regardless of the infection status of a partner but would only reciprocate with uninfected individuals (see above; Webster et al., 2003). These data would appear to be evidence against the prediction that reciprocal mating behavior may be unconditional as predicted by the Eager Male model (see Table 3; above; Connor, 1992; Pongratz and Michiels, 2003).

There is also evidence from several systems that hermaphrodites prefer to mate in the female role. In a series of experimental observations using groups of three individuals, Leonard and Lukowiak (1991) found that the opisthobranch Navanax inermis were unlikely to initiate male courtship behavior when they were already copulating as females and that they were more likely to terminate intromission as males when they got an opportunity to mate in the female role. In a later study, Michiels et al. (2003) also concluded that the evidence favors a preference for the female role in Navanax. Reise (1996) described mating behavior in stylomatophoran limacid slugs, of the genus Deroceras in which copulation is typically reciprocal, and if it is not, the slug that performed intromission will follow and bite the defector. Karlsson and Haase (2002) demonstrated in the opisthobranch Aeolidiella glauca, which transfers external spermatophores, that although 30% of spermatophores fell off before sperm had penetrated into the body of the recipient, spermatophores were more likely to remain attached if there had been a reciprocal exchange. Comparative data from a group of planarian species comes from the work of Michiels and colleagues (see above, review in Michiels, 1998; Michiels and Bakovski, 2000; Pongratz and Michiels, 2003); who have demonstrated that planarians give sperm preferentially to partners that reciprocate with sperm. These authors have concluded that, in these species, individuals donate sperm in order to obtain sperm. There is strong evidence, then, that the preferred sexual role varies among taxa. Sexual conflict in hermaphrodites may stem from a species-typical preference for either the female or the male role.

**What determines the preferred role?**

The empirical evidence from many species of pairing hermaphrodites suggests that sexual conflict over a preferred sexual role has led to the evolution of mating systems based on conditional reciprocity. There are several theories that would explain why a particular sexual role should be preferred. Bateman’s...
principle (Table 1, above), in its simplest form, would predict that the male role should be preferred (Charnov, 1979); that hermaphrodites would be eager to mate as males because fitness in the male role would have a linear correlation with the number of mates, whereas fitness in the female role would be limited by the resources available for egg production. That is, hermaphrodites should prefer the male role because it has the greatest “upside-potential” (see discussion in [Leonard, 1999]). More sophisticated applications of Bateman’s principle argue that the preferred role will be the role with the lower energy investment in matings, which may be either role, depending on circumstances (see below). In contrast, application of Gillespie’s principle (Table 1, Gillespie, 1974, 1977; see above) to hermaphrodites predicts that hermaphrodites will achieve higher fitness through the sexual role with the lower variance in reproductive success, the role with the lower “downside potential” (Leonard and Lukowiak, 1991; Leonard, 1999). Where the two roles have equal mean fitness, as must be true for male and female function, the lower variance role will offer higher fitness because individuals assuming that role will be less likely to experience reproductive failure (see discussion in Leonard, 1999; Gillespie, 1974, 1977). Both principles have practical limitations in that it is not possible to predict which sexual role will be preferred without having information on either a) the energy expenditures in the two sexual roles (Bateman’s principle) or b) the variance in reproductive success in the two sexual roles (Gillespie’s principle). That is, both principles have great explanatory power but little predictive power unless one applies them in the simplistic but paradoxical form of predicting that the male role will always be preferred under Bateman’s principle but that, if Bateman’s principle holds, the female role will always be preferred due to Gillespie’s principle. Since the empirical evidence demonstrates that the role preference varies among hermaphroditic taxa, neither principle, in its most simplistic form, can explain sexual conflict.

Direct tests of Gillespie’s principle will require more data on the relative variances in reproductive success through the two sexual roles for hermaphrodites. At present, very few data are available. Fischer (1981) estimated the reproductive success in both roles in the externally-fertilizing hamlet, *H. nigricans* and found little difference in variance. There have only been two studies using microsatellites to determine paternity in hermaphrodites (Locher and Baur, 2001; Pongratz and Michiels, 2003) and neither examined variance in lifetime reproductive success. One might expect that if reciprocal mating systems effectively link male and female reproductive success for an individual there may be little difference in variance between the sexual roles averaged across the population. However, more complex mating systems such as the harem polygamy systems of some serranines may well offer opportunities for the uncoupling of male and female reproductive success, as may systems with substantial partitioning of sexual roles over the lifespan (e.g., protandry in *Achatina fulica* [Tomiyama, 2002] or *Arion subfuscus* [Fernandes, 1988]). The need to measure lifetime reproductive success, in both roles, severely limits the predictive power of Gillespie’s principle. The mating rate hypothesis (Baylis, 1981) suggests a third explanation of the preferred role; i.e., that hermaphrodites should prefer mating in the role that requires less time between matings. That will usually be the female role in hermaphrodites that store sperm and do not need to form eggs until sometime after mating, and the male role in hermaphrodites that yolk up clutches of eggs between matings, but again the mating rate hypothesis requires knowledge of the time required to form an ejaculate and/or clutch of eggs and therefore does not yield *a priori* predictions. Gamete trading (Table 3), based on considerations of control of fertilization (Alexander and Borgia, 1979) was developed as a more predictive model (Leonard and Lukowiak, 1984).

**Gamete trading or energy trading?**

In an attempt to reconcile the apparent preference for the male sexual role in *H. nigricans* with the preference for the female role in *Navanax inermis*, Leonard and Lukowiak (1984, 1985) developed a general model of sexual conflict in simultaneous hermaphrodites, “gamete-trading” which predicts the preferred sexual role on the basis of control of fertilization. As Alexander and Borgia (1979) pointed out, one of the fundamental differences between the sexes is that in general females maintain control of the fate of their gametes to a greater extent than do males. That is to say, particularly with internal fertilization, insemination may not lead to fertilization and males may have very low certainty of paternity. One of the factors that reduces male control of fertilization is simply sperm competition. When females mate multiple times, a male’s expected reproductive success from a given mating may be drastically reduced, increasing the effort required to produce a single offspring and reducing certainty of paternity, thus creating conditions where male fitness is not proportional to the number of mates (see Shuster and Wade, 2003). Eberhard (1985, 1996, 2004) has documented the many ways in which females may exert “cryptic choice” and manipulate received ejaculates, reducing male control of fertilization and certainty of paternity. The gamete-trading model (Table 3) predicts that pair-mating hermaphrodites will evolve mating systems based on conditional reciprocity resolving sexual conflict based on a preference for the sexual role that offers the greater control of fertilization (Leonard and Lukowiak, 1984, 1985, 1991; Leonard, 1991, 1993). That is, in species such as the serranines, or hermaphroditic *Ophryotrocha* species, which have external fertilization with the eggs being spawned first, the individual in the male role has control of fertilization, since it has information as to when eggs are available (see discussion in [Leonard, 1993]). On the other hand, *Navanax*, like many...
euthyneuran gastropods, has internal fertilization with long-term sperm storage and a gametolytic gland which serves to digest stray gametes and may be used to digest excess or unwanted sperm. In such a case, an individual giving sperm to a partner has no guarantee that the recipient will use the sperm to fertilize eggs. The sperm may simply be digested or may remain in storage past their period of viability. The gamete-trading model predicts therefore that hermaphrodites prefer to mate in the sexual role that gives the greater certainty, through control of fertilization, that whatever investment is made in the mating in terms of energy, time, risk of predation, etc. will increase the individual's reproductive success.

The gamete-trading model then can explain both the preference for the male role in serranines (but see [Fischer, 1987]; discussed in [Leonard, 1993]) and Ophyrotrocha spp., and the preference for the female role found in Navanax, and the planarians studied by Nico Michiels and colleagues, since these planarians also have sperm storage and the ability to digest foreign sperm. The gamete-trading model's predictions for a variety of euthyneuran gastropods have been reviewed elsewhere (Leonard, 1991). It appears to be consistent with the available data and is a predictive model; that is the role preference can be predicted from a basic knowledge of the reproductive anatomy and physiology of the species in question, rather than explained after a detailed study of the energy used in the male relative to the female role, and/or variance in lifetime reproductive success. The gamete-trading model is consistent with Gillespie's principle and the principles of the Modern Portfolio theory (see Leonard, 1999 for discussion) in that it assumes that hermaphrodites will be risk-averse in their mating strategy. It predicts which sexual role will offer the temptation to cheat in the Hermaphrodite's Dilemma model of sexual conflict (Leonard, 1990). The observations of conditional reciprocity in the female role in resistant Biomphalaria glabrata (Webster et al., 2003) appear to be inconsistent with the gamete-trading hypothesis, which would predict sperm-trading for this species. However, it may be the case that schistosome infection alters control of fertilization, or the probability of surviving to egg laying, in some way. Further work on this system will offer an opportunity for a critical test of the gamete-trading hypothesis. Lüscher and Wedekind (2002) have hypothesized that the internally-fertilizing cestode, Schistoccephalus solidus, prefers the male role, which will also offer a critical test of the gamete-trading model.

In dioecious species, mating systems that are in clear violation of Bateman's principle are usually explained in terms of unusual expenditure of energy by males (see Trivers, 1972; reviews in Thornhill and Alcock, 1983; Andersson, 1994; Simmons, 2001; papers in Tang-Martinez, 2005; but see Jones et al., 2000, 2005). That is, sexual selection, through male-male competition and/or female choice, may force males to invest energy in matings in the form of nuptial gifts, sperm competition, parental care, etc., so that costs for males come to equal or exceed those of females. (For critical reviews of this perspective see Shuster and Wade [2003] and Gowaty and Hubbell [2005]). There are certainly well-studied cases in which males produce a nutrient-rich spermatophore that contains energy that is used by the female to produce eggs (see Simmons, 2001 for review). It has been argued that internally-fertilizing hermaphrodites, such as planarians and some of the euthyneuran gastropods that have the ability to digest sperm and/or ejaculates, may be trading sperm to use as food for egg production (Michiels, 1998; Pongratz and Michiels, 2003).

However, there are two reasons why an energy-trading mating system in hermaphrodites would be evolutionarily unstable. The first is that a pair of hermaphrodites trading sperm (or any other metabolic product) would come out of the encounter with both individuals having a net loss of energy. This stems from basic thermodynamics. Even if we assume a high rate of conversion efficiency, 80% for example, a hermaphrodite which consumes 100 calories of food will be able to make 80 calories of sperm (or seminal product). If it then transfers that 80 calories of sperm to the partner, the partner will be able to make only 64 calories of eggs as a result of the "nuptial gift." A pair of sperm-trading hermaphrodites then would each end up with 16% fewer calories of eggs than if they had not traded sperm. If reproductive success in the female role is limited by the resources available to make eggs, à la Bateman's principle and/or the production of sperm is expensive, resource trading between hermaphrodites should not be evolutionarily stable, unless a resource could be traded without incurring a metabolic cost (hypothetically, hermaphrodites could trade nest materials or something of that sort). Energy trading between hermaphrodites would only be evolutionarily stable if energy limited reproductive success through neither sexual role. Therefore, it seems unlikely that sperm-trading in hermaphrodites represents an exchange of energy (or any metabolically produced resource) to make eggs or gametes. The more likely scenario is that, as predicted by Leonard and Lukowiak (1984, 1985, 1991), sperm trading is a mating system that allows each individual to gain sperm to use for fertilizing its own eggs. This does not mean that paternity per se is traded (see Pongratz and Michiels, 2003), in that each individual sires an equal number of the partner's offspring, but rather that each individual that exchanges sperm with a partner has a higher probability of getting its own eggs fertilized than it would otherwise (Leonard and Lukowiak, 1984; Leonard, 1991).

The second problem with the energy or resource trading hypothesis is that it assumes that hermaphrodites respond to the risk that their sperm will be wasted by increasing the amount of sperm transferred (Greeff and Michiels, 1999). In a theoretical paper, Greeff and Michiels (1999) argued that if the partner is likely to digest sperm, hermaphrodites should pro-
duce and transfer very high volumes of sperm to compensate for the anticipated loss as a way of increasing probability of paternity. This would increase male mating costs to the point where individuals may become more energy-limited through the male role than the female role and explain why some internally-fertilizing hermaphrodites trade sperm. However, Greeff and Michiels failed to consider that where females are promiscuous and sperm competition, through whatever mechanism, is high, an increase in investment in sperm may not lead to greater fitness for males and they would be expected to evolve other mechanisms for improving their reproductive success, such as mate guarding, etc. (Shuster and Wade, 2003). Greeff and Parker (2000) did consider, explicitly, the theoretical problems posed by "spermicide" and demonstrated that where females are likely to destroy or digest sperm rather than use it to fertilize eggs, males should evolve to restrict the amount of sperm given to the partner during mating, unless it is the case that the female destroys only a fixed amount of the sperm received. That is, where sperm passed to a partner are at risk, males pouring more and more sperm into a partner that may not use it for fertilization would be committing the "Concorde fallacy" (Dawkins and Carlisle, 1976). It seems likely that hermaphrodites, which need to use metabolic energy to make eggs, would be even less likely than pure males to benefit by evolving massive and expensive ejaculates under conditions of sperm competition and female promiscuity. The gamete-trading model (Leonard and Lukowiak, 1984, 1985; Leonard, 1991) predicts that where a hermaphrodite mating in the male role is unsure of achieving paternity, it should limit the amount of sperm given to the partner in each mating, that is, male-acting hermaphrodites should "parcel" sperm, as serranines parcel eggs (Leonard and Lukowiak, 1984). Evidence that planarians trade sperm by volume (Vreys and Michiels, 1997) is consistent with this prediction and would not be expected under the Greeff and Michiels model. Observations on Navanax inermis suggest that individuals collected from the field are often allosperm depleted (Michiels et al., 2003). Also, single spermatophores may not be sufficient to fertilize a clutch of eggs in the opisthobranch, A. glauca (Karlsson and Haase, 2002). Pollen is known to be a limiting resource for seed production in many hermaphroditic angiosperms (Willson and Burley, 1983). These observations are consistent with the fundamental prediction of the gamete-trading model (Table 3) which is that where control of fertilization is through the female role in hermaphrodites, hermaphrodites acting as males will restrict sperm transfer, making sperm a limiting resource for zygote production.

Although these considerations make it seem unlikely that mating systems in internally-fertilizing hermaphrodites will be based on resource trading rather than gamete-trading, there may be circumstances in which a "nuptial gift" could be adaptive in hermaphrodites. There is a report in slugs of the genus Derotites. There is a report in slugs of the genus Maphroditis of unilateral copulation followed by the male-acting individual severing its own penis and presenting it to the partner as a nuptial gift which is then eaten (Rzymhanov, 1994). The mating system that makes such a behavior adaptive is not clear, but with unilateral mating a male-acting hermaphrodite, perhaps nearing the end of a protandric phase (see Fernandes, 1988, 1990), could increase its success through male function by using the penis as a nuptial gift before turning its energies to laying eggs. Another possible example of hermaphrodites bearing nuptial gifts is the famous case of the love-dart or sarcobelum in helicids. Charnov (1979) predicted that the calcareous dart that is shot into, or at least toward, the partner’s body in helicids, might act as a gift of calcium for egg production. The eggshell of helicids is heavily calcified and egg laying requires a large mobilization of calcium (Tompa and Wilbur, 1977). Rogers and Chase (2001, 2002) have demonstrated that receipt of a dart increases both sperm storage from the mating and the number of offspring sired by the dart donor in Helix aspersa, consistent with Charnov’s hypothesis (but see Baminger et al., 2000 for contrary data in another helicid). However, the amount of calcium contained in the dart of Helix aspersa has been shown to be sufficient to produce only one eggshell (Koene and Chase, 1998), making it unlikely that dart shooting, which often does not result in the dart getting into the recipient’s body (see discussion in Leonard, 1992), increases the shooter’s fitness by increasing its partner’s ability to form eggshells. An intriguing possibility is that exchange of love darts may stabilize reciprocal mating systems in helicids by acting as an indication of good faith and commitment by the donor (see Zahavi, 1977, 1987; Leonard, 1992; Carmichael and MacLeod, 1997). Carmichael and MacLeod (1997) have demonstrated, in a game theoretical study, that exchange of gifts at the beginning of an interaction can promote cooperative behavior, if and only if, the gift is more expensive to the donor than it is valuable to the recipient. Because the gift is expensive to produce and not particularly valuable to the recipient, individuals that have initiated an encounter with an exchange of such gifts will be unlikely to desert their partner. Carmichael and MacLeod’s model is consistent with the “honest-signaling” hypothesis of Zahavi (1977, 1987) but does not, however, explain either egg- or sperm-trading mating systems, with their repeated alternation of sexual roles (see above). Energetic considerations suggest that in these systems, hermaphrodites are trading gametes for fertilization, rather than trading gametes for energy for gamete production. The energy trading predicted by Pongratz and Michiels (2003) on the basis of Bateman’s principle could, paradoxically, be evolutionarily stable only where gamete production is not limited by energy availability; i.e., Bateman’s principle does not apply.

**Bateman’s Principle and Hermaphrodites**

Although Charnov (1979) used Bateman’s principle to correctly predict that sexual conflict would be im-
important in pair-mating hermaphrodites, Bateman’s principle does not offer an adequate explanation of the form that sexual conflict takes. Bateman’s principle produces a paradox in that it hypothesizes, on the basis of assumptions about energy requirements, that hermaphrodites will compete for the male role because of its greater “upside potential” although Gillespie’s principle demonstrates that where two strategies have equal mean fitness (as must the two sexual roles in a sexual population) the strategy with the lower variance (the female role according to Bateman’s principle) will have greater fitness. Neither Bateman’s principle nor Gillespie’s principle in their simplest forms correctly predict the observed sexual role preferences in hermaphrodites. Either or both principle(s) may be able to explain these observations a posteriori but the gamete-trading model (Leonard and Lukowiak, 1984, 1991) based on the prediction that sexual conflict will stem from control of fertilization (Alexander and Borgia, 1979; Eberhard, 1985; etc.) seems to have the most predictive power at present. A limitation of all of these models is that they assume that a single sexual role will be preferable for all individuals in a species. There is ample evidence that size and/or age matter in hermaphrodites (Tomiyama, 2002; Lüscher and We dekind, 2002; Schärer and Ladurner, 2002; Angeloni, 2003; Angeloni and Bradbury, 1999; Ohbayashi-Hodoki et al., 2004; Michiels et al., 2001, etc.) and future development in the field will need to incorporate this complexity. Mutual assessment during sexual encounters (Landolfa, 2002) is also an issue that needs attention.

Therefore, although Bateman (1948) predicted that his principle would apply to hermaphrodites, Charnov’s (1979) prediction that hermaphroditism would commonly occur where Bateman’s principle did not apply may well be correct. His predictions, based on Bateman’s principle, as to the distribution and occurrence of hermaphroditism are inconsistent with the data. In conclusion, although Bateman’s principle has been a very fruitful source of falsifiable predictions about hermaphrodites and hermaphroditism, it does not offer a useful framework for constructing a general theory of sexual selection that would include both hermaphroditic and dioecious systems, as Bateman (1948) predicted. Since Bateman’s principle was based on observation of the sexual behavior of dioecious species, observations of eager males and coy females in such systems do not constitute tests of the idea(s). Bateman (1948) suggested extension to hermaphrodites as a test of the principle and the tests discussed above, along with the many exceptions from systems with separate sexes (see Shuster and Wade, 2003; Gowaty and Hubbell, 2005), suggest that alternative explanations of sexual selection are needed. The idea that there is sexual conflict over control of fertilization, discussed above for hermaphrodites and for dioecious species by Alexander and Borgia (1979) and Eberhard (1985, 1996) may offer a useful alternative. Cases in which the two hypotheses make conflicting predictions may be used to test the theory.

ACKNOWLEDGMENTS

Thanks are due to Zuleyma Tang-Martinez for organizing the symposium and inviting a delegate from Pluto to speak. I also thank Peter Souzou for introducing me to the Carmichael and MacLeod paper and Heike Reise for alerting me to the Rymzhanov reference and providing an English translation. I would also like to thank NSF for providing funding for participation in the symposium and Dr. Gary Griggs and the staff of Long Marine Laboratory at UCSC for providing a pleasant and stimulating work environment.

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