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Sneaking from a female perspective

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Alternative male mating tactics in species with external fertilization are often viewed as coercive matings by low-quality males, when a male, unable to attract a female himself, steals fertilizations from a spawning pair by adopting 'sneaky' mating tactics, thereby eroding the interests of both the pair-mating male and female. Although a cost of sneaking to guarder males is inevitable, we highlight emerging evidence that females may actually seek and benefit from mating with sneaking males. Sneaking may thus be a means by which females gain access to resources critical for reproduction when these are defended by males adopting a guarder tactic, while maintaining some control over indirect (genetic) benefits through mate choice. We consider a range of potential costs and benefits that females may obtain from matings that involve sneakers and review empirical studies on female responses to sneaking. We show that the outcome of the trade-off between costs and benefits is context specific and may vary among mating systems, species, populations within species, and individual females within populations. This emerging evidence undermines the view that sneaking necessarily represents forced fertilizations and that sneakers are always low-quality males making 'the best of a bad job'. When females prefer to spawn in the presence of sneaker males, the distinction between deliberate polyandry and sneaking becomes ambiguous and females may only be limited in the expression of their mating preferences by resource monopolization or mate guarding by dominant males, resulting in an intersexual conflict.

Keywords: external fertilization; mate choice; mate guarding; polyandry; reproductive behaviour; sexual conflict; sexual selection; territoriality

Sexual selection consists of two components; competition within the sexes (typically among males) for access to mates or resources critical for reproduction (intrasexual selection), and mate choice from a pool of available individuals of the opposite sex (intersexual selection, typically female choice). These two mechanisms of selection, acting both before and after mating, have traditionally been considered to operate in concert (Andersson 1994). Males successful in intrasexual competition for high quality resources (direct benefits) are also expected to confer superior genetic quality (indirect benefits) to females. Therefore, the argument goes, it should be adaptive to females to choose dominant males. However, recent work has highlighted the fact that although there are many cases when females may benefit from choosing dominant males, with male–male contests facilitating female choice (Andersson 1994; Candolin 1999), in other cases the costs to a female of choosing a dominant male may outweigh the benefits (Berglund et al. 1996; Moore & Moore 1999; reviewed in Qvarnström & Forsgren 1998). Consequently, female choice may not discriminate between dominant and subordinate males (Kangas & Lindström 2001; Spence & Smith 2006), or females may consistently prefer mating with subordinates (Ophir & Galef 2003). Thus, in some instances the high reproductive success of dominant males may arise simply as a consequence of dominant males monopolizing access to females, thereby reducing the opportunity for female choice to operate (Reichard et al. 2005). A consequence might be a conflict between the outcome of the

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intra- and intersexual components of sexual selection, with important implications for the strength and direction of sexual selection.

The role that females play in sexual selection has often been overlooked. However, recent work has demonstrated sophisticated ways in which females may influence the outcome of conflicts over mating, transforming our view of how sexual selection operates. Female often solicit extra-pair copulations (Griffith et al. 2002) and may bias sperm use in favour of particular males (Evans et al. 2003; Pizzari et al. 2003). Yet, most studies of female roles in the outcome of sexual conflicts have largely come from taxa with internal fertilization (Arnqvist & Rowe 2005) where females encounter males sequentially. In contrast, external fertilization usually demands the simultaneous release of sperm and ova because of a short time window for fertilization to occur; the viability of sperm is usually severely compromised once released. This time constraint limits the degree of control that a pair-spawning male and female can have over the success of additional males that adopt alternative mating tactics and attempt to participate in a mating, either through force, or by 'sneaking' fertilizations. Such males effectively parasitize the courtship effort and resource use of pair-spawning males (Perrill et al. 1978; Taborsky 1994, 1998). Males adopting alternative mating tactics potentially also undermine female choice. However, we argue here that a cost to females is not inevitable, and alternative mating tactics may actually enhance female reproductive success in some circumstances.

We review the consequences to females of male alternative mating tactics in species with external fertilization; that is when the deposition of gametes occurs outside the female reproductive tract in an external environment. Alternative mating tactics have traditionally been seen as coercive mating by low-quality males, when a male, unable to attract a female himself, steals fertilizations from a spawning pair, thereby eroding the interests of both the pair-spawning male and female (van den Berghe et al. 1989; Taborsky 1998; Byrne & Roberts 1999). Associated with this view Taborsky (1994, 1997) suggested the collective term 'parasitic males' for disparate labels given to males that exploit the reproductive investment of other males, and 'bourgeois' males for dominant males possessing territories and investing in primary access to females, but which can also act as parasitic males (Taborsky 1994, 1997). While we think they are useful collective terms that incorporate all variations of the two basic male tactics, given the scope of our review and attention we pay to particular spawning situations rather than the long-term tactic used by a male, we use the terms 'guarder' and 'sneaker' males (Parker 1990, 1998). A guarder is a male in possession of a resource or females that have been acquired through aggressive defence. Guarders typically also engage in courtship displays. A sneaker is a male that, in a given mating scenario, participates in mating but neither guards a resource nor engages in courtship behaviour. Sneaking does not necessarily infer furtiveness, since sneakers may often be highly obvious in their behaviour to guarders and females. The essential distinction between a guarder and sneaker role is the control of a resource by guarders at a given mating.

Contrary to the prevailing view, we highlight accumulating evidence that females may actually seek and benefit from mating with subordinate males, with sneaking the means by which females might gain access to resources critical for reproduction when these are defended by guarders, while maintaining some control over indirect (genetic) benefits through mate choice. Given that external fertilization occurs exclusively in the aquatic environment, we illustrate our ideas using examples of fish, anuran and marine invertebrate mating systems. However, we believe that our review has more general implications pertaining to theoretical concepts of sexual selection, mating system evolution and sexual conflict. Although female-solicited sneaking resembles aspects of extra-pair copulations in taxa with internal fertilization, the essential difference stems from the fertilization environment and simultaneous participation of all mating individuals.

In our review we first discuss the cost and benefits of sneaking to females. We review empirical studies showing female responses to sneaking and go on to address the role of sneaker quality in female mating decisions. We conclude that there is a range of situations where sneaking may confer direct and indirect benefits to females and highlight potential future directions into research on the role of females in the evolution of alternative mating tactics.

FEMALE BENEFITS AND COSTS OF SNEAKING

We consider a range of potential indirect (genetic) and direct (fertilization rate, paternal care, male harassment) benefits and costs to females that mate in the presence of sneakers. Indirect benefits to females, acquired by mating with males of superior genetic quality, may be independent of female genotype (additive genetic effects, 'good genes') or arise from an interaction between male and female genotypes (nonadditive genetic effects, 'complementary genes') (Neff & Pitcher 2005).

Additive Genetic Quality of the Offspring

So-called 'good genes' models of intersexual selection predict that in a situation when males provide no direct resources, females choose males of a higher additive genetic quality (Andersson 1994; Kokko et al. 2002). Such genetically superior males often advertise their status by costly signals, ability to win fights or a higher rank in male dominance hierarchies (Andersson 1994). Although 'genetic quality' is a difficult term to define, dominant, guarder males are considered to be those that are genetically superior (Andersson 1994; but see Qvarnström & Forsgren 1998). Good genes models of sexual selection are a controversial aspect of sexual selection theory, and their importance and validity has been questioned (Kirkpatrick & Barton 1997; Cameron et al. 2003; Hall et al. 2004; Parker 2006). Notwithstanding the debate associated with these models of sexual selection, there may be a role for female costs and benefits to sneaking in the context of the broadly defined good genes model.

Additive genetic male quality may be related to higher viability of the offspring (e.g. faster growth, resistance to disease, better predator avoidance; i.e. factors related to natural selection), but may also stem from its higher potential reproductive success (increased access to females by male progeny or higher fecundity of female progeny; i.e. factors related to sexual selection). Female often choose males with more developed sexually selected traits (Andersson 1994), although the evidence of fitness benefits of female choice for males of superior intrinsic quality is surprisingly weak in taxa where males provide no direct resources or paternal care (Kirkpatrick & Barton 1997; Møller & Alatalo 1999).

In the lekking cichlid, *Lethrinops parvidens*, from Lake Malawi, a species in which males provide no resources to females, bower height (the supposed sexually selected signal) was positively correlated with the number of female visits, although the relationship with the number of eggs laid was low (Kellogg et al. 2000). In a half-sib experimental design, with offspring raised without parental care, progeny of brightly coloured male three-spined sticklebacks, *Gasterosteus aculeatus*, had a slower growth rate than offspring of duller males, although they were more resistant to parasite infection (Barber et al. 2001). Similarly, in the grey treefrog, *Hyla versicolor*, offspring of long-calling males showed better larval and juvenile performance than offspring sired by short-calling males (Welch et al. 1998). In a study on the Alpine whitefish, *Coregonus* sp., that used a full breeding design, offspring sired by males with the most extensive breeding ornamentation (the putative signal of ‘good genes’) showed higher survival rates following bacterial infection at the egg stage, regardless of female identity. In contrast, offspring mortality arising from developmental problems was related to specific male–female combinations, suggesting partial incompatibilities between parental haplotypes (Wedekind et al. 2001, see below). Whitefish scatter their eggs over the substrate in spawning groups, with no mate guarding or parental care. Such a mating system is prone to sneaking, but there is no information on whether male whitefish form dominance hierarchies, whether dominant males are characterized by a more pronounced breeding ornamentation, or whether females exert mate choice. On the contrary, other research has shown that offspring survival was not related to sire sexual ornamentation. This includes studies on cod, *Gadus morhua*, and roach, *Rutilus rutilus*, fishes with similar mating system to whitefish (Kortet et al. 2004; Rudolfsen et al. 2005), and Chinook salmon, *Oncorhynchus tshawytsha* (Pitcher & Neff 2007). In Atlantic salmon, *Salmo salar*, offspring sired by sneaker males had higher viability and grew faster than progeny of guarder males implying a higher additive genetic quality of sneaker males (Garant et al. 2002).

Thus, although there is overwhelming evidence that mating with dominant males provides females with direct resources of superior quality (Andersson 1994), male dominance and control of resources may be a poor overall predictor of the benefits that mating with a dominant male can bring (Qvarnström & Forsgren 1998; Moore & Moore 1999). If the case, this implies that female choice of dominant males may be more likely to arise through direct benefits, rather than benefits that accrue through superior sire genetic quality (Cameron et al. 2003). Consequently, the female cost/benefit ratio of mate choice has an ambiguous outcome with respect to male dominance and will depend on the temporal and spatial distribution of resources and ability of guarder males to monopolize matings. The prediction is that high monopolization potential without an underlying requirement for high intrinsic quality in monopolizing guarder males leads to an increased probability of female benefits from sneaking.

Sperm–Egg Compatibility (Nonadditive Genetic Quality)

Sperm competition arising through sneaking may also increase fertilization rates and offspring fitness via a higher probability of compatibility between sperm and egg. Zeh & Zeh (1996) suggested that genetic incompatibility arising from intragenomic conflict is widespread and may substantially decrease fertilization rate and offspring viability. Notably, soliciting of sneaker males to ensure sperm–egg compatibility does not predict these additional males to be of a higher intrinsic quality than guarder males, the logic that is otherwise inherent in all ‘good genes’ models (Kokko et al. 2006). Therefore, the sperm–egg compatibility hypothesis predicts that females should benefit from an increase in the number of mating partners regardless of their additive genetic quality (Zeh & Zeh 1996). Although the sperm–egg compatibility hypothesis has been proposed for viviparous females with internal fertilization (Zeh & Zeh 1997), it may equally apply to externally fertilizing species (Neff & Pitcher 2005).

The simplest case of reduced genetic compatibility is mating between close relatives resulting in inbreeding. Inbreeding may lower offspring viability through several mechanisms (reviewed in Jennions & Petrie 2000; Fisher et al. 2006). Female Atlantic salmon with a higher number of mates produced more outbred offspring and enjoyed increased reproductive success through higher survival of their offspring (Garant et al. 2005). Tregenza & Wedell (2002) showed that eggs of female crickets, *Gryllus bimaculatus*, mated to two sibling males had significantly reduced hatching success compared with the hatching success of females mated to two nonrelative males. Importantly, when females were mated to one sibling and one unrelated male, no decrease in hatching success was detected, suggesting an efficient mechanism of selection for nonsib sperm (although see Jennions et al. 2004). Studies on externally fertilizing marine invertebrates (sea urchin, *Heliocidaris erythrogramma*, and polychaete worm, *Galeolaria caespistosa*) also support an increase in costs to females arising from fertilization by incompatible sperm (Evans & Marshall 2005; Marshall & Evans 2005).

Recent work suggests that females may choose genetically compatible mates through olfactory cues based on MHC-specific odours (Jordan & Bruford 1998), and a substantial body of empirical evidence for major histocompatibility complex (MHC)-based mate choice has accumulated (see Neff & Pitcher 2005; Piertney & Oliver 2006 for review). For example, Aeschlimann et al. (2003) showed that female three-spined sticklebacks chose males with the most complementary MHC profile to their own. The mechanism appears to be through using a self-referential process that involves detection of MHC peptide ligands (Milinski et al. 2005). MHC-based preferences are not restricted to premating choices, but pertain also to fertilization (Tregenza & Wedell 2000). Proteins coded for by MHC genes appear to be expressed on sperm, and in vitro fertilization experiments in mice and fish have revealed that eggs are capable of MHC-haplotype-dependent selection of sperm (Wedekind et al. 1996; Skarstein et al. 2005). Consequently, benefits to females from mating with both guarder and sneaker males, resulting in sperm competition, may arise through an increased probability of compatible parental haplotypes in the offspring.

In contrast, in cases when a female bases choice of the guarder male on a signal that accurately reveals compatibility between herself and a potential mating partner (e.g. a MHC-related odour), sneaker males decrease female fitness if they successfully fertilize a portion of her eggs. Here, the sneaker would sire offspring with a lower viability than the chosen guarder. The resolution of this ambiguity is similar to that of additive genetic quality of guarder/sneaker males.

Enhanced Genetic Variability among Offspring (Genetic Bet-Hedging)

Another potential benefit to females from the participation of sneaker males in mating comes from a higher genetic diversity among their offspring (Watson 1991). If increased genetic diversity is advantageous, females may, as with sperm–egg compatibility, benefit from multiple paternity per se, regardless of the intrinsic quality of a mate. The survival, viability and fitness advantages for offspring are often environmentally dependent, making polyandry beneficial although genetic bet-hedging (Watson 1991; Jennions & Petrie 2000). In externally fertilizing species like fishes, anurans and aquatic invertebrates there is typically extremely high fecundity matched by high embryonic mortality (Wootton 1998). Many females are unable to split their clutches and the participation of sneaker males in a mating may be the only means to secure polyandry. Thus, the benefits from multiple paternity may come from spatially and temporally unpredictable gene–environment interactions. Females may also respond to fluctuations in environmental conditions favouring different phenotypes between generations. For example, when a sneaker role has some genetic component (e.g. in salmon, Aubin-Horth & Dodson 2004) and its success is frequency dependent (Gross 1985), interannual variability in the frequency and, hence, the success of guarder and sneaker males may vary unpredictably. Females whose eggs have been fertilized by both guarder and sneaker males may thereby benefit through bet-hedging, at least in species with a heritable component to male mating tactic as shown by Alonzo & Sinervo (2001).

Although the advantage of polyandry stemming from genetic bet-hedging has been questioned, especially when it incurs a cost to females (Yasui 1998), there is empirical evidence of reduced parasite load and higher fitness payoffs resulting from a genetic bet-hedging (Baer & Schmid-Hempel 1999). Further, a direct cost of multiple mating may be substantially lower in externally fertilizing species compared to species with internal transfer of sperm (Arnqvist & Rowe 2005), although there may be indirect costs to females associated with male behaviour, such as aggression, refusal to spawn, or decreased paternal care (see below).

Sperm-Limited Fertility

Participation by sneaking males in a pair mating may confer direct benefits to females through insurance of fertilization. Infertility rates in nature can be high (Wedell et al. 2002) and are often explained, although sperm depletion following multiple ejaculations in males that enjoy high mating success (Nakatsuru & Kramer 1982; Warner et al. 1995; Preston et al. 2001) or have a finite quantity of sperm (Damiens & Boivin 2006). Males are often able to tailor ejaculate expenditure in a given mating to trade-off current and future reproductive success (Wedell & Cook 1999; Pilastro et al. 2002; Smith et al. 2003). Lower sperm delivery by a male may decrease the proportion of eggs fertilized in a given mating, while maximizing reproductive success of that male in the longer term (Warner et al. 1995; Smith & Reichard 2005). Increased intensity of sperm competition results in a higher number of sperm delivered in total as well as by an individual male (Parker 1998), decreasing the probability of sperm-limited infertility. Therefore, inciting sperm competition may be adaptive for females that would otherwise suffer from incomplete fertilization of their eggs, as reported for the lemon tetra, *Hyphessobrycon pulchripinnis* (Nakatsuru & Kramer 1982), bluehead wrasse, *Thalassoma bifasciatum* (Warner et al. 1995), European bitterling, *Rhodeus amarus* (Smith & Reichard 2005), common frog, *Rana temporaria* (Vieites et al. 2004), and several marine invertebrates (reviewed in Levitan & Petersen 1995; Levitan 1998).

In the European bitterling, which spawns on the gills of freshwater mussels (Smith et al. 2004), females suffered a 20% reduction in fertility of their eggs when spawning with a solitary guarder male compared with a group of four males (Smith & Reichard 2005). In a separate study with this species, more developing embryos were recovered in experimental treatments that involved participation by multiple males (Reichard et al. 2004a). Since there is a positive correlation between the number of preoviposition ejaculations and fertilization success in bitterling (Reichard et al. 2004a), and failure of fertilization is common (Smith et al. 2000; Reichard et al. 2005), it is possible that increased fertility arose from a higher number of spermatozoa released into mussel gills by multiple males. In individual spawnings guarder male bluehead wrasse released an order of magnitude fewer spermatozoa than sneaker males (Warner et al. 1995). Furthermore, guarder males with the highest spawning success released fewer spermatozoa than guarders with a lower mating rate, implying sperm limitation in the most successful males. Despite the potential for limited fertility, female bluehead wrasse appear to prefer spawning with particular guarder males (Warner et al. 1995), although other work suggests that direct benefits to females from spawning in preferred spawning territories are more important than mating with particular guarder males (Warner 1987). Similarly, in the common frog, *R. temporaria*, males that are not in amplexus seek egg clutches and attempt to fertilize them; thereby increasing the proportion of fertilized eggs by 15–20% (Vieites et al. 2004). In contrast, in the quacking frog, *Crinia georgiana*, females suffered significantly reduced fertilization of eggs when amplexed by more than a single male, perhaps because of a suboptimal position of male cloacae during ejaculation (Byrne & Roberts 1999). These studies suggest that sneakers may have ambiguous effects on sperm-limited fertility, although most empirical evidence shows females benefit from enhanced fertility rates because of increased sperm numbers arising from sperm competition.

Spawning Disruption and Reduced Spawning Rate

When guarder males are confronted by sneakers it may be adaptive for them to cease courtship and drive sneakers away rather than attempt to mate. Disruption to pair matings by sneakers can considerably prolong the time between female approach to a spawning site and oviposition (Reichard et al. 2004b). Guarder males may even decline a spawning opportunity altogether when the prospect of sneaking interference is high (Alonzo & Warner 1999). Exceptionally, female anurans can be drowned by amplexed males (Davies & Halliday 1979; Byrne & Roberts 1999).

Territorial male Mediterranean wrasse, *Symphodus ocellatus*, refused to spawn with females when their nests were surrounded by sneakers, although they were capable of spawning and they did spawn immediately after sneakers were removed (Alonzo & Warner 1999). Similarly, guarder male three-spined sticklebacks reduced courtship effort in the presence of a sneaker male (Le Comber et al. 2003), and a reduction in courtship because of sneakers results in fewer female visits to the territories of guarder male sticklebacks (van den Assem 1967). The same pattern was observed with zebrafish, *Danio rerio* (Spence & Smith 2005). In the European bitterling, the number of spawning attempts that failed to result in a successful oviposition increased significantly when sneaker density was high (Reichard et al. 2004b). This effect was because of elevated aggression rates by guarder males to sneakers. In contrast, the courtship effort of guarders in the black goby, *Gobius niger*, and grass goby, *Zosterisessor ophiocephalus*, was not affected by interference from a single or four sneakers, although guarders responded to them aggressively (Scaggiante et al. 2005).

These examples suggest that reduced spawning rates may result from a direct response by guarder males to the presence of a sneaker (Alonzo & Warner 1999), or may result from a trade-off between territorial defence/mate guarding and courtship (Reichard et al. 2004b). In extreme cases, male–male aggression can lead to physical injuries and incidental female mortality (Davies & Halliday 1979; Byrne & Roberts 1999).

Lower Parental Effort

Guarder males may provide paternal care to developing eggs and embryos. Parental care theory predicts that males should modulate parental effort according to the level of perceived paternity (Westneat & Sherman 1993). In the bluegill sunfish, *Lepomis macrochirus*, guarder males adaptively adjust their parental effort (Neff & Gross 2001), and this adjustment is dynamic (Neff 2003). During the egg phase guarder males modify their effort according to the number of sneaking males near their nest during spawning. However, once the offspring have hatched guarder males use olfactory cues to judge paternity and correct their level of paternal care relative to the proportion of offspring they have fathered (Neff 2003). Similarly, simulated intrusions by sneaking males led to an increase in filial cannibalism and decrease in parental effort by guarder male scissortail sergeant, *Abudefduf sexfasciatus* (Manica 2004). The paternity level of guarder males was positively correlated with nest defence effort in pumpkinseed sunfish, *Lepomis gibossus*, although it was not associated with other paternal care components, such as egg fanning effort and defence of the hatched offspring (Rios-Cardenas & Webster 2005). Male four-spined sticklebacks, *Apeltes quadracus*, took longer to begin postspawning nest repairs in the presence of a rival male, which resulted in a reduction in hatching success. However, reduced paternal care as a consequence of a decrease in paternity may also have taken place (Willmott & Foster 1995). In contrast, no relationship between paternity and parental effort or hatching success was observed in the fifteen-spined stickleback, *Spinachia spinachia* (Östlund-Nilsson 2002). We are not aware of any study that has attempted to measure the relationship between parental effort and paternity level in externally fertilizing species with biparental care.

TRADE-OFFS FOR FEMALES OF SNEAKING

Participation by sneaker males in pair-spawning may bring a range of costs and benefits to females (Table 1). The positive effect of the presence of sneaker males may arise from (1) increased genetic variability within the clutch, and (2) delivery of higher sperm numbers under sperm competition. Positive or negative effects can result from the alteration of genetic quality of the offspring, either through sneaker males being of (3) higher/lower additive genetic quality than guarder males (in accordance with 'good genes' ideas of sexual selection), or (4) enhanced/reduced genetic compatibility between parental haplotypes (complementary genes). Negative consequences of mating with sneakers may arise from (5) intensification of male–male competition and resultant disruption to spawning, and (6) the risk of reduced paternal investment in offspring care. The outcome of the trade-off between costs and benefits is likely to be context specific and may vary among mating systems, species, populations within species, and individual females within populations.

Table 1. Consequences for female fitness of sneaker participation in spawning

Variable	Consequence for female fitness			Source
	S < G*	S = G†	S > G‡	
Fertilization insurance	Benefit	Benefit	Benefit	Nakatsuru & Kramer 1982, Warner et al. 1995, Smith & Reichard 2005
Genetic bet-hedging	Benefit	Benefit	Benefit	Kellog et al. 1995, Garant et al. 2005
Additive genetic quality of offspring	Cost	No cost	Benefit	Welch et al. 1998, Wedekind et al. 2001, Garant et al. 2002, Pitcher & Neff 2006
Nonadditive genetic quality of offspring (including sperm–egg compatibility)	Cost	No cost	Benefit	Wedekind et al. 2001, Evans & Marshall 2005, Marshall & Evans 2005, Skarstein et al. 2005
Spawning disruption	Cost	Cost	Cost	Alonzo & Warner 1999, Reichard et al. 2004b
Lower parental effort	Cost	Cost	Cost	Willmott & Foster 1995, Neff & Gross 2001, Neff 2003, Manica 2004, Rios-Cardenas & Webster 2005

*Sneaker of lower genetic ‘quality’ than guarder.
†Sneaker and guarder of equivalent genetic ‘quality’.
‡Sneaker of higher genetic ‘quality’ than guarder.

Females should suffer the highest potential costs from sneaking when (1) resources essential for reproduction (e.g. nesting sites) are not limiting to males, (2) females are not constrained by males in their mate choice, (3) sneaking elicits aggressive responses by guarder males that substantially disrupt female spawning rate or fertilization success, and (4) when incidents of sneaking subsequently decrease guarder male expenditure on paternal care. Here, sneaking clearly undermines a female’s direct and indirect benefits of mate choice.

In contrast, females are predicted to benefit most from sneaking when (1) a small number of guarder males are able to obtain exclusive access to resources essential for reproduction or females themselves (i.e. high spatial and low temporal clustering of fertilizations), (2) guarder males become sperm depleted and/or (3) there is a high incidence of sperm–egg incompatibility (e.g. in small and inbred populations), (4) there is no paternal care, and (5) offspring genetic variability is advantageous (e.g. fluctuating environment or negative frequency-dependent selection) and females cannot readily share fertilizations among males. In these situations sneaking may augment rather than undermine female choice, and females are predicted to engage in behaviour that could influence the probability and success of sneaking from particular males. Females may then mate in high quality territories (with consequent direct benefits), but at least some offspring may be sired by preferred nonguarder males (indirect benefits). Notably in individual spawning acts, sneaker males often sire a higher proportion of offspring than guarder males (Fu et al. 2001), probably because sneakers face a higher risk of sperm competition than guarders and are better adapted to compete in this way (Parker 1998; Stoltz & Neff 2006). Several of these criteria are met in the European bitterling, and sneaking does appear to be both common and successful in this species, with females appearing to solicit matings from sneaker males (Smith & Reichard 2005). An outcome of female benefits of sneaking is a three-way sexual conflict between females and guarder males, and sneakers and guarder males (see also Alonzo & Warner 2000a), perhaps resulting in the evolution of cryptic female complicity in sneaking.

Under certain circumstances it may be adaptive for females to respond to sneaker male quality and modulate their response accordingly. In mating systems with flexible male mating tactics, males that possess their own territory and act as guarders can also often successfully engage in sneaking (Jennions et al. 1992; Reichard et al. 2004a), typically in the territories of neighbouring males. Females may solicit participation of these males (as well as sneaker males without their own territories) in spawning, by lengthening the prespawning period and timing oviposition to increase the probability of fertilization by sneaker males. So far, female behaviour that increases the probability of sneaking has only been documented in the European bitterling (Smith & Reichard 2005), although we expect that further research will identify this behaviour as more common feature of some mating systems, comparable with the widespread recognition of the role of female solicitation in extra-pair mating in birds (Griffith et al. 2002).

In mating systems where male mating tactics are not flexible, but instead male role is determined by genetic factors or by achieving some threshold during ontogenetic development (i.e. with alternative mating strategies sensu Gross 1996), males with higher growth rates as juveniles often develop into sneaker males (Thorpe 1986; Gross 1991; Garant et al. 2002; Neff 2004). In these cases, sneaking may have evolved as a strategy because it allows males to circumvent the costs associated with a guarder role (e.g. energetically expensive territorial aggression, longer time to the onset of reproduction, risky migration; Gross 1985). This emerging view of alternative strategies further undermines the view that sneaker males are always low-quality males making ‘the best of a bad job’, since the reverse often appears to be the case.

FEMALE RESPONSE TO SNEAKING

Unfortunately, the female role is often overlooked in studies on alternative male mating behaviour (Alonzo &

Warner 2000a), and few studies have directly addressed female responses to sneaker males in mating systems with external fertilization. Studies that have addressed sneaking from a female perspective have yielded varied results. Females of the Mediterranean wrasse and East Atlantic peacock wrasse, *Symphodus tinca*, were shown to avoid spawning with sneaker males (van den Berghe et al. 1989; Alonzo & Warner 2000b). Experimental reduction in the number of sneaker males resulted in an immediate five- to eight-fold increase in spawning rate of the guarder males with reduced sneaker abundance (van den Berghe et al. 1989). The higher spawning rate cannot be attributed to the increased visitation rate of females but comes from the decision of females whether to lay their eggs or not after inspecting a particular nest (Alonzo & Warner 2000b).

In cases where males modulate their level of parental care in relation to perceived paternity of offspring (Westneat & Sherman 1993; Sheldon 2002; Neff 2003), females are predicted to show a negative response to sneakers, yet they often fail to show any sneaking-avoidance behaviour. For example, in the sand goby, *Pomatoschistus minutus*, female spawning choices were unaffected by the presence of sneaking males near the nest (Svensson & Kvarnemo 2005). Similarly, although female quacking frogs suffer a significant cost of reduced fertilization success and appear to gain no genetic benefit when mating in the presence of sneakers, they show no sneaker-avoidance behaviour (Byrne & Roberts 1999, 2000).

In the Azorean rock-pool blenny, *Parablennius sanguinolentus parvicornis*, females were more responsive to male courtship in the nests of territorial males with an associated subordinate male (that also participated in spawnings) and such nests received five times more spawnings than nests with a solitary guarder male (Oliveira et al. 2002). Unfortunately, the design of the study cannot exclude the possibility that subordinate males preferentially associated with successful guarder males rather than demonstrating a female preference for nests with associated subordinate males. However, the nests with subordinate males suffered less sneaking intrusions from other nonassociated sneaking males (Oliveira et al. 2002), reducing the possibility that females directly preferred an increase in the number of spawning males (e.g. to ensure high fertilization rate).

More robust evidence of a preference for sneaking males by females comes from field studies on coho salmon, *Oncorhynchus kisutch*, and bluegill sunfish, and experimental manipulations in the European bitterling. Female coho salmon performed more digging behaviour (a measure of mate choice) when accompanied by sneaker males. Further, females oviposited for longer (and therefore, perhaps, laid more eggs) when sneaker males took part in spawning (Watters 2005). Females appeared to prefer mating with sneaker males to avoid direct costs of mating that are imposed on them when spawning with aggressive guarder males (Watters 2005). Similarly, female bluegill sunfish laid three times more eggs when sneaker males participated in spawning and females have never been reported to show any sneaking-avoidance behaviour (Fu et al. 2001). A recent empirical and modelling approach demonstrated that high quality female bluegill sunfish preferentially spawned in nests with optimal rates of sneaking and thereby trade-off genetic benefits of sneaker paternity against costs from reduced paternal care of guarders (Neff in press). Notably, females do respond to sneaker quality and prefer mating with older sneakers mimicking females rather than small sneakers that dart into nest and release sperm over the eggs (Neff in press). This female preference reduces costs associated with decreased paternal care that is observed only in the latter case of sneaking fertilization (Neff & Gross 2001). In the European bitterling, pair-spawning females significantly preferred spawning close to a sneaker male and engaged in a specific behaviour that signals that a female is about to oviposit ('skimming' behaviour). Notably, this behaviour is associated with the arrival of sneaker males both under experimental conditions and in the field (Smith & Reichard 2005).

CONCLUSIONS

We have examined the costs and benefits that accrue to females of externally fertilizing species from matings that involve sneaker males, and reviewed empirical studies that have addressed female responses to sneakers. We believe that there is compelling evidence that, under certain circumstances, females may benefit from sneaking. For guarder males the net costs associated with sneaking are implicit (for exceptions see Oliveira et al. 2002; Hamilton & Taborsky 2005), creating a potential sexual conflict between guarder males and females over the role of sneakers. The resolution of the conflict can be affected by characteristics of a given mating system (distribution of nest sites and other resources, potential for sperm limitation, population size, environmental fluctuations, level of paternal care, potential for sneaking deception), with context-specific variability in predicted female responses. We show that females can enhance their reproductive success by increasing the probability of sneaking and show that females of at least three unrelated fish species do prefer to mate in the presence of sneaking males.

A wealth of empirical and theoretical studies support the concept of sexual conflicts; conflict of evolutionary interests between the sexes (Parker 1979; Arnqvist & Rowe 2005). Our review provides evidence that the evolution of alternative male mating tactics leads not only to intrasexual conflict, but also to intersexual conflict. We call for studies to investigate the role of female behaviour in influencing the reproductive success of sneaker males, and we predict such studies will bring important new insights of the female role in the evolution, maintenance, and success of alternative male mating tactics. When females prefer to spawn in the presence of sneaker males, the distinction between deliberate polyandry and sneaking becomes ambiguous, and sneaking does not necessarily represent forced fertilization. In this situation, females are only limited in the expression of their mating preferences by resource monopolization or mate guarding by dominant males resulting in an intersexual conflict.

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