

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-