Female Sneak Copulation

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Synonyms

Sneaky mating; Undetected extra-pair copulation

Definition

Undetected copulation with the partner of another female or in defiance of the dominant female; often punished if detected.

Introduction

A female sits with her partner, or with a dominant male. She is able to reproduce and benefits due to her partner's parental care and protection. Another female – of low rank, in a female-driven dominance hierarchy – has failed to find a partner and has yet to mate. In both cases, the females can increase their reproductive fitness by mating with an additional male (or with additional males) or by mating for the first time. But in order to do so, each must overcome various forms of resistance. In the first case, the partner of the female, or the dominant male, will not want her to "cheat" on him. Likewise, the partners of her additional mates will not want "their" males to cheat on them. Finally, in the case of the low-rank female, the dominant female will not want her to win over reproductive access, because this could lead to a dilution of the benefits that she receives both in terms of parental care and protection.

Here then is the basis for two broad forms of female sneak copulation (FSC). One is based on a female's attempt to "have her cake and eat it," in which a female tries to obtain the benefits of additional mates – such as additional parental care or genetically diverse offspring – while also attempting to avoid the costs of discovery, which are likely to result in lower parental investment by her partner or even physical punishment. Another arises when a female attempts to break rank, to the same end but with similar risks. Yet cut across these two forms is another division. In the first case, the punishment (i.e., fitness loss) is meted out not only by the male partner but also by the *female* partners of her additional mates. In the second, punishment is administered by the dominant *female*. The rest of this section focuses on these female-female interactions linked to female sneak copulation (FSC), where a female tries to ensure additional, secretive reproduction, in defiance of other females.

The Lay of the Land

Many aspects of the female-female contest for copulation are understudied, and the same is true of FSC (Neff and Svensson 2013). Indeed, there is practically no direct evidence on this topic at all. Nonetheless, it is plausible that FSC could be common. And if so, it could well have been important in evolution of animal behavior, cognition, and psychology, and maybe in particular in humans. Given the dearth of direct evidence, the approach taken here is to first provide an overview of the evolutionary requirements of FSC. This is followed by a brief review of the direct and indirect evidence in favor of each form of FSC (in relation to the partners of other males and in defiance of dominant females). A discussion of the behavioral mechanisms that could facilitate the operation of FSC in nature is then provided, along with a discussion of the relevance of FSC to human evolution. A conclusion is then provided that looks to the future, at the questions that remain to be addressed.

Female Multiple Mating (FMM)

FSC requires that there are benefits to female multiple mating. In males, multiple mating is expected to arise due to the linear relation between the number of matings that a male secures and a male's total paternity. Just such a relationship was found in Bateman's classic study on the fruit fly, *Drosophila melanogaster* (Bateman 1948). In contrast, females have been viewed as the limited sex, with fitness being determined by reproductive output rather than the mating rate. Yet even in 1948, Bateman was able to find evidence that females increased their reproductive success with the addition of extra mates. Moreover, females have been observed to mate multiple times with multiple partners in multiple species across multiple taxa. Ascribing this all to male activity with the implication that the female is just a passive vehicle now seems absurd (Trivers 1972), and recent work has rightly rejected this simplistic dichotomy. Multiple mating is as much a female mating strategy arising from female action as it is a male mating strategy based on male action.

But why do females mate multiple times? The act of copulation is associated with a number of costs (Jennions and Petrie 2000; Forstmeier et al. 2014). Copulation itself can be associated with direct damage to the female reproductive tract, for example, in species where the male penis carries spines, or it may simply use up a crucial resource – time. Likewise, precopulatory behavior can injure females. Postcopula, there are further risks resulting from the transmission of sexual diseases by multiple mating, while female longevity has been shown to decline due to the transfer of male-derived ejaculate products that raise a male's paternity at the costs of female survival. Mixed ejaculates are also associated with increased risk of embryo mortality via polyspermy. And there may be additional dangers if predation risk is increased in copula (or if a female suffers costs due to attacks by her partner or by other females). Given this, there must be clear benefits to FMM.

The most obvious direct benefits arise when the female herself benefits from mating, because the male provides a nuptial gift, such that more mating results in greater resource acquisition. Another example is the increased parental care that a female can obtain if she mates with more males, as a larger number of males will have a stake in her brood. Mating may also cause a reduction in male harassment or a decrease in the risk of male-driven infanticide. A final – special – example is that of fertility assurance. Females may become sperm limited in situations where some males have reduced fertility, where males invest few sperm per copulation (due to the partitioning of their resources across multiple females), or where there are limits to the length of time sperm remain viable. All of these benefits provide reasons for females to mate multiple times: to accrue benefits to themselves in terms of resources or to ensure all of their eggs are fertilized (Jennions and Petrie 2000).

In addition to these direct benefits to the female, females can obtain indirect genetic benefits to their offspring via multiple mating. A female can mate with a more ornamented male to obtain "attractiveness genes" (in so far as the male ornament is preferred by other females) or "viability genes" (where ornament size correlates with male genetic quality). A female can thus trade up genetically by multiple mating if she mated first with a low attractiveness or low genetic quality male. In other cases "compatible genes" will be more important. Here, multiple mating can open up postcopulatory mechanisms that can select for compatibility (based on relatedness, MHC complexes, selfish element suppressors; Forstmeier et al. 2014). Alternately, multiple mating can be a simple bet-hedging strategy to increase the genetic diversity of a female’s offspring. In this case, multiple mating can either compensate for nonperfect female choice or increase the chances that some offspring fit their environment (Fox and Rauter 2003). As a final indirect genetic benefit, it is notable that, postcopula, “cryptic female choice” and “male sperm competition” are enabled by multiple mating and may simply select for sons that are good at fertilization – as such sons will inherit their father’s more competitive sperm.

Extra-Pair Copulation and FSC

As seen above, there are various benefits to multiple mating that are necessary for FSC. However, FSC also requires that multiple mating takes place in a social context. It is not possible to “sneak” in isolation. A simple social context is the monogamous pair bond. Here, a female is joined in a social pair with a male, and they jointly raise their offspring. However, the benefits of female multiple mating remain in this monogamous context. This can lead to selection for female alternate mating strategies, such as extra-pair copulation (EPC), as well as FSC, which is in this context a subclass of EPC.

EPC arises when a male or female mates with an individual other than their partner. It can be driven by males or females. Males can force females to mate with them in the face of true female resistance (forced copulation, coercion) or females may solicit males to mate with them (Griffith 2007; active female solicitation). Usually the interaction between the sexes reveals that males search and display to females and that the females passively accept such advances, or put up a threshold of resistance (Westneat et al. 1990). The females’ behavior is presumably a reflection of the costs and benefits associated with extra-pair paternity. It is in this context that FSC might evolve.

A classic example of this FSC-EPC was provided by Kempenaers et al. (1992), who combined behavioral and genetic data to show that female-driven EPC was common in monogamous pairs of the blue tit, *Parus caeruleus.* In the wild population studied, 31 % of clutches included extra-pair paternity. Further, of the 7 EPCs (out of 90 copulations) observed, more than 70 % were classified as female driven. In these cases, females moved onto the territory of neighbors and were either chased off by the resident female or – if undetected – were sometimes able to solicit and take part in an EPC. The observation that resident females showed aggression toward intruders highlights the extra costs to this form of EPC, which must nonetheless be outweighed by the benefits, and provides evidence of a selective pressure that could promote the evolution of costly female sneak behaviors leading to copulation.

Primate Tactical Deception and FSC

Another class of species in which FSC-EPC could be important is primates. Exclusive pair bonds are rare in most mammals (around 3 %). But they are relatively common in primates, with 14–18% of species forming monogamous sexual bonds (Drea 2005), while the percentage is even higher if nonexclusive “pair” bonds nested within hierarchies are included (such as when a male has exclusive access to several females, see “Hierarchies and Defiant FSC” below). Female- driven EPC has been observed in several primate species, and male mate guarding behavior is known to be common (Drea 2005). Females are also known to take part in competitive interactions with other females, as well as to use various forms of physical and social punishments (Stockley and Campbell 2013). Hence, the FSC forms of EPC could be common in primates.

An advantage to recent studies on EPC in primates is that a number have started to provide insight into the psychological processes and cognitive mechanisms that underlie EPC. For instance, Overduin-de Vries et al. (2015) found evidence of EPC based on tactical deception in captive populations of the macaque species *Macaca mulatta* and *Macaca fascicularis*. They observed that females appear to deliberately create distance between themselves and other females before EPC events – a more complex level of cognitive processing than chance exploitation of a peripheral location but less complex than taking the perspective of other females into account (e.g., by deliberately hiding out of view behind screens). Similar tactical concealment was also observed in a wild Ethiopian population of the gelada monkeys, *Theropithecus gelada*, in recent study by le Roux et al. (2013). As tactical deception is known to occur in relation to food and other nonsexual contexts in fish, corvids, apes, and monkeys (Overduin-de Vries et al. 2015), this behavior could also be widespread in FSC contexts of EPC. But at present there is little direct evidence for FSC-EPC in primates or of the role of tactical deception in this. This is due mostly to a lack of studies. Hence, such mechanisms *could* often be utilized in an FSC-EPC context, and there remains a need for further studies on this issue to determine if this is the case.

Hierarchies and Defiant FSC

Another social context in which FSC might appear is that based on rank and social hierarchy seen in a variety of species, including cetaceans, elephants, corvids, and primates (Overduin-de Vries et al. 2015). A diverse array of such hierarchical systems exists. But the most relevant in terms of the evolution of human psychological processes are the primates. Here, hierarchies are based on both male and female rank (Drea 2005). Higher-ranked females often have higher reproductive success.

And such females are also known to suppress the reproduction of lower-ranked females (Drea 2005). Hence, another type of FSC that could be important is that of "defiant FSC" – where a lower-ranked female mates with a male, in defiance of a higher-ranked female. As in the case of tactical deception, there is little direct evidence about defiant FSC. Nonetheless, a number of studies have provided indirect evidence that this could be common. For instance, both Overduin-de Vries et al. (2015) in macaques and le Roux et al. (2013) in gelada monkeys found evidence of male rank-related audience effects on EPC – females and lower-rank males were less likely to copulate when a male of higher rank was nearby and were often punished by these males if sighted. Female rank-related audience effects were not observed in either case. However, these are the first studies of their kind and highlight the potential for such defiant FSC to arise in nature.

FSC in Humans: "Woman Beware Woman"

It has also been suggested that FSC is likely to be common and important in humans. Like other primates, humans have complex social structures and form close pair bonds. Females (women) have flatter "hierarchies" than males (men) (Sidanius et al. 1994) but are known to enforce these via subtle social as well as physical means (Campbell 2013; Stockley and Campbell 2013). Women are also known to "cheat" on men and are known to punish this behavior in other women, especially if the target of the FSC-EPC was "their" man. In street "gangs" such punishment can even lead to the death of another woman (Campbell 2013). Hence FSC is likely to be important in humans and could well involve – or have been involved in the evolution of – the complex psychological processes and cognitive systems that define humans. But once again there is very little solid observational or experimental work that would establish human FSC beyond anecdotal reports; so more studies are needed.

Conclusion

Female sneak copulation (FSC) is likely to be common in nature. However, all female-female sexual competitive interactions remain relatively poorly investigated, and FSC is no exception. Nevertheless, the field is starting to move forward, and it is likely that within the next 5–10 years the mechanisms of FSC, its prevalence in nature, and its importance in human evolutionary psychology will be better known. The results are awaited with anticipation!.

Cross-References

Evolution of *Homo sapiens*

Extra-Pair Mating

Female Deception

Female Dominance Hierarchies

Female-Perpetrated Violence

Inclusive Fitness

Intrasexual Competition

Multiple Mating

Reproductive Strategies

Sneak Copulation

References

<!-- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, *2*, 349-368. -->

A. J.
Bateman

1948
Intra-sexual selection in *Drosophila*
Heredity
2
349

368

<!-- Campbell, C. (2013). The evolutionary psychology of women's aggression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20130078. -->

C.
Campbell

2013
The evolutionary psychology of women's aggression
Philosophical Transactions of the Royal Society, B: Biological Sciences
368
20130078

<!-- Drea, C. M. (2005). Bateman revisited: the reproductive tactics of female primates. *Integrative and Comparative Biology*, *45*, 915-923. -->

C. M.
Drea

2005
Bateman revisited: The reproductive tactics of female primates
Integrative and Comparative Biology
45
915
923

<!-- Forstmeier, W., Nakagawa, S., Griffith, S. C., & Kempenaers, B. (2014). Female extra-pair mating: adaptation or genetic constraint. *Trends in Ecology and Evolution*, *29*(8) 456-464. -->

W.
Forstmeier

S.
Nakagawa

S. C.
Griffith

B.
Kempenaers

2014
Female extra-pair mating: Adaptation or genetic constraint
Trends in Ecology & Evolution
29
8
456
464

<!-- Fox, C. W. & Rauter, C. M. (2003). Bet-hedging and the evolution of multiple mating. *Evolutionary Ecology Research*, 5, 273-286. -->

C. W.
Fox

C. M.
Rauter

2003
Bet-hedging and the evolution of multiple mating
Evolutionary Ecology Research
5
273

286

<!-- Griffith, S. C. (2007). The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. *American Naturalist*, *169*, 274-281. -->

S. C.
Griffith

2007
The evolution of infidelity in socially monogamous passerines: Neglected components of direct and indirect selection
American Naturalist
169
274
281

<!-- Jennions, M. D. & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, *75*(1), 21-64. -->

M. D.
Jennions

M.
Petrie

2000
Why do females mate multiply? A review of the genetic benefits
Biological Reviews of the Cambridge Philosophical Society
75
1
21
64

<!-- Kempenaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C., & Dhondt, A. A. (1992). Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, *357*, 494-496. -->

B.
Kempenaers

G. R.
Verheyen

M.
Broeck
Van den

T.
Burke

C.
Broeckhoven
Van

A. A.
Dhondt

1992
Extra-pair paternity results from female preference for high-quality males in the blue tit
Nature
357
494
496

<!-- le Roux, A., Snyder-Mackler, N., Roberts, E. K., Beehner, J. C., & Bergman, T. J. Evidence for tactical concealment in a wild primate. *Nature Communications*, *4*, 1462. -->

A.
Roux
le

N.
Snyder-Mackler

E. K.
Roberts

J. C.
Beehner

T. J.
Bergman

2013
Evidence for tactical concealment in a wild primate
Nature Communications
4
1462

<!-- Neff, B. D., & Svensson, E. I. Polyandry and alternative mating tactics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20120045. -->

B. D.
Neff

E. I.

Svensson

2013
Polyandry and alternative mating tactics
Philosophical Transactions of the Royal Society, B: Biological Sciences
368
20120045

<!-- Overduin-de Vries, A. M., Spruijt, B. M., de Vries, H., & Sterck, E. H. M. (2015). Tactical deception to hide sexual behaviour: macaques use distance, not visibility. *Behavioral Ecology and Sociobiology*, *69*(8), 1333-1342. -->

A. M.
Overduin-de Vries

B. M.
Spruijt

H.
Vries
de

E. H. M.
Sterck

2015
Tactical deception to hide sexual behaviour: Macaques use distance, not visibility
Behavioral Ecology and Sociobiology
69
8
1333
1342

<!-- Sidanius J., Pratto, F., & Bobo, L. (1994). Social dominance orientation and the political psychology of gender: a case of invariance? Journal of *Personality and Social Psychology*, *67*, 998-1011. -->

J.
Sidanius

F.
Pratto

L.
Bobo

1994
Social dominance orientation and the political psychology of gender: A case of invariance?
Journal of Personality and Social Psychology
67
998
1011

<!-- Stockley, P. & Campbell, A. (2013). Female competition and aggression: interdisciplinary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20130073. -->

P.
Stockley

A.
Campbell

2013
Female competition and aggression: Interdisciplinary perspectives
Philosophical Transactions of the Royal Society, B: Biological Sciences

368
20130073

<!-- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man: 1871-1971*, Chicago: Aldine-Atherton. -->

R. L.
Trivers

1972
Parental investment and sexual selection

B.
Campbell

Sexual selection and the descent of man
Aldine-Atherton
Chicago
1871
1971

<!-- Westneat, D. F., Sherman, P. W., & Morton, M. L. (1990). The ecology and evolution of extra-pair copulations in birds. *Current Ornithology*, *7*, 331-369. -->

D. F.
Westneat

P. W.
Sherman

M. L.

Morton

1990
The ecology and evolution of extra-pair copulations in birds
Current Ornithology
7
331
369