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On the adaptive function of gamete trading in the black hamlet *Hypoplectrus nigricans*

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ABSTRACT

Explanations for the sexual behaviour of gonochoristic (dioecious) and hermaphroditic animal species differ. Gonochore sexual behaviours are generally understood in the context of sexual signals, whereas those of hermaphrodites have been explained by sexual conflict resolution. Specifically, the alternation or simultaneity of mating roles observed in some hermaphroditic species has been attributed to conditional reciprocity, in which an individual's donation of gametes (eggs or sperm) appears to depend on its partner's release of that same gamete type. Because it appears that individuals 'give gametes to get gametes' so as to avoid being cheated, this phenomenon is known as 'gamete trading'. Here, the observations from the original report analysing the egg trading behaviour of the sea bass *Hypoplectrus nigricans* are re-interpreted within the context of modern sexual signalling theory. Questions raised by the gamete trading hypothesis are resolved once the observed behaviours are viewed as sexual signals. I therefore propose that 'giving gametes to get gametes' represents conventional sexual signalling. Generalization of the hypothesis to other hermaphroditic mating systems, combined with empirical support, should contribute to a consistent theory of sexual signalling that is applicable to all animal mating systems.

Keywords: egg trading, gamete trading, good genes, hermaphrodites, sexual signals.

INTRODUCTION

Descriptions of bizarre sexual behaviours in hermaphroditic animals are numerous. Before mating, pairs of earthworms perform tugs-of-war on the surface between their burrows as well as making mutual burrow visits (Nuutinen and Butt, 1997); planaria flatten and spread their already not-too-thick selves against each other to gauge the size of their partner (Vreys and Michiels, 1997, 1998a); marine flatworms stab at each other with their penes to inject sperm subcutaneously (Michiels and Newman, 1998); shelled land snails thrust calcified darts through their partner's body walls (Lind, 1976; Chung, 1987; Adamo and Chase, 1988; Landolfa, 2002); and shell-less land snails flagellate one another with swollen accessory sex organs (Reise, 1995) or hang suspended on slime strings while exchanging sperm at the tips of their intertwined penes (Falkner, 1993; Baur, 1998). Myriad

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other hermaphroditic species from diverse taxa exhibit equally bizarre but less notorious behaviours (Michiels, 1998). Although many of these behaviours are well described, in many cases their adaptive functions are as yet largely undetermined.

However, one particular adaptive explanation for a subset of hermaphroditic sexual behaviours involving alternating or simultaneous fertilization has found favour among behavioural ecologists. ‘Gamete trading’ (Leonard and Lukowiak, 1984) has been proposed to obtain in such disparate taxa as a family of sea basses (Serranidae: Fischer, 1980, 1984; Pressley, 1981; Petersen and Fischer, 1986; Fischer and Petersen, 1987; Petersen, 1990, 1995), a genus of polychaete annelid (*Ophryotrocha diadema*: Sella, 1985, 1988; Sella and Lorenzi, 2000; *O. gracilis*: Sella *et al.*, 1997), an opisthobranch mollusc (*Navanax inermis*: Leonard and Lukowiak, 1984, 1985) and two species of planarian (*Dugesia gonocephala*: Vreys and Michiels, 1998b; *Schmidtea polychroa*: Michiels and Streng, 1998; Michiels and Bakovski, 2000). The observed sexual behaviours are superficially distinct, but all involve conditional reciprocity: the occurrence or amount of gametes donated by each individual of a mating pair appears to be conditioned by the occurrence or amount of donation of the same gamete type by its partner. For example, in the form of gamete trading practised by the black hamlet, *Hypoplectrus nigricans*, one member of the mating pair initially spawns eggs that the other member fertilizes with its sperm; within minutes the partners then switch roles, the initial ‘male’ spawning eggs for the initial ‘female’ to fertilize. Alternation of mating roles may occur several times within a single spawning bout. The mating roles of the polychaete *Ophryotrocha* are similarly alternated but over longer time-scales. In these two cases, fertilization is external and the release of eggs by each individual appears to be conditioned by the opportunity to fertilize the eggs of its partner, hence the term ‘egg trading’ (Fischer, 1980). In contrast, the sea slug *Navanax* and the planarians *Dugesia* and *Schmidtea* engage in intromission and internal fertilization. In these species, it is the donation of sperm that appears to be conditioned by the like behaviour of partners, hence the term ‘sperm trading’ (Leonard and Lukowiak, 1984).

What can an individual gain by basing gamete release on its partner’s like behaviour? Conditional gamete donation is believed to be adaptive via its mitigation of ‘cheating’ (Leonard, 1990, 1991): by basing gamete donation on gamete receipt, both mating partners mutually force each other to give gametes to get gametes. In egg-traders, cheating is defined as spawning as a male only – that is, without making a reciprocal offer of eggs. The biological incentive for cheating in egg-traders is that reproduction via sperm is materially less costly than via eggs (at least in non-role-reversed systems) while providing the same genetic (i.e. fitness) payoff. The basing of egg release on egg receipt mitigates against cheating by mutually enforcing roughly equal non-genetic investment by the partners in offspring. In sperm-traders, cheating consists of declining to donate sperm or donating far less sperm than one’s partner, which might be adaptive if sperm production were costly or if female reproduction were limited by sperm availability. As a result of the supposed role that conditional gamete exchange plays in resolving the sexual conflict arising when all members of the population ‘prefer’ to mate in the same sexual role, it has been proposed that conditionality stabilizes hermaphroditism in those mating systems in which it exists (Fischer, 1980; Leonard, 1990; Petersen, 1995; Sella *et al.*, 1997; Michiels, 1998).

Here, I suggest an alternative adaptive function for those behaviours previously explained by gamete trading. I address egg trading in particular, focusing on the mating system of the black hamlet *H. nigricans* (Fischer, 1980) because the sexual behaviours of this species and of other serranids are relatively well characterized. As investigations of hermaphrodite sexual behaviour and its evolution since Fischer (1980) have relied heavily on the conclusions drawn by that analysis, my comments are likely to be applicable to all mating systems for which gamete trading and conditional reciprocity have been proposed. For egg trading, the hypothesis extended here is that egg release (i.e. spawning in the female role) functions in part as a conventional sexual signal indicating phenotypic viability and/or sexual attractiveness, which themselves may correlate with genotypic quality (Andersson, 1994). Signal receivers use the information contained in their partners' egg spawns to make adaptive decisions about mate choice and/or relative investment in a given pairing. For systems in which mates appear to trade sperm, the hypothesis proposes that the amount of sperm donated is the sexual signal. My thesis is that the behaviours previously explained by gamete trading represent conventional sexual signalling in exactly the same sense that the extravagant displays of peacocks and male frogs, as well as the sexual behaviours exhibited by females in sex-role-reversed species (e.g. Berglund *et al.*, 1997), function as sexual signals in gonochores. The appearance of conditionality may be an artifact of the simultaneous, sequential or alternating generation and receipt of conventional sexual signals by the two mates, each of which engages in the pairing as both signaller and signal receiver.

SEX IN THE BLACK HAMLET

Here, I review briefly the typical sexual behaviours of the black hamlet *H. nigricans* (Fischer, 1980). In the following section, I cite several characteristics of these behaviours that are not adequately explained by gamete trading. These features become comprehensible upon re-interpretation using conventional sexual signalling (see pp. 1195–1197).

Black hamlets are small sea bass (*c.* 10 cm standard length) that forage by day on Caribbean reefs. In the late afternoon, individuals migrate to the reef edge to spawn; pair formation and mating occur only within the two hours before sunset. Individuals may spawn with usually one or at most three partners per day. Pairs probably form based on chance, mutual inspection and previous experience with a given partner. Fischer (1980) found that the same individuals could be found pairing together on successive days. During pair formation, the two prospective partners approach each other, allowing mutual observation of sexual behaviours. Non-aggressive behaviours performed before and during spawning bouts are of two types (a spawning bout consists of the set of spawns performed by a given pair on a given day). The first is called 'forward pitch', in which the performing individual faces away from its partner and swims forward and downward a short distance, raising its caudal fin slightly to the side. Forward pitch probably gives the partner an unobstructed view of the displayer's vent area, which may be swollen with eggs. The second behaviour is called 'head snap', in which the focal individual faces away from its partner, raises its head slightly, and snaps its head rapidly from side to side (Fischer, 1980: fig. 2). Both partners generate these behaviours repeatedly before (forward pitch and head snap) and during (usually head snap only) the spawning bout.

The performances of the sexual behaviours do not occur at random, but are temporally correlated with the spawning roles assumed in the succeeding spawn. Forward pitch is usually performed by one or both prospective partners before initial spawning attempts – that is, within the loosely defined period between pair formation and spawning. It is performed less frequently once spawns have commenced. Head snapping, in contrast, is almost always (98% of cases; Fischer, 1980) performed repeatedly just before each spawn by the individual releasing eggs in that spawn – the 'initiator' (Barlow, 1975). Spawning begins with the initiator facing away from the 'follower', rising in the water and performing head snaps repeatedly. The follower generally swims close behind, positioning its head near the initiator's vent region. The partners then orient closely side by side, facing in opposite directions with the follower's nose still adjacent to the initiator's vent (Fischer, 1980: fig. 1). Head snapping ceases to occur once the partners are nose-to-tail. The curvatures of the partners' bodies create a space between them. The follower visibly clenches its jaws (the function of which is unknown), after which the initiator begins the spawn by rowing backward with its pectoral fins, rolling towards the horizontal and releasing eggs into the space between the partners. The follower sheds sperm while maintaining its position relative to the initiator. After spawning (1–2 s in duration), both fish swim suddenly and quickly to the substrate. There is no parental care and the eggs disperse in the plankton.

After a brief interval, the same partners usually switch roles: the follower now becomes initiator, repeatedly generating head snaps and perhaps forward pitch before spawning eggs. The original initiator takes on the role of follower, attending to its partner's behaviour before shedding sperm on the new initiator's spawned eggs. The same pair may alternate sex roles as many as 17 times in a single spawning bout (i.e. a maximum of 9 spawns in each role; mean number of egg spawns per day 4.7; Fischer, 1980). Alternation is not always perfect, however; occasionally, the same individual spawns eggs twice or more in succession. Additionally, the pair may break up before either or both fish have exhausted their gametes for that day. One or both individuals may then pursue spawns with other mates. Further information on the mating system of *H. nigricans* is given in Fischer (1980).

QUESTIONS ABOUT EGG TRADING IN THE BLACK HAMLET

Gamete trading behaviours have been explained by the presumed need, derived from selection against being cheated, for individual partners to ensure reciprocity (Fischer, 1980; Leonard, 1990, 1991; Michiels, 1998). However, certain puzzling aspects of the behaviour and mating system of serranids are not adequately explained by gamete trading. The first of these is that sexual signalling appears to be performed by the 'wrong' sex: in *H. nigricans*, it is the incipient female (egg donor) that generates the putative sexual signals just before the spawn (Fischer, 1980), whereas the incipient male (sperm donor) generates no obvious signal. This contrasts with conventional systems, in which males generate explicit signals conveying their viability and/or attractiveness, and females observe signalling males so as subsequently to perform mate choice based on their receipt of the information contained in those signals. If the serranid mating system is not role-reversed, why do egg-releasing, female-acting individuals, and not sperm-donating, male-acting ones, appear to produce sexual signals? Although male mate choice may be present to some extent in non-role-reversed mating systems, the apparent complete reversal of sexual signalling roles in the serranid system implies that we either misunderstand the mating system or have an incorrect conception of the adaptive function(s) of the observed behaviours.

Related to the question of who is signalling is the sort of information the signals are conveying. For the purposes of this discussion, the term 'sexual signal' is restricted to those behaviours or traits that convey information regarding the performer's viability and/or attractiveness (Andersson, 1994). Sexual selection – differential reproductive success – functions in part to secure the reproductive fitness advantage conveyed by mating with high viability partners. Sexual signals have evolved because they reveal, or even magnify, the otherwise imperceptible viability/quality differences among potential mates. Forward pitch is usually performed by both partners before the first spawn (it is also performed at a lower frequency throughout the spawning bout); it affords the partner an unobstructed view of the signaller's vent region, which may be visibly distended by eggs (Fischer, 1980). To the extent that distension of the vent region correlates with the number of eggs held, forward pitch may be a conventional sexual signal indicating viability and/or fecundity.

An explanation for head snapping is more problematic, as it is unclear how this behaviour could convey viability or attractiveness. Fischer (1980) suggested two possible functions for head snapping. First, because the behaviour is performed consistently by the female-acting partner just before egg release, it signals the onset of this event to the follower or male-acting partner. This proposed function is inconsistent, however, with the varying number (1–9) of head snaps that may be performed before an egg spawn (Fischer, 1980: table 2). If the behaviour were to serve to signal the onset of the spawn, then a single head snap might be expected to suffice; indeed, variable numbers of iterations should corrupt the signal's timing function. Even allowing that head snapping signals the onset of the female spawn, serving this function would not qualify this behaviour as a conventional sexual signal of mate quality, as defined above. Second, Fischer (1980) speculated that head snapping might communicate that an individual has eggs to give up in exchange for the chance to fertilize those of mates. However, its function in this manner would be open to cheating, as there is no apparent reason why an individual unprepared to spawn eggs should be incapable of snapping its head – that is, nothing about head snapping indicates that its performance should correlate with viability or attractiveness.

A third puzzling question, posed by Fischer (1980) himself, is why it pays to reciprocate. That is, once an individual has received and fertilized its partner's first egg spawn, why should that individual remain with the same partner, rather than desert and search for another dupe? Such a male-biased strategy could offer relatively higher overall reproductive success if the cost of finding another partner were less than the cost of producing egg spawns. The density and mobility of hamlets both seem sufficient to allow greater mate desertion and promiscuity than found (Fischer, 1980); although some hamlets mated with two (34%) or three (10%) partners per spawning period, most (56%) mated with only one. Furthermore, the mating success (as measured by total number of spawns) of fishes that mated with one, two or three partners in a spawning period did not differ. What, then, does a first-acting sperm donor gain by remaining with a first-acting egg spawner and reciprocating with that individual by generating its own female spawn? Fischer (1980) speculated that an individual is likely to fertilize more eggs in total if it reciprocates than if it does not, but this is not a satisfying explanation of the observed mate fidelity. For *H. nigricans*, the gamete trading hypothesis does not explain why an individual benefits by remaining with a particular partner after shedding sperm rather than deserting.

SPAWNING EGGS AS A CONVENTIONAL SEXUAL SIGNAL

The adaptive function of sexual behaviors in gonochores is generally understood within the context of sexual signalling of either viability (as indicators of good genes) or attractiveness (via the Fisherian runaway mechanism; Andersson, 1994). In contrast, the possibility that the sexual behaviours of hermaphrodites represent conventional sexual signals has not been thoroughly explored (but see Charnov, 1979; Landolfa, 2002). Rather, existing adaptive explanations for hermaphrodite sexual behaviours are based on conditional reciprocity, a phenomenon for which no analog exists for gonochores. Are the selective pressures on, and the evolutionary responses of, gonochoristic and hermaphroditic mating systems really so distinct (but see Greeff and Michiels, 1999)? Do gonochores alone generate and heed sexual signals, and do hermaphrodites alone engage in conditional reciprocity? The adaptive function proposed here for egg trading in the black hamlet, if successfully validated and extended to other hermaphrodite mating systems, may reconcile our understanding of mating systems in gonochores and hermaphrodites.

The explanation of black hamlet sexual behaviour presented here is that an individual's viability/attractiveness is signalled to potential mates via its spawning of eggs; potential partners base mate choice and/or gamete investment decisions on receipt of this sexual signal. Implementation of the hypothesis resolves the three questions raised above that were inadequately explained by gamete trading.

First, assuming that the serranid mating system is not role-reversed, why does the female-acting (egg-spawning) partner appear to perform conspicuous signals, but not the male-acting (sperm-donating) one? In the original presentation of the gamete trading hypothesis, Fischer (1980) reasoned that because head snapping precedes spawning, it functions as a sexual signal. This interpretation is unlikely to be correct, however, because there is no reason to think that the behaviour contains information regarding attractiveness or viability. What possible function could head snapping serve if it is not a sexual signal? The side-to-side head movement may simply be the initiator's means of keeping the follower within its visual field as it prepares to commence the spawning clasp; that is, head snapping is the initiator's way to check that the follower is 'paying attention'. Close observation of the initiator's head and eye movements during head snapping and of the relative position of the follower might reveal whether this hypothetical function is plausible. In addition, one of Fischer's (1980) explanations for head snapping, that it signals the initiator's readiness to begin the spawning clasp as an egg donor, may still apply. Whether head snapping serves an orientation, intentional or some other role, it is unlikely to function as a conventional sexual signal. But which behaviour or trait, if any, does serve as a sexual signal in this system?

To answer this we turn to the second question, regarding the information contained in black hamlet sexual behaviours. Behaviours or traits whose magnitudes correlate with genetic quality or attractiveness may function as conventional sexual signals. Forward pitch may represent such a sexual signal, as it allows the prospective mate – the one about to shed sperm – a clear view of the signaller's vent area. For forward pitch to be considered a reliable signal of viability or female reproductive potential, the frequency with which the display is performed and/or the extent of swelling, local colour/reflectance change, or other signal parameter should be correlated with the number of eggs spawned – a testable hypothesis. However, the exclusive use of forward pitch as the sexual signal could leave signal receivers vulnerable to bluffing if individuals with strong forward pitch signals were unable or unwilling to spawn eggs. Thus a more reliable signal of viability and/or attractiveness may be the actual spawning of eggs, about which the performance of forward pitch provides preliminary information. The sequence of the behaviours (forward pitch followed by spawning) is consistent with this interpretation.

Finally, why should a follower that has just fertilized the initiator's first egg spawn remain and reciprocate with that partner, instead of deserting to replay the male role with another dupe? If the egg spawn functions in part as a sexual signal, the incentive to reciprocate is clear: the initiator's (egg spawner's) high-magnitude sexual signal (many spawned eggs) indicates a mate of high viability/attractiveness and will, accordingly, be assessed positively by the follower. Just as female gonochores receive and assess signals generated by males, the follower evaluates the initiator based on the latter's egg spawn signal. A positive evaluation induces the follower to remain with the same partner and to have its eggs fertilized by it – a testable hypothesis (Sella and Lorenzi, 2000), but one that will be difficult to differentiate from conditional reciprocity. The curious situation presented by the egg-spawn-as-sexual-signal hypothesis is that the initiator's egg spawn serves both a female function (female gamete production) and a traditionally male function (sexual signal). Similarly, the follower performs two roles simultaneously – shedding sperm (male function) and assessment of its partner's sexual signal (female function).

CONCLUSIONS

My intent has been to re-interpret the sexual behaviours of the hermaphroditic black hamlet, *H. nigricans*, from the perspective of modern sexual signalling theory, which is well-accepted as an explanation for most mating behaviours in gonochores. This re-interpretation suggests that conventional sexual signalling, in which individuals (usually males) express traits that are perceived and used by potential partners (usually females) as the bases for mate choice, may profitably be applied as well to hermaphroditic sexual behaviours. Although the available evidence certainly does not refute gamete trading (conditional reciprocity to mitigate against cheating and ensure mating in both sexual roles) as an explanation for hermaphroditic sexual behaviours, I have tried to show that conventional sexual signalling is able to address specific characteristics of the *H. nigricans* mating system that are not well explained by gamete trading.

Performing definitive tests of the conventional sexual signalling hypothesis in the black hamlet system will be difficult because of this species' experimental intractability. Nonetheless, existing and new observational data may be marshalled to support or refute the hypothesis. For example, the fact that the smaller of the two partners of a mating pair spawns more frequently as a female (Fischer, 1980) is puzzling, unless the female spawn represents a conventional sexual signal. The hypothesized functions of head snapping – that it is either a means by which the initiator monitors the follower or a signal of proximate intention – might be substantiated by close observation of mating pairs. Also testable is the proposed correlation between the magnitude of forward pitch and the number of eggs spawned. For the purpose of manipulating the number of eggs perceived by partners (to test their signal values), the annelid *Ophryotrocha* (Sella *et al.*, 1997) may be a more tractable experimental system than *H. nigricans* or other serranids. The variations among the mating systems of the multiple species within both the serranids (see references in Petersen, 1995) and *Ophryotrocha* (Sella and Lorenzi, 2000) represent useful material for comparative studies.

Studies addressing the questions posed above might distinguish the relative contributions of conventional sexual signalling and gamete trading in the evolution of the relevant mating systems, thus having wider implications for the understanding of mating systems in general.

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