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## COMMENTS

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### CRITERIA FOR DEMONSTRATING POSTCOPULATORY FEMALE CHOICE

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The recent discussion of Birkhead (1998) may cause confusion regarding the nature of cryptic female choice and how to test for its occurrence. Here I attempt to (1) clarify the distinction between cryptic female choice and “sperm choice,” the primary focus of Birkhead’s discussion; (2) present more appropriate criteria for demonstrating cryptic female choice; (3) describe errors resulting from an either-or approach to male and female effects on sperm usage; and (4) discuss the usefulness of the kinds of indirect evidence that are often crucial in testing evolutionary hypotheses. I will treat each of these points in turn.

#### *Inconsistent Use of Terms*

Although the term cryptic female choice appears in Birkhead’s title, most of the text is dedicated to discussing what he calls “sperm choice.” Unfortunately he uses this term inconsistently. At first, Birkhead defines sperm choice broadly, as “the postcopulatory ability of females to favor the sperm of one conspecific male over another, that is, sperm choice” (his abstract), a definition that would seem to make sperm choice synonymous with “cryptic female choice” sensu Thornhill (1983) and Eberhard (1985, 1996) (I will assume throughout, as has been customary in previous discussions, that “postcopulatory” refers to events following initiation of copulation, and thus includes processes that occur during as well as following copulation). Overlap between sperm choice and cryptic female choice is emphasized in Birkhead’s first paragraph, where he claims that sperm choice is “a necessary component of postcopulatory female choice.” But then later Birkhead uses a much narrower definition of sperm choice that includes only a subset of the ways in which females may be able to bias paternity after copulation has begun: “The simultaneous recognition of and discrimination between sperm of different males, either on the basis of the males’ phenotype or that of their sperm constitutes sperm choice and is the focus of this review” (p. 1213). This results in his proposing very narrow criteria for demonstrating what is usually treated as a broader phenomenon. Finally, Birkhead returns in his discussion to the broader definition in apparently equating sperm choice with cryptic female choice (p. 1217), which implies (misleadingly) that the same narrow criteria apply to both.

The narrow definition of sperm choice is incompatible with the broader definition because “simultaneous recognition of and discrimination between sperm of different males” is in no way necessary for many of the female processes that can

affect the “postcopulatory ability of females to favor the sperm of one conspecific male over another.” These additional processes (which are summarized with lists of concrete examples in Eberhard 1996) include, among others, refraining from discarding the current male’s sperm from her body, allowing intromission or spermatophore attachment to last long enough for maximal amounts of sperm and other seminal products to be transferred, discarding or digesting sperm from previous copulations, transporting sperm stored from previous copulations to sites where the current male can remove or otherwise inactivate them, failing to reject subsequent sexual advances of other males, allowing larger or smaller amounts of sperm from future copulations to be transferred and to be retained, rapidly maturing immature eggs, ovulating, and promptly ovipositing following copulation. (This last was the context in which the phrase “cryptic female choice” was first used [Thornhill 1983]). These processes can all have direct effects on sperm. A female that fails to ovulate within the survival period of sperm in her reproductive tract will have killed those sperm just as surely as if she flooded them with phagocytes. Birkhead mentions the existence of some of these processes and states that their effects on paternity appear “to be well established” (p. 1213). But he seems not to have realized that they too can affect the “postcopulatory ability of females to favor the sperm of one conspecific male over another” that he was attempting to evaluate.

The effect of this switching between broad and narrow definitions of sperm choice confuses the issue of establishing criteria for demonstrating postcopulatory female choice in general, as Birkhead claims to have done in his title and abstract. Birkhead was discussing criteria for a certain restricted subset of female mechanisms, not for postcopulatory female choice in general, as he implies. Birkhead’s criteria are thus inappropriate for evaluating the existence of cryptic female choice in the wide sense in which this phrase has been used by other authors since its invention (e.g., Thornhill 1983; Eberhard 1985, 1996; Sakaluk and Eggert 1996; Dickinson 1997; Peretti 1997; Telford and Jennions 1998; Johnson et al. 1999; Tadler 2000).

#### *Mistaken Criteria*

Even if one uses Birkhead’s narrow definition of sperm choice, his discussion of criteria is overly restrictive for two reasons. He emphasizes that unless the effects of sperm competition are controlled for, sperm choice cannot be demonstrated (e.g., p. 1213), and he proposes particular experi-

mental protocols in which such controls are included. But several female processes that can be influential after copulation has begun are not likely to be confused with competition among sperm if one observes animals directly. These include sperm dumping, interruption of copulation before maximum numbers of sperm are transferred, production by the female of physical plugs that promote retention of the sperm of the current male or prevent access of sperm from subsequent males to her reproductive tract, and female removal or degradation of such plugs (for concrete illustrations and references, see Eberhard 1996; Eberhard and Huber 1998). Thus Birkhead's criteria and the experimental protocols he proposes are inappropriate for testing the existence of several possible mechanisms of sperm choice, even in its *sensu strictu* meaning. In many cases research on other topics, such as functional morphology, may be more useful in resolving doubts. A concrete example comes from the yellow dung fly, *Scathophaga stercoraria*, which Birkhead judged not to be a convincing case for female effects. Recent morphological data, however, have provided strong evidence for a female postcopulatory role in sperm usage that has proven persuasive even to former skeptics (Simmons et al. 1999; for further recent evidence supporting this female role in *S. stercoraria*, see Otronen et al. 1997; Hosken and Ward 2000). The question of whether females systematically bias their effects in favor of particular types of males is still under investigation (Eberhard 1996; Ward 1998; Parker et al. 1999).

Second, Birkhead argues that in order to demonstrate postcopulatory female effects on sperm usage, one must demonstrate a significant effect on sperm usage patterns ( $P_2$  values) that is due to differences among females. This criterion reduces to the unconvincing proposition that female effects are only important if there is variation in choice among females. For instance, if all pea hens have an equally strong preference for males with long tails, is one to conclude that there is no female choice on tail length (see Jennions and Petrie 2000)? A more reasonable position is that demonstration that the differences among females affect  $P_2$  values is indeed evidence of a female effect (e.g., Price 1997; Wilson et al. 1997), but that such a demonstration is not a necessary condition for concluding that a female bias occurs.

A hypothetical experiment of a type proposed by Birkhead can serve to illustrate in more detail the inadequacy of the female variation criterion. Let us say that known numbers of sperm from two males (say 50% from male A and 50% from male B) were artificially introduced into a series of 10 females (a technique cited by Birkhead as appropriate to control for sperm competition effects in the search for female choice effects), and that male A fathered exactly 80% of the offspring of each of the females. Setting aside for the moment the fact that this experimental procedure is woefully inadequate to test for possible female-imposed biases (it eliminates most or all of the stimuli normally associated with copulation that might trigger differences in female responses such as differential transport, ovulation, etc.), what should one conclude? There is no variance in  $P_2$  attributable to females, so the conclusion, using Birkhead's criteria, is that sperm choice is not occurring; the pattern of sperm use in this species is apparently to be explained by sperm competition (assuming

there is no biased abortion). The sperm of male A are better at fertilizing eggs than are the sperm of male B.

But this is only a partial answer to the question of why the males and females of this species have the traits that they do. The competition between sperm occurs in a female environment, and it is likely that the degree of superiority of male A's sperm is influenced by their interactions with and adjustments to many different female-determined conditions. If, for instance, the female ducts are long and transport time to storage or fertilization sites is long, then long-lived sperm that could swim long distances might be favored over short-lived sprinters. A conservative list of other such female traits that could influence the outcome of sperm competition *sensu strictu* and that are known to occur in nature (for examples and references, see Eberhard 1996; Gomendio et al. 1998) includes the viscosity of the contents of the female's reproductive tract, the pH of the contents, the direction in which these contents flow, the temperature, the presence or absence of materials in the tract that adhere to sperm and slow their movements, nutrients, cells such as phagocytes that can kill sperm, sperm activating factors, folds or cracks where sperm can shelter, contractions of the ducts that facilitate (or inhibit) transport, and the properties of the egg membrane and the materials surrounding it that affect the sperm's motility and ability to adhere. Sperm that are competitively superior in one environment are unlikely to be superior in all others. Changes in these female-imposed environmental conditions, whether induced by the male or whether occurring in past or future evolutionary time, could change the outcome of competition between sperm from males A and B. Indeed, female-imposed bias in the past is a likely explanation for the traits currently found in the sperm of male A. Wiley and Poston (1996) made a similar point regarding the inevitable female influence on eventual winners in the context of precopulatory competition among males. For instance, male-male battles at leks will only have reproductive consequences for the males if females behave in particular ways: if they visit leks, and if they allow males to copulate with them there and not elsewhere.

*It Takes Two to Tango: A Misleading Dichotomy between Sperm Competition and Female Choice*

This last point can be placed in a more general context. Birkhead's line of reasoning is that "the most plausible way to demonstrate the occurrence of female sperm choice is to control for both differential abortion and sperm competition" (p. 1213). He mentions that different combinations of sperm competition via sperm interactions and female sperm choice can occur (p. 1213), but the implication of this type of analysis is that male effects can occur in the absence of female effects, and vice versa. Neither extreme is possible, however; sperm competition *sensu strictu* is between male products that are inside the female's body. Its outcome must always depend on interactions between the sperm and the female environment in which they find themselves. If one type of sperm wins out, it is because that type is better adjusted to perform under the particular conditions present in conspecific females (e.g., Eady 2000). In an analogy with sporting events, the male competition occurs on playing fields whose characteristics are determined by females. A common temptation has been to treat a female's traits as an unstudied "given"

when discussing interactions among ejaculates, and to neglect to ask why it is that she has one particular set of traits instead of another.

This problem of an either-or approach is exemplified in Birkhead's criticism of the possibility that female sperm choice occurs in the beetle *Chelymormpha alternans* based on the length of the male's long thin genitalic flagellum. He cites the alternative explanation that "males with a longer flagellum may simply be more efficient at getting their sperm to the best place to achieve fertilization" (p. 1214). However, females of this beetle have a very long, highly convoluted and complex spermathecal duct, thus Birkhead's proposal is not an alternative, but rather a statement regarding payoffs for different male behavioral and morphological strategies once the female has set the playing field (in this case the tortuous female duct).

Questions about which sex controls processes that result in differences in paternity will have different answers, depending on the level of analysis (Eberhard 1998). Differences in the lengths of male organs in *C. alternans* and presumably their ability to deposit sperm at particular sites in the female do explain some of the variance in paternity in this beetle. At a deeper level, the reason why the lengths of male organs affect paternity this way can be explained by the details of the design of the female. Another recent example emphasizes the interactive nature of male and female effects in the now classic context of sperm removal by male damselflies. In at least some species, the male's chances of removing the sperm of previous males are influenced by female ejection of sperm from deep within her spermatheca where his genitalia cannot reach, and this ejection is, in turn, influenced by male copulatory stimulation of the female (Cordoba-Aguilar 1999). Female traits lurk behind many explanations based on male traits and, of course, vice versa. An "either-or" approach is not appropriate for studying male and female traits involved in sexual interactions. By setting up a contrast between sperm competition and postcopulatory female choice, Birkhead focuses attention in a way that tends to perpetuate this kind of erroneous dichotomy.

#### What Constitutes "Sound" Evidence?

A final point of difference concerns the scientific value of different types of data. Birkhead's use of the loaded phrase "sound evidence" (p. 1212) in introducing his criteria implies that other types of evidence presented previously regarding cryptic female choice (e.g., ch. 5–7 of Eberhard 1996, where predictions of general patterns derived from theoretical considerations are checked against the data from many different groups) are somehow "unsound," and implies that a phenomenon is of dubious importance unless one has directly observed or demonstrated experimentally that it occurs at present. But one need not blow up the side of a mountain experimentally to deduce that landslides are powerful forces of nature: the importance of landslides can also be deduced from observing their consequences. It is worth remembering that in *The Origin of Species*, Darwin did not directly "demonstrate" the creation of a single species, nor did he experimentally prove that natural selection caused changes in any given species. Rather he amassed data and compared their

patterns with the expected consequences of evolution by natural selection. Darwin's technique of checking predictions of hypotheses against general trends in biological data continues to be valid (e.g., Brandon 1996), and arguments derived from this technique should not be ignored unless one presents direct, specific demonstrations of errors of fact or interpretation. This does not mean that experimental studies of sperm precedence will not be useful for understanding phenomena related to sperm usage—they are likely to be fascinating. But this is not the only type of test that is useful and, as shown above, incautious interpretation of such data can even lead to serious mistakes in evaluating the importance of postcopulatory or cryptic female choice.

In summary, Birkhead's inconsistent use of the term sperm choice led him to draw inappropriately general conclusions regarding postcopulatory female choice on the basis of data related to only a narrow range of possible female effects. These conclusions are not appropriately applied to the more general interpretation of cryptic female choice that has been used throughout the history of this term, as implied in his title. Birkhead's statement (his first paragraph) that sperm choice is "a necessary component of postcopulatory female choice" is simply wrong, no matter which of his definitions is used, because it fails to take into account many postcopulatory female processes. By presenting sperm competition and sperm choice as "alternatives," Birkhead confused the issues of the evolution of male and female effects on paternity and how they can be established. Differences among females are not necessary for female choice to occur, as his criteria imply. Because fertilization results from an *interaction* between the two sexes, the effects of both sexes are inextricably interrelated, and female traits are not appropriately taken as static "givens" in these interactions. Birkhead is correct in proposing that further studies of the mechanisms determining sperm usage promise to provide interesting and exciting results, but his position that direct observation of current biases are necessary to provide "sound" evidence for the existence of postcopulatory female choice is unjustified.

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#### LITERATURE CITED

- Birkhead, T. R. 1998. Cryptic female choice: criteria for establishing female sperm choice. *Evolution* 52:1212–1218.
- Brandon, R. N. 1996. *Concepts and methods in evolutionary biology*. Cambridge Univ. Press, Cambridge, U.K.
- Cordoba-Aguilar, A. 1999. Male copulatory sensory stimulation induces female ejection of rival sperm in a damselfly. *Proc. R. Soc. Lond. B* 266:779–784.
- Dickinson, J. 1997. Multiple mating, sperm competition, and cryptic female choice in leaf beetles (Coleoptera: Chrysomelidae). Pp. 164–183 in J. Choe and B. Crespi, eds. *The evolution of mating systems in insects and arachnids*. Cambridge Univ. Press, Cambridge, U.K.
- Eady, P. E. 2000. Sperm competition, sperm selection and speciation. *J. Zool.* *In press*.
- Eberhard, W. G. 1985. *Sexual selection and animal genitalia*. Harvard Univ. Press, Cambridge, MA.

- . 1996. Female control: sexual selection by cryptic female choice. Princeton Univ. Press, Princeton, NJ.
- . 1998. Female roles in sperm competition. Pp. 91–116 in T. R. Birkhead and A. P. Møller, eds. Sperm competition and sexual selection. Academic Press, New York.
- Eberhard, W. G., and B. A. Huber. 1998. Courtship, copulation, and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. *J. Arachnol.* 26: 342–368.
- Gomendio, M., A. H. Harcourt, and E. R. S. Roldán. 1998. Sperm competition in mammals. Pp. 667–755 in T. R. Birkhead and A. P. Møller, eds., Sperm competition and sexual selection. Academic Press, New York.
- Hosken, D. J., and P. I. Ward. 2000. Copula in yellow dung flies (*Scathophaga stercoraria*): investigating sperm competition models by direct observation. *J. Insect. Physiol.* *In press.*
- Jennions, M., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* *In press.*
- Johnson, J. C., T. M. Ivy, and S. K. Sakaluk. 1999. Female mating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans*: a mechanism of cryptic female choice. *Behav. Ecol.* 10:227–233.
- Otronen, M., P. Reguera, and P. I. Ward. 1997. Sperm storage in the yellow dung fly *Scathophaga stercoraria*: identifying the sperm of competing males in separate female spermathecae. *Ethology* 103:844–854.
- Parker, G. A., L. W. Simmons, P. Stockley, D. M. McChristie, and E. L. Charnov. 1999. Optimal copula duration in yellow dung flies: effects of female size and egg content. *Anim. Behav.* 57: 793–805.
- Peretti, A. V. 1997. Evidencia de cortejo copulatório en el orden Scorpiones (Arachnida), con un análisis en *Zabius fuscus* (Buthidae). *Rev. Soc. Entomol. Argent.* 56:21–30.
- Price, C. S. C. 1997. Conspecific sperm precedence in *Drosophila*. *Nature* 388:663–666.
- Sakaluk, S., and A.-K. Eggert. 1996. Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. *Evolution* 50:694–703.
- Simmons, L. W., G. A. Parker, and P. Stockley. 1999. Sperm displacement in the yellow dung fly, *Scathophaga stercoraria*: an investigation of male and female processes. *Am. Nat.* 153: 302–314.
- Tadler, A. 2000. Selection of a conspicuous male genitalic trait in the seedbug *Lygaeus simulans*. *Proc. R. Soc. Lond. Ser. B.* *In press.*
- Telford, S., and M. Jennions. 1998. Establishing cryptic female choice in animals. *Trends Ecol. Evol.* 13:216–217.
- Thornhill, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am. Nat.* 122:765–788.
- Ward, P. I. 1998. A possible explanation for cryptic female choice in the yellow dung fly, *Scathophaga stercoraria* (L.). *Ethology* 104:97–110.
- Wiley, R. H., and J. Poston. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* 50: 1371–1381.
- Wilson, N., S. C. Tubman, P. E. Eady, and G. W. Robertson. 1997. Female genotype affects male success in sperm competition. *Proc. R. Soc. Lond. Ser. B* 264:1491–1495.

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## DISTINGUISHING BETWEEN FEMALE SPERM CHOICE VERSUS MALE SPERM COMPETITION: A COMMENT ON BIRKHEAD

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Sperm competition has received a lot of attention from behavioral ecologists in the past decade (Birkhead and Møller 1998). In the strict sense, it can be defined as the competition among spermatozoa from different males for the fertilization of a set of ova (Parker 1970). Sperm competition can thus be seen as the postcopulatory form of competition among males for access to females and might therefore be an important mechanism for sexual selection (Andersson 1994; Møller 1998). Although there is obviously a lot at stake for males (in terms of reproductive success), it has become clear that females also play an important role. Female behavior and reproductive physiology are shaped by selection to reduce the fitness costs to females of male adaptations to sperm competition (Rice 1996) and to increase the benefits of having eggs fertilized by particular males (Keller and Reeve 1995). Among evolutionary biologists, interest arose in the possibility that females can exert postcopulatory choice on who

fathers their offspring (e.g., Eberhard 1996). If sperm competition occurs, that is, if sperm from different males is present within the female reproductive tract, females might be able to discriminate between and differentially utilize the sperm of different males, a process referred to as “sperm choice” (Birkhead 1998; Olsson et al. 1999). Just as competition among males for access to females is more obvious than subtle female choice for a particular male, sperm competition seems more obvious and easier to study than female sperm choice.

Birkhead (1998) proposes that three criteria need to be fulfilled to unequivocally demonstrate female sperm choice and he describes the types of experiments needed. This is an important contribution, because—as Birkhead’s review of studies shows—the current evidence for sperm choice is limited and a clarification of the criteria needed to demonstrate it is clearly valuable. However, we believe that the proposed