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Letter

Cryptic Female Choice Revisited: A Response to Firman *et al.*

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The timely and welcome overview of cryptic female choice (CFC) by Firman *et al.* [1] will help guide future research. But their conclusion that CFC has 'seldom . . . been clearly demonstrated' may be at least partially due to their strong focus on sperm usage to test for CFC and on studies of vertebrates and *Drosophila* (cf. the recent review [2] of CFC in other arthropods). CFC can involve many intermediate mechanisms that affect eventual sperm usage, such as: morphogenesis, which determines the biases of the female 'playing fields' for male–male competition [3]; short-term effects on oviposition, as in a soldier fly in which male copulatory courtship induces females to oviposit more promptly and results in greater paternity [4]; and female cooperation in the deposition and removal of sperm plugs that affect the female's chances of remating (as well as male survival) [5]. It is true that technical difficulties have plagued many attempts to document CFC [1], but a few complementary ideas can help ease these problems.

Arthropods present important advantages for CFC studies. For example, experimental manipulations of portions of the male's body that are specialized to contact the female in sexual interactions (including both genitalic and non-genitalic 'contact courtship' structures) are especially easy in many arthropods; these traits tend to diverge especially rapidly and are thus probably often under sexual selection [6]. Importantly, because these structures presumably often stimulate the female via tactile stimulation on her external surface, especially powerful experimental tests for selection by CFC on these male structures (including male genital structures that remain on the female's outer surface during copulation) can combine experimental blocking or inactivation of female touch receptors with modification of the male structure itself. Because the tactile stimulation provided by male contact courtship structures is highly localized, experimental modifications of female receptors can also be highly localized, leaving her otherwise largely unaffected [7].

Experimental manipulations of males and females in these ways can help overcome several of the problems mentioned by [1], including difficulty in observing key events that occur hidden within the female, incidental correlations with other traits, and the difficulty of disentangling male and female effects. They also make it feasible to make strong tests for CFC even in the absence of data on difficult variables such as sperm velocity (of dubious significance in any case, especially when measured outside the female reproductive tract) and male and female genotypes (Box 1).

Another powerful technique particularly accessible in arthropods is to use the tendency for male traits under sexual selection by CFC to diverge rapidly [6] as a guide to distinguish which male traits may be important in CFC. Or, if a particular male trait is suspected to be important, one can check for divergence in close relatives to confirm that the trait has indeed probably been under sexual selection. Checks of this sort are often feasible in arthropods, because male genitalia and contact courtship structures have traditionally been used by taxonomists to distinguish closely related species.

The details of male and female behavior during copulation, including the extremely widespread male courtship behavior during copulation and its positive effects on male reproduction [4,8] and copulatory dialogs [9], were not emphasized by [1] but can provide additional useful information. One test of hypotheses regarding particular male traits (morphological or otherwise) being under CFC is to ascertain whether it is feasible for the female to sense them during sexual interactions. A further check is whether the male's behavior is appropriate to emphasize the stimulation the female receives from this trait. During copulation in tsetse flies, for instance, there are sustained, powerful, rhythmic squeezing movements by the male genitalia on the female's outer surface and similarly sustained, highly patterned, and forceful thrusting movements inside her body (with no likely functions in sperm transfer *per se*) [7]. Doubts [1] concerning male rather than female control of cloaca pecking in dunnocks are reduced by noting the behavioral context of sperm ejection [10]: the female is not coerced, but stands in front of the male and actively displays her cloaca to be pecked [11].

In sum, assessments of CFC can benefit from including data on morphology, taxonomy, and behavior and studies of

Box 1. Trends in the Review

The Firman *et al.* review [1] revealed two interesting trends. The first was the rarity of studies documenting Fisherian payoffs to females when they exercised choice (one of 14 payoffs mentioned for only one of 22 species), despite expectations that such payoffs are common [6]. This trend is probably related to the technical difficulty of demonstrating Fisherian payoffs and to the current unfortunate bias among students of sexual selection in favoring hypotheses that involve natural selection [12]. Second, although genitalia were emphasized in CFC studies from the outset [5], the review [1] indicates that CFC on male genitalia is virtually absent (one of the 22 species mentioned above). Genitalia were related to only one (penises in ducks) of 31 male traits mentioned in the text, which included male relatedness with the female (a trait not likely to be under sexual selection), and ten traits of sperm and seminal fluid. This bias may be due to the review's emphasis on sperm and vertebrates: genitalia figured prominently in 11 of the 15 data chapters in the arthropod book on CFC [2].

arthropods can facilitate understanding CFC in several ways, providing more opportunities to reject CFC hypotheses and making critical tests more convincing.

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