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Forum

Bateman's principles: why biology needs history and philosophy

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My aim in Hoquet (2020) was to examine the fate of Bateman's (1948) paper in a diachronic study. I wanted to provide the readers with an overview of the fate of this important article, presented as a 'paradigm' (Kuhn, 1970). I did this especially through an examination of the citation rates and concluded that, in spite of receiving many theoretical criticisms, Bateman (1948) still exhibits a high level of citations. I was not trying to make a case for or against Bateman (1948), but I presented the major aspects of an ongoing debate that began about 50 years ago (1972 to today). In fact, following Trivers's rediscovery of Bateman in 1972, one of the earliest critiques was by William Sutherland (1985), on purely theoretical grounds. More recent critiques can be interpreted as building on Sutherland's original concerns.

In a comment published as forum discussion (Morimoto, 2020, this issue), Juliano Morimoto expressed some frustration that there were some missing parts in my story: he emphasized the fruitfulness of Bateman's principles and cited many papers that empirically confirmed Bateman's gradients. He concluded that by criticizing Bateman's paper, my historical and philosophical study might eventually be detrimental to the field – especially by depriving field biologists of a useful metric. Bateman, he claimed, got accidentally embroiled with sex stereotypes, but should not be blamed – much less rejected – on this account.

Here I must emphasize that the roots of the discontent are not philosophical, but biological. My analysis does not rely that much on philosophical tools. Apart from a reference to Thomas Kuhn's 'paradigms' as providing a general framework, my analysis was entirely based on the fieldwork and theoretical work of several biologists (e.g. Hrdy, Gowaty, Roughgarden, Wade, Shuster, etc.). I focused on their differing positions. My paper emphasized that there is an ongoing debate *among biologists*. I reviewed some works that have directly addressed this debate, and attempted to present both sides of the ongoing discussion.

<H1>WHAT IS AT STAKE WITH BATEMAN (1948)?

Reference to Bateman is tricky in many ways. The ongoing debate is actually at least two-

levelled, bearing both on Bateman's original 1948 experimental design, and on the broader validity of Bateman's gradients and Bateman's principles.

<H2>(1) *The Validity of Bateman's (1948) Paper*

Alluding to Gowaty et al. (2012), Morimoto (2020, p. e2) claims 'it is almost irrelevant that some studies might have failed to replicate Bateman's original experimental design'. This stance suggests that Bateman's original study and methodology is immune to any kind of refutation, because his 'principles' have been otherwise confirmed since.

Bateman's (1948) paper aimed at showing that the male sex is the one experiencing the most intense form of sexual selection. He did this by different measures. First, Bateman was concerned with variance in the number of mates: 'Statistically speaking, the variance in number of mates is higher in males than in females' (Bateman, 1948, p. 360). But he also considered that while 'the fertility of the males increases steadily with the number of mates [, t]here is a much weaker correlation between fertility of females and number of mates' (Bateman, 1948, pp. 360–361). Here Bateman drew a very thin line, especially when he wrote: 'There is an obvious sex difference, the females not responding so markedly to increases above one in number of mates' (Bateman, 1948, p. 361). The first part of Bateman's sentence emphasized 'an obvious sex difference', while the second part was subtler, noting that the difference is only of degree ('not [...] so markedly').

Bateman's gradients were interpreted as a biological signature of sexual selection. Bateman's aim was to demonstrate that intrafeminine sexual selection was *low* and to explain why polyandry is a rather *uncommon* mating system (Bateman, 1948, p. 352). But he committed a fateful mistake: he chose to emphasize the 'obviousness' of the sex difference and in order to do so, he isolated and aggregated two of his experimental series (series 5 and 6), in order to make 'the difference [...] even more noticeable' (Bateman, 1948, p. 362). This decision has been repeatedly pointed out as a methodological mistake by several biologists (especially Snyder & Gowaty, 2007; Tang-Martínez & Ryder, 2005). Bateman did not have any reason to separate series 1–4 from series 5–6, except that these seemed 'more comparable with one another than with the other series' (Bateman, 1948, p. 362).

Based on this methodological artefact, Bateman drew two different graphs and, discarding the results of series 1–4 (synthesized in graph 1a) he concluded, on the sole base of series 5–6 (synthesized in graph 1b) that ‘the males show direct proportionality between number of mates and fertility’ while ‘the females [...] show *absolutely no effect* of number of mates’ (emphasis added). This methodological fault was especially fateful as graph 1b exhibiting a clear plateau for females would later be cited and reprinted more often in textbooks (Tang-Martínez & Ryder, 2005). For many readers, Bateman had empirically demonstrated that female reproductive success *did not benefit* from mating with more than one male – in other terms: that there was no benefit of polyandry for females. But this was not the case: he had only created an artefact by pulling together data from series 5–6 and building them into a separate graph.

Beside the failed attempt of replication (Gowaty et al., 2012), it is also noteworthy that several populations in Bateman (1948) fail to meet Mendel’s laws – hence showing a strong bias in Bateman’s methodological design (Gowaty et al., 2013). These methodological critiques and the inability to replicate Bateman’s experimental design are not at all dispensable or superfluous. They are a central piece of evidence documenting the progress of biological thinking. Even a recent meta-analysis (Janicke et al., 2016, p. 1) aiming to ‘demonstrate that, across the animal kingdom, sexual selection, as captured by standard Bateman metrics, is indeed stronger in males than in females’ had to paradoxically exclude Bateman’s original study from its pool of candidate studies. The faults in Bateman’s original study must be taken seriously.

<H2>(2) *The Validity of Bateman’s Principles*

The main thrust of Morimoto’s (2020, this issue) critique is that my original paper (Hoquet, 2020) did not cite the increasingly large numbers of empirical papers using Bateman’s gradients as convenient metrics of sex differences. I cited neither the ones with results that support Bateman, nor the ones with results that do not support Bateman. My aim was to capture the fact, that in spite of a host of empirical papers *supporting* Bateman’s principles, there are huge debates within the field not only about the validity of Bateman’s conclusions but also about *the definition of the principles*. It is

precisely this historical debate that I attempted to address, in part because it is informative of scientific debates more generally, and because it illuminates the ways that scientific hypotheses and theories evolve and change over historical time. First of all it should be noted that the definition of ‘Bateman’s principles’ has varied across time (Dewsbury, 2005 ; Gerlach et al., 2012). The term ‘Bateman’s principle’ was originally limited to the claim (1) that ‘the variance among individuals in male reproductive success exceeds the variance among individuals in female reproductive success’ (Wilson et al., 1994, p. 284). Later, Arnold (1994, pp. 126–127) showed that, besides the greater variance of males in offspring number, Bateman’s results generated two other predictions regarding sexual selection: (2) that males should display greater variance than females in number of mates and (3) that the correlation between number of mates and number of offspring should be stronger in males than in females.

Regardless of these distinctions, Morimoto’s comment gives a standard version of Bateman’s principles, or ‘metrics’. Morimoto takes Bateman’s principles to be a measure of the intensity of sexual selection as indicated by higher variance in offspring numbers and higher variance in the number of mates (hence principles 1 and 2). He mentions that more and more additional field studies are produced that seem to confirm ‘Bateman’s principles’. But what if the theoretical analysis is all wrong as Hrdy, Gowaty, Tang-Martínez, Roughgarden and others have argued? To tell the truth, Morimoto’s long list of papers apparently supporting or confirming Bateman’s gradients or principles appears a little bit like ‘white swans’ in the old problem of induction. The phrase ‘all swans are white’ seems sound as long as the idea of anything other than a white swan is preposterous, but one ‘black swan’ is sufficient to refute the old belief. So the right question is not: how many white swans have we found? But rather: what shall we do with the black ones? In other terms: in the face of theoretical debates, what is the value of field studies? A common conception of scientific work is that science is like a town made of a plurality of edifices (laws, explanations), and that its builders (the scientists) have to assemble bricks (facts) in a correct fashion. This view of the nature of scientific work has led to the development of a prosperous industry of brickmaking. But what if the bricks are faulty or badly assembled (Forscher, 1963)? Biologists should be prone to sweep away systems when they are like castles built on sand.

<H1>HOW TO ACHIEVE A CONSENSUS?

Another issue bearing on the validity of Bateman's principles regards what Kant called the 'modality' of statements: are Bateman's principles only *possibly* true, or are they *necessary* laws? I concur with Wilson et al. when they wrote: 'We do not now dispute that Bateman's principle (or something like it) is true *in some cases*, but we are concerned that it is being treated as *generally, or even axiomatically*, true' (1994, p. 284, emphasis added). To avoid the trap of universality, Morimoto mentions that, in Bateman's gradients, the slope is *often* steeper in the sex experiencing stronger sexual selection. But 'often' is a perplexing term as it suggests again that Bateman's gradients, even though they do not always hold up, are almost by definition, impossible to refute: the black swans exist but are discounted because 'often' the swans are white! Bateman himself used the trick of 'almost' when he referred to the greater dependence of males for their fertility on frequency of insemination as being 'in fact *an almost universal attribute* of sexual reproduction' (Bateman, 1948, p. 364, emphasis added).

To achieve robustness, some have claimed that the right method and a clear sign of scientific cogency was 'strong inference' (Platt, 1964). Strong inference argued that careful experiments capable of disproving a hypothesis were important. I am fully aware that the value of this method has been debated (O'Donohue & Buchanan, 2001). However, the important question here, in my opinion, is the question of *disproof*: some possible occurrences (Popper, 1959 spoke of 'basic statements') are ruled out so that we can say that if they happen, the scientific theory is false. In front of any 'brick' (or 'swan'), the right question should be: 'what hypothesis does your experiment *disprove*?' – with a marked emphasis on the '*dis*' (Platt 1964, p. 352).

As we have seen in the case of Bateman (1948), the interpretation of papers can be fraught with complexity and different readers can disagree on what a paper demonstrates. This also applies to more recent literature. Morimoto (2020, p. e1, this issue) mentions that 'there are many studies that do find support for Bateman's principles in a wide variety of species, including in humans'. I will take one example from the ones cited by Morimoto as being in favour of Bateman's principles: Gerlach,

McGlothlin, Parker, and Ketterson (2012). Can this paper be interpreted as supporting Bateman's ideas? It starts with a contrasted appreciation regarding the empirical testing of Bateman's first principle: the authors emphasize that while a number of studies confirm that variance in reproductive success is greater in males than in females, a number of other studies from an equally broad taxonomic distribution have nevertheless found that males and females do **not** differ in variance in reproductive success. Similarly, these authors noted that Bateman's third principle, that the relationship between mating success and offspring number should be strong and positive in males but not in females, has received 'mixed support'. Finally, they concluded (Gerlach et al., 2012, p. 1083) that 'positive Bateman gradients may arise from many other mechanisms' apart from sexual selection acting directly on traits. They suspected that the correlation may be taken too hastily for causation, and they cautioned their readers that 'the extent to which a positive Bateman gradient reveals something about sexual selection may also depend in large part on the life history of the organism in question' (p. 1085). Their analysis is subtle in the way that it does not 'support' Bateman's principles but reflects on what Bateman's gradients actually measure, and how positive slopes can actually be taken as a 'signature of sexual selection'. Thus, Gerlach et al. (2012) is a classic example of the widespread existence of alternative interpretations of the same paper; while Morimoto sees it as supporting traditional Bateman gradients, other authors (e.g. Tang-Martínez, 2016) regard it as persuasively challenging traditional formulations of Bateman gradients.

<H1>SEPARATING BATEMAN FROM SEX STEREOTYPES?

'Bateman's principles' are not an ahistorical entity: they are the product of a controversial history (aspects of which go all the way back to Darwin), and my approach is based on the work and debates that have occurred among biologists precisely about definitions and about the applicability of Bateman's ideas in real animals under different conditions. Morimoto builds a claim that Bateman's principles (and among them, the graphs known as 'gradients') have nothing to do with sex stereotypes. According to his account, 'the scientific appeal of Bateman's principles to the community [is] independent of sex stereotyping' – at least in their actual guise: 'sex stereotypes were not coined by

Bateman himself but instead were linked to Bateman's principles by the interpretation of other individuals' (Morimoto, 2020, p. e1, this issue). In other words, Bateman's principles should not be the innocent victims of 'misuse' – just like, say, Darwin's 'natural selection' should not be confused with another case of 'misuse': 'social Darwinism'. That is, one should cautiously distinguish between 'science' and 'ideology'. I must make several comments on this.

<H2>(1) *Anisogamy and the 'Sexual Cascade' Hypothesis*

The underlying assumption under Bateman's metrics is that animal behaviours are best explained when individuals are divided into two different sets, called 'males' and 'females'. Of course, sex differences and similarities may be measured in many different ways. But supporters of Bateman believe that his views lead to a clear-cut sex divide, namely: 'a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females' (Bateman, 1948, p. 365). More than that, 'anisogamy' or gamete size dimorphism is the ultimate ratio under Bateman's methodology. Geoff Parker (2014) called this 'the sexual cascade' – a phrase that has been taken up by supporters of Bateman's principles (e.g. Janicke et al., 2016). This focus on 'anisogamy' was not imposed on Bateman (1948) by ulterior male chauvinist followers but rather it was unquestionably in the original paper. As mentioned, Bateman focused on eagerness in males and coyness in females: while he believed that these roles were only 'widespread' or 'almost universal', he also stated that they were rooted in anisogamy. He argued for instance that 'the differentiation into male and female gametes is the basis of intramasculine selection' (Bateman, 1948, p. 365). Similarly, a recent meta-analysis confirming 'Darwinian sex roles' across the animal kingdom (Janicke et al., 2016) described a 'sex role syndrome', 'rooted in anisogamy' and cascading into typical sex roles through stronger sexual selection on males. However, their 'Discussion' section is full of caveats: 'Although the here-depicted 'sex role syndrome' appears *generally* valid for the animal kingdom, there are *many exceptions* emphasizing that the realized sex biases in sexual selection can still diverge from the primordial contribution of anisogamy' (Janicke et al., 2016, p. 4, emphasis added).

<H2>(2) *Sex Roles, Reversed or Not*

A major break was introduced on this point by R. Trivers, when species with sex-role reversals were accommodated into the behavioural framework. This is a crucial fact as it demonstrated that anisogamy is not the only factor that determines a species' mating system or sexual behaviours. On this account, Morimoto is absolutely correct that, under the conditions of Jones et al. 's experiments (e.g. Jones et al., 2000 ; Jones et al., 2005), the sex-role-reversed pipefish *Syngnathus typhle* conforms closely to Bateman's predictions. But, it should always be kept in mind that sex roles are plastic. For instance, in *S. typhle*, Berglund, Widemo, and Rosenqvist (2005) found that depending on environmental and demographic conditions, both males and females can be choosy and competitive. Consequently, they suggested that sex roles involve males and females being able to show both choosy and competitive behaviours in different combinations under different conditions. Although this was *not excluded* by Bateman's findings, it must be acknowledged that Bateman largely discounted the importance of these cases. He rather focused on explaining the rarity of those cases.

Let us now consider Fritzsche and Arnqvist's (2013) study appropriately called 'Homage to Bateman'. They looked at Bateman gradients in conventional and sex-role-reversed species of seed beetles. For the most part, the results were highly consistent with Bateman's predictions as far as the females were concerned. However, males in sex-role-reversed species had steeper gradients than females, a result that is contrary to Bateman's predictions. The overall results, although usually lauded as strongly confirmatory of Bateman (1948), actually offer only partial support for Bateman's formulations. That is, results for the males do not correspond to the expected pattern.

These examples demonstrate the complexity of the predictions and of nature when one considers all relevant factors. And I think they show the difficulties that can happen in the interpretation of results. That is, these examples also show how different observers can interpret the same results in different lights and arrive at different conclusions.

<H2>(3) *Revising Bateman's Principles*

To salvage Bateman's principles from the fact that there are so many species that depart from the 'sex role syndrome' and that the 'sexual cascade' does not universally or deterministically proceed from anisogamy to sex roles, some authors have strived to distinguish two different premises in Bateman (1948) (Wade & Shuster, 2005): (1) due to anisogamy, sexual selection favours increased promiscuity of males but not of females; (2) the male variance in mate number is the fundamental cause of a sex difference in fitness variance, with males having greater variance than females.

By presenting these two premises as different, Wade and Shuster (2005) attempted to argue that, while Bateman may have been incorrect about rooting typical sex roles in anisogamy, he was, nevertheless, correct about intrasexual selection acting mostly on males. Others, such as De Lisle (2019), tried to integrate models focusing on differences originating from anisogamy ('the Darwin-Bateman paradigm') and other models 'agnostic of anisogamy'. Morimoto concurs in the conclusion that (1) arguments based on anisogamy were mere 'speculation about patterns of parental investment' (Wade & Shuster, 2005, p. 945) and he widens the second claim stating that (2) variance in offspring production and variance in the number of mates are clear signs of 'the sex' (be it 'males' or 'females') experiencing stronger sexual selection. Even if Bateman's gradients have been broadened and reworked in order to accommodate species with sex-role reversal and the benefits for females of polyandry, two hypotheses are always lurking in the background, as a potential root for 'typical' sex roles : anisogamy and the 'sexual cascade'. On this account, it should be noted that several biological theoreticians promoted the use of gender-neutral assumptions in the study of individual animal behaviours (Ah-King & Nylin, 2010 ; Gowaty & Hubbell, 2005, 2009). The basic assumption here is that because of social and ecological constraints, 'it is unlikely that focal individuals actually mate with all potential mates who are acceptable to them' (Gowaty & Hubbell, 2009, p. 10020); in other words, all individuals, regardless of sex, 'may change their behavior – from moment to moment – to fit dynamically changing circumstances (Gowaty & Hubbell, 2005, p. 931; see also Ah-King, 2011).

Finally I want to emphasize that, as the understanding of differences between the sexes is a transdisciplinary issue, the evaluation of Bateman's gradients is not restricted to biology but also includes psychology and medicine. Bateman constantly combined claims to universality with adverbs restricting the validity of his claims: he wrote that his predictions were '*almost universal*' and he thought that in 'unisexual' (i.e. gonochoric) organisms, 'there is *nearly always* a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females' (Bateman, 1948, p. 365, emphasis added). He also extended this result to humans: 'even in derived monogamous species (e.g. man) this sex difference might be expected to persist as a relic' (Bateman, 1948, p. 365). What is left of a behavioural trait when it 'persist[s] as a relic'?

Anisogamy or dimorphism in gamete size is an important fact as it forms a functional sex binary between males and females (Hoquet 2016). However, as Roughgarden (2009, p. 26) put it: 'The biggest error of biology today is uncritically assuming that the gamete size binary implies a corresponding binary in body type, behavior, and life history. No binary governs the whole individuals who make gametes'. In real organisms, anisogamy is not the sole element relevant to defining sex. For instance, in humans, chromosomes, hormones, internal sex organs and genitalia are also important constituents of the sex of an individual – and these various elements are not always necessarily concordant with one another. And, in this regard, several intersex conditions challenge the dualistic presentation of the sexes (Fausto-Sterling, 2000). This allowed developmental biologist Fausto-Sterling (1993) to claim that 'Male and Female are not enough'.

In summary, in Hoquet (2020), acting as a historian and an observer of science, I collected and presented the disagreements in the field, among *scientists* – and I did this because I believe it helps scientists to understand how science works and evolves. Science progresses through the questioning of accepted ideas – and a healthy science should welcome respectful debates. Readers may remember that in his 1795 *Philosophy in the Bedroom* (*La philosophie dans le boudoir*), the Marquis de Sade included a lengthy philosophical pamphlet called: 'Frenchmen, Some More Effort If You Wish To Become Republicans'. Happily plagiarizing his statement, my final words could be: 'Biologists, Some More Effort If You Wish To Understand Behaviors!'

The so-called ‘science wars’ that pitted scientists against philosophers/historians are, I hope, a thing of the past. A recent paper (published in *Proceedings of the National Academy of Sciences*) that explains ‘why science needs philosophy’ (Laplane et al., 2019, p. 3948) quotes Einstein: ‘A knowledge of the historic and philosophical background gives that kind of independence from prejudices of [their] generation from which most scientists are suffering. This independence created by philosophical insight is – in my opinion – the mark of distinction between a mere artisan or specialist and a real seeker after truth’. Within this framework, I hope my work can contribute to the progress of biology, in the wake of what Einstein suggested.

I take this opportunity to correct an error in Hoquet (2020). Although Robert Trivers was very close to Irven DeVore, and even co-taught some of his courses, he was never officially DeVore’s graduate student. Trivers’s thesis was on the behaviour of anolis lizards in Jamaica and his advisor was the herpetologist Ernest Williams (1914–1998) in the Department of Organismic and Evolutionary Biology at Harvard.

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