

The Darwin-Bateman Paradigm in Historical Context¹

DONALD A. DEWSBURY²

Department of Psychology, University of Florida, Gainesville, Florida 32611-2250

SYNOPSIS. I introduce the term “Darwin-Bateman Paradigm” to include several proposals stemming from the writings of Charles Darwin and A. J. Bateman, including the notions that (a) male reproductive success is more variable than that of females, (b) males gain more in reproductive success from repeated matings than do females, and (c) males are generally eager to mate and relatively indiscriminate whereas females are more discriminating and less eager. I trace this paradigm from Darwin’s *The Descent of Man* through Bateman’s research and beyond. I try to clarify the terminology used in applying Bateman’s results and discuss both the impact and the criticisms the paradigm has engendered. I then broaden the context of the Darwin-Bateman Paradigm to show related conceptions in disparate fields that evolved in parallel with it. I conclude that gender stereotypes appear to have influenced these conceptions. The paradigm has been of great heuristic value but is in need of further empirical investigation in view of numerous exceptions to these general rules.

INTRODUCTION

What I call the Darwin-Bateman Paradigm is a set of interrelated hypotheses stemming from the work of Charles Darwin and Angus Bateman that can be viewed in the broader context of the study of sex differences. Together, these form a view of the sexes that has affected the ways in which they have been conceptualized in much scientific research but that were deeply embedded in the cultures in which these the two Englishmen lived. I begin with some of Darwin’s foundational thinking, then discuss Bateman’s work and its impact, return to Darwin, and finally consider the gender-related issues that provide some context for this work. The generality of some of the cornerstones of the paradigm are being called into question and the role of androcentric conceptions is becoming increasingly prominent.

Some basics from Darwin

Darwin’s treatment of what he called sexual selection was presented primarily in his (1871) *The Descent of Man and Selection in Relation to Sex*. He treated sexual selection as fitness that “depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” (v.1, p. 256) and used the principle especially to explain the evolution of such characters as the ornamentation of males. Darwin divided sexual selection into two processes, male-male competition and female choice. He believed that males generally pursued females, writing, for example, “that males of all mammals eagerly pursue the females is notorious to every one” (v.1, p. 272) but that “the female, on the other hand, with the rarest exceptions. . . is coy, and may often be seen endeavoring for a long time to

escape from the male” (v. 1, p. 273). Darwin explained this difference as originating in plants and lower animals because differences in mobility between large ova and small sperm. He believed that the habit of males approaching females and of their “strong passions” (p. 274) grew out of this difference in transportability. Darwin backed up his conclusions with many observations of sex differences in both morphology and behavior across a broad range of taxa.

Darwin discussed cases of sex “reversals” in which females are ornamented and males are choosy (*e.g.*, v.1, pp. 263, 276) and considered but rejected the possibility that male coercion might be an important factor in female passivity. Darwin’s ideas on sexual selection generally languished with relatively little acceptance and appreciable criticism for many years before exciting scientific interest.

BATEMAN’S CONTRIBUTIONS

A. J. Bateman

Angus John Bateman (1919–1996) was an English geneticist who received his B.Sc. in 1940, Ph.D. in 1946 and D.Sc. in 1956 in botany from King’s College, London (Debus, 1968). He was affiliated with several laboratories during his career; in 1948 he was with the John Innes Horticultural Institute in Merton Park, London. Bateman was known for research on a dominant lethal procedure for *in vivo* testing for mutagenicity, studies of cross pollination in seed crops, and the genetics of quantitative characteristics in barley and rye in addition to his several studies with animals.

Bateman’s 1948 experiment

Bateman reported his study of sexual selection in an article entitled “Intra-Sexual Selection in *Drosophila*” in the *Journal of Heredity* in 1948. Bateman’s logic was framed by Darwin’s ideas on sexual selection. He contended that the evidence in favor of sexual selection was circumstantial and that alternative explanations were possible. He noted that Darwin supported

¹ From the Symposium *Bateman’s Principle: Is It Time for a Reevaluation?* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 5–9 January 2004, at New Orleans, Louisiana.

² E-mail: dewsbury@ufl.edu

the ardent male-coy female hypothesis solely on the basis of behavioral observations and contended that Darwin “was at a loss, however, to explain this sex difference” (p. 350).

Bateman studied small groups of equal numbers of male and female *Drosophila melanogaster*, carrying distinctive marker chromosomes, confined in small bottles and allowed to mate *ad lib*. He conducted six experimental series with 4–9 replications per series, 3–5 fruit flies of each sex in each replicate, and with females allowed 3–4 days of laying. He then classified the offspring with regard to genotype. Bateman reported two primary phenomena. First, he found that the variance of reproductive success was greater for males than for females. In all, just 4% of the females, as compared to 21% of the males, failed to produce any progeny. He regarded this as “a *sign* of intra-masculine selection” (p. 362). Second, Bateman reported that male fertility increased in a linear manner as a function of the number of copulations achieved, whereas the fertility of females showed little increase as a function of the number of copulations beyond the first. Bateman regarded this as “the *cause* of intra-masculine selection” (p. 362, italics in original).

In essence, Bateman believed that female reproductive success appeared to be limited by the number of eggs that can be produced, whereas for the male he suggested that “fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him” (Bateman, 1948, p. 364). Like Darwin, Bateman saw the variance difference as suggesting greater action of sexual selection on males than on females; he suggested that this was due to the sex differences in the cost of producing gametes.

Problems of interpretation

It should be noted that all of Bateman’s conclusions were based on differences in the representation of marker genes in progeny. He did not conduct systematic behavioral observations. Thus, as he noted, if a female mated with a male but no progeny resulted from that mating, the mating would have escaped detection. Further, Bateman could not distinguish single- and multiple- inseminations involving the same pair of flies. As he noted, “it might be possible when two matings occurred in quick succession for no progeny from the first mating to appear” (pp. 353–354). Thus, his estimates of the number of mates and matings must be regarded as minima. In fact, when Bateman wrote of the number of “mates,” he actually measured the number of partners with which the individual produced offspring, not the number of individuals with which she mated or the number of times it did so.

For most animal behaviorists, a “mate” is a partner with which an animal copulates and/or pairs. Bateman’s use of the term “mate” is misleading. Given the usual meaning of the word, it is a mistake, therefore to write that “he established that the relative strength of sexual selection in males and females is determined

by the relationship between mating success (*number of copulation partners*) and reproductive success (offspring production)” (Cunningham and Birkhead, 1998, p. 1312; italics added). What Bateman studied was the relationship between reproductive success and the number of partners with which individuals produced progeny, not the number with which they copulated. Further, Bateman’s questionable use of the term “mate” has been carried forth in research he stimulated and in theoretical statements regarding the relationship between “reproductive success” and “mating success (number of mates)” (e.g., Jones *et al.*, 2002).

As noted, Bateman apparently made only casual observations of the actual behavior of his flies (pp. 356–357). I can find no basis in Bateman’s (1948) article for Thornhill and Alcock’s (1983) statement “all males exhibited courtship behavior and every female was vigorously courted” (p. 55) or for Trivers’ (1972) statement that the females that “failed to copulate” (which should read ‘failed to produce progeny’) “were apparently courted as vigorously as those who did copulate” (p. 137) or that the 21 per cent of males who failed to reproduce showed no disinterest in trying to copulate, only an inability to be accepted (p. 138). I find no such observations reported.

Terminology

Although Bateman’s work has been quite influential, the literature is confused as to exactly which term should be used to refer to which aspect of Bateman’s (1948) results. I use the term “Bateman’s principle,” in the sense of Wilson (1975), who appears to have coined the term, to mean that “the variance of reproductive success is greater in males than in females” (Wilson, 1975, p. 325). What has been termed the “Bateman gradient” (e.g., Jones, *et al.*, 2001) refers to the differential benefits to reproductive success to be gained by males and females with repeated matings. Yet a third aspect of this complex, the “ardent male-coy female hypothesis,” is best attributed to Darwin as it was this hypothesis that Bateman was trying to validate and explain.

Some authors use the terms in different ways. Jones *et al.* (2002) refer to “Bateman’s principles” as entailing differences in the variance in reproductive success, differences in the variance of mating success, and the relationship between them and Tang-Martinez, 2000 used “Bateman’s principle” quite broadly. Hrdy (1986) used the term “Bateman paradigm” as the aggregate of the ideas that a.) male variance of reproductive success exceeds that of females, b.) males have more to gain from multiple matings, and c.) males are generally ardent and females coy. Here, I adopt Hrdy’s term and rename it the **Darwin-Bateman Paradigm** because it is derived from both scientists.

Strictly speaking, we might couch these principles not in terms of males and females but of the sex experiencing the weakest or strongest sexual selection (e.g., Darwin, 1871; Jones *et al.*, 2002). However, Bateman himself so emphasized the roles of males and

TABLE 1. Citations of Bateman's (1949) article in 5-year blocks.

Years	Number of citations
1949–1953	8
1954–1958	2
1959–1963	2
1964–1968	6
1969–1973	6
1974–1978	20
1979–1983	84
1984–1988	128
1989–1993	89
1994–1998	135
1999–2002*	145
Total	625

* 4-year block.

Data from combined on-line *Citation Indexes: Science Citation Index plus Social Sciences Citation Index plus Arts & Humanities Citation Index* at <http://isi1.isiknowledge.com/portal.cgi/wos>. Note that the years given for each citation are those when they were entered into this database and, typically, a few each year get credited to the next year.

females per se that it would appear appropriate to employ the simpler terminology as long as the effects of so-called sex reversals are remembered.

THE IMPACT OF BATEMAN'S PAPER

One measure of the impact of an article is its frequency of citation. Typically, a paper receives the bulk of its citations in the few years immediately after publication. Bateman's has an unusual history (see Table 1). I found a total of 625 citations, with a mean of 11.6 per year, between 1949 and 2002. However, for the first 30 years after its publication, the article received just 44 citations, or an average of just 1.5 citations per year. Ever since, it has received at least a dozen citations every year, reaching a peak of 55 in 2002, more than the total for the first 30 years after publication and more than a half-century later.

Although the article was cited in passing by Williams (1966), it appears that Trivers' (1972) article, in which the concept of parental investment was developed, followed by Wilson's (1975) book brought the work of Trivers and Bateman to a broader audience. The concept of Parental Investment (PI) and Bateman's research became standard fare in many textbooks and courses in the field.

TESTS AND CRITICISMS

The validity of Bateman's principle per se is a matter for empirical test. One need only compare the variances of reproductive success for females and males. Such differences occur in many studies (e.g., Clutton-Brock, 1988; Jones, *et al.*, 2002) but not in others (e.g., Hafernik and Garrison, 1986; Sheridan and Tamarin, 1988). Clutton-Brock (1988) concluded both that "variation in female breeding success is substantial" (p. 472) but that "standardized variance in male success commonly exceeds variance in female success" (p. 475). The exceptions to this generalization are important, however.

Support for the Bateman gradient was found in such species as rough-skinned newts by Jones *et al.* (2002) and in the sex-role-reversed pipefish by Jones *et al.* (2001).

In reality, it is not the sex difference in variability of reproductive success per se that makes the principle of such great interest. Rather, it is the implications of these results for the entire Darwin-Bateman paradigm. One can ask whether the sex difference in variance necessarily implies that sexual selection has operated or that this explains or implies "undiscriminating eagerness in males and discriminating passivity in females" (Bateman, 1948, p. 367). Both Sutherland (1985) and Hubbell and Johnson (1987) argued that the expected sex differences in variance can occur even when there is random mating and thus that Bateman's data can be explained without any reference to inter-male competition and female choice. Gowaty (2003) noted that "what was most important about Sutherland's model was that it showed that sex differences in variance in the number of mates should not count as evidence for indiscriminate males and coy, choosy females" (p. 908). She concluded that "credible, sex-neutral alternatives to parental investment theory exist, and those interested in social behavior must eliminate these alternatives before concluding that parental investment patterns alone account for selection on sex roles" (p. 911).

A key belief in the development of PI theory was the assumption that male capacity to produce ejaculates was virtually unlimited. One could thus read that "fertility is seldom likely to be limited by sperm production" (Bateman, 1948, p. 364), or that "the word excess has not meaning for a male" (Dawkins, 1976, p. 176). However, beginning in the early 1980s a literature evolved showing that male reproductive capacity is limited and that males might be selected for prudent allocation of their available ejaculates (e.g., Dewsbury, 1982; Nakatsuru and Kramer, 1982). Because males' production of ejaculates entails some costs and is limited, males may be more choosy in mating than had generally been believed. Indeed, scattered evidence of male choice was considered by both Darwin and Bateman. There are now many data concerning limited male capacity, the complex factors affecting prudent male allocation, and the implications for females of limited sperm delivery by males and this information is being taken seriously in discussions of sexual selection (e.g., Harris and Lucas, 2002; Pizzari *et al.*, 2003; Wedell, *et al.*, 2002). Males also incur many costs besides that of the individual sperm. This line of research has served to erode some of the thinking about continuously "ardent" males.

Complementary to this work on the costs to males, the roles of females have been reexamined. Females are sometimes active in soliciting copulation. Thus, the view that females are necessarily coy has been seriously challenged. Beach (1976) termed female solicitation of copulation "proceptivity."

Females of some species, especially primates, often

solicit matings with multiple males (e.g., Hrdy, 1986, 1997). Although this has been known in insects for some time, the issue has become so prominent as to be featured in *Newsweek* magazine under the title “Sex and the Single Fly” (Begley, 2000). The benefits of such multi-male matings have been re-examined. Among the benefits that have been proposed for multi-male mating are renewal of depleted sperm supplies, improvement of the genetic quality and diversity of a female’s offspring, increased access to resources, and increased lifetime offspring production (Arnqvist, 2000; Birkhead, 2000; Jennions and Petrie, 2000). Most important, it has become apparent that in some of Bateman’s experiments females did, in fact, gain increased fertility through repeated matings (Arnold and Duvall, 1994; Birkhead, 2000).

As with the ardent male, the growing literature has cast doubt upon the universality validity of the concept of the coy female. Gowaty (2003) suggested that male and female roles are more flexible than suggested by Bateman’s inferences. It is likely that the ardent male-coy female perspective may hold for more species than does the reverse. However, the growing literature regarding exceptions to these generalizations is important for the development of a truly comprehensive theory.

MORE FROM DARWIN

The Darwin-Bateman paradigm can be viewed in the broader context of sex differences and gender politics (see also Zuk, 2002). Darwin was a man of his time whose views might easily be labeled sexist in today’s context. His ideas may have led directly to, but certainly at least set the occasion for, a number of developments, including the Bateman research. Among Darwin’s views, as expressed in *The Descent of Man* were the following:

Men and women differ in temperament

Darwin wrote that “Woman seems to differ from man in mental disposition, chiefly in her greater tenderness and less selfishness; and this holds good even with savages . . . Man is the rival of other men; he delights in competition, and this leads to ambition which passes too easily into selfishness . . . with woman the powers of intuition, of rapid perception, and perhaps of imitation, are more strongly marked than in man” (v.2, pp. 326–327).

Men are more intelligent than women

“The chief distinction in the intellectual powers of the two sexes is shewn by man attaining to a higher eminence, in whatever he takes up, than woman can attain—whether requiring deep thought, reason, or imagination, or merely the use of the senses and hands . . . if men are capable of decided eminence over women in many subjects, the average standard of mental power in man must be above that of woman” (v.2, p. 327).

The sex difference in intelligence is the product, at least in part, of sexual selection

“Without the higher powers of the imagination and reason, no eminent success in many subjects can be gained. But these latter as well as the former faculties will have been developed in man, partly through sexual selection—that is, through the contest of rival males, and partly through natural selection, that is, from success in the general struggle for life; and as in both cases the struggle will have been during maturity, the characters thus gained will have been transmitted more fully to the male than to the female offspring. Thus, man has ultimately become superior to woman” (v.2, p. 328).

Females may be more primitive, evolutionarily and developmentally, than males

“Some, at least, of these faculties [that are strongest in women] are characteristic of the lower races, and therefore of a past and lower state of civilization” (v.2, pp. 326–327). In addition, he wrote that “throughout the animal kingdom, when the sexes differ from each other in external appearance, it is the male which, with rare exceptions, has been chiefly modified; for the female still remains like the young of her own species, and more like the other members of the same group” (v. 1, pp. 271–272) and “in most cases the young of both sexes resemble each other; and the female resembles her young offspring throughout life” (v. 2, p. 397).

Males are generally more variable than females

Darwin introduced the issue of variability, suggesting that “variations are more apt to occur in the male than in the female sex” (v.2, p. 128) and provided much evidence of this phenomenon. Elsewhere, Darwin wrote of “the frequent and extraordinary amount of variability presented by secondary sexual characters” (v. 1, p. 278) of males and he concluded from his studies of domesticated animals that “the male is more liable to vary than the female” v.1, p. 275). He reasoned that “all these contingencies are highly favourable for sexual selection” (v.2, p. 128).

Sex differences are not limited to traits related to reproduction

Darwin did not limit his discussion of sex differences in variability to obviously secondary sexual traits. Of humans he suggested that “the numerous measurements of various other races with respect to stature, the circumference of the neck and chest, and the length of the back-bone and arms, which were carefully made, nearly all shewed that the males differed much more from each other than did the females” (v. 2, p. 321; see also v. 1, p. 275). He also discussed studies in which various abnormalities, such as supernumerary digits, occurred more frequently in men, noting that the data might be biased if women were more likely to conceal such effects.

Thus, Darwin’s treatment of, and reliance upon, sex-

ual selection was wide-ranging. I have not yet determined whether it is possible to disentangle the origins of Darwin's conceptions of sex differences in humans *versus* other species. It is probably impossible to determine which came first. It seems quite likely, however, given the culture in which Darwin lived (Houghton, 1957), that his ideas of sex differences in non-human animals were shaped, at least in part, by the views he shared with many others of his time regarding gender differences in humans. The notion that females are characterized by a lack of certain qualities ("the presence/absence metaphor") has been traced back as far as Aristotle and St. Thomas Aquinas (Faus-to-Sterling, 2000). In Victorian culture, boys up to the age of 5 were often treated as part of the feminine side of the family and this phase was regarded as an important stage in the development of masculinity (Nicholson, 2003). Women were viewed as providing a "haven of stability" (Davidoff, 1973, p. 16). The Darwin-Bateman paradigm originated in this context.

BROADER IMPACT OF DARWIN'S EMPHASES

The Darwin-Bateman paradigm can be treated as part of a family of related developments stemming from Darwin's views regarding sex differences variability, developmental state, and intelligence. Although none of these ideas was originated by Darwin, surely his prominence helped the coalescence of a somewhat integrated view of sex differences. Although they may perhaps be traceable to Darwin's writings, this says nothing conclusive about their utility. Sexist hypotheses need not necessarily be viable or inviable. They may be subjects of empirical inquiry. The origins should foster such inquiry given the possibility that these approaches emerged as a product of 19th-century sexism.

The variability hypothesis

According to the so-called variability hypothesis, there may be no innate differences in intelligence, and other characteristics, between men and women but men are more variable. As a result, there are more men at each tail of the normal distribution. As a consequence, it is argued, the prevalence of men in positions of prominence in society is the result not of overall gender differences in intelligence or of power and privilege but because there are more men with extraordinary innate abilities. The hypothesis had been controversial for more than a century (Shields, 1975, 1982). The notion that male intelligence is the more variable is thus a cousin to the notion that male reproductive success is the more variable.

Ellis (1894) developed the variability hypothesis following Darwin writing that "since Darwin wrote the evidence has accumulated, and the greater variational tendency of males has never been questioned" (p. 359) and that "men represent the more variable and the more progressive element, women the more stable and conservative element in evolution" (p. 367). Pearson (1897) argued against Ellis's conclusions. Geddes

and Thomson (1889) explained the difference in terms of anabolic and catabolic traits. Debate among psychologists continued early in the 20th century (*e.g.*, Hollingworth, 1914; Thorndike, 1906). The hypothesis remains controversial today with supporting data published by several authors (*e.g.*, Feingold, 1992; Hedges and Nowell, 1995). By contrast, Noddings (1992) opposed this "pernicious hypothesis" (p. 85) and suggested that "it is hard to avoid the conclusion that interest in the variability hypothesis was part of an effort to maintain the notion of women as undifferentiated beings—alike and thus interchangeable, designed only for reproduction" (p. 86). Like the Darwin-Bateman paradigm, the variability hypothesis appears to have been derived, at least in part, from Darwin's notion of the sex difference in variability.

The Trivers-Willard hypothesis

The Trivers-Willard hypothesis can be seen as a corollary of the Darwin-Bateman paradigm. Because sexual selection is believed to act more strongly on males, such characteristics as size, health, and strength would be expected to be more important for reproductive success in males than in females. This should affect the preferred sex ratio if a mother could control the sex of her offspring. According to Trivers and Willard (1973), females in good condition and able to invest heavily in their offspring would be favored to produce males; those less able to invest in offspring should produce females. Put another way, if a mother is able to produce an offspring that is really special, she should produce a male; if she is only able to produce an average offspring she will be better off producing a female. A marginal female will probably have some reproductive success; a male weakling is likely to have little. Some appreciable support has been generated for this hypothesis but it seems greatly over-simplified and remains highly controversial (Bercovitch, 2002; Cameron and Linklater, 2002; Carranza, 2002). Cameron and Linklater (2002) suggested that "currently there is a sex bias in studies of sex-biased maternal investment." This hypothesis appears to be a reflection of Darwin's view of the differential action of sexual selection on males and females.

Sex differences in development

The Darwin-Bateman paradigm may also have affected conceptions of the development of sex differences. Recall that Darwin proposed that females were more primitive and less variable than males. Following Darwin, Spencer (1896) wrote of females as displaying an "arrest of development" and of an "earlier cessation of individual evolution" [*i.e.*, development] (p. 374). As a result, "there is a perceptible falling-short in those two faculties, intellectual and emotional, which are the latest products of human evolution" (p. 374).

More recently, a similar perspective can be seen in the literature on the effects of early hormones on the differentiation of both sexual morphology and behav-

ior. Much relatively early literature suggested that the female behavioral pattern was the more basic one and additional action was needed if maleness was to be developed. As noted by Bermant and Davidson (1974) "the rat is born with a potential capacity to manifest both male and female behavioral patterns in adulthood, on exposure to the appropriate hormones. Testicular hormone secreted in the first few days of life suppresses the capacity to manifest the female pattern and develops the capacity for male behavior . . . estrogen is presumed not to play any role, and the female pattern is 'basic'" (p. 195). In essence, then, the female pattern was viewed as the default condition. Male behavior required additional action.

Later studies showed, somewhat paradoxically, that estrogens are important in the masculinization of behavior. In more recent developments, evidence suggesting an active role for ovarian hormones in feminization during development has been uncovered, thus weakening the view of the female phenotype as the "default" condition (e.g., Fitch *et al.*, 1998). The view of females as the "default" condition consistent with "the presence/absence metaphor" in general and Darwin's views of females as less developed than males in particular.

Bateman's work thus fits within this family of lines of research stemming from *The Descent of Man*. One can see similar elements in this family tree of hypotheses regarding differences between the sexes regarding their variability, degree of primitiveness, and susceptibility to sexual selection. The Darwin-Bateman paradigm developed in the context of related developments with similar origins but in other spheres, not in a vacuum.

CONCLUSION

Many of the aspects recent thinking regarding sexual selection that have been attributed to Bateman had their roots in the writings of Charles Darwin; thus, I introduced the term "Darwin-Bateman paradigm." Its core includes the sex difference in variance of reproductive success, the sex difference in benefits to be gained from repeated matings, and the ardent male-coy female hypothesis. However, it was a part of a broader view of the sexes. I have tried to trace the origins of the paradigm, show how it evolved, place it in broad context, and to show that other lines of research appear to have had similar roots.

Bernstein (2003) put it nicely: "it was much easier when I understood Darwin to say that macho males fight each other to claim females, and that the females choose the winners because these will be the best fathers for their sons. It does not seem quite that simple any more . . . there are entirely too many animals that appear to violate that rule" (p. 82).

The Darwin-Bateman paradigm has been of great heuristic value. It probably holds in more cases than it fails. However, given its origins and the significant exceptions to its hypotheses, reevaluation is important. This is likely to yield a perspective that is both more

complex and more comprehensive. I think it likely that when these proposals are seen in their cultural context and when further research is carefully conducted, we may get a very different understanding of males and females.

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