

## FORUM

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**Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours?**

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In an earlier paper, I proposed the use of unified functional terms for the description of alternative reproductive behaviours (Taborsky 1994). Here I aim to explain why I regard this as useful for our understanding of the functional and evolutionary background of alternative mating tactics, and I argue that the pair of terms “bourgeois – parasitic” is probably most adequate.

Animals may either invest to gain access to a resource directly or they may try to gain access by exploiting the investment of others. Specialization in one or the other possibility may exist at all different levels, from taxonomical entities like species (producers and scroungers) down to individuals, or even successive actions of individuals (see Barnard 1984). In reproduction, for example, males may invest to gain primary access to females by direct monopolization via defence, by monopolizing resources important to females, or by using attracting traits such as courtship or secondary sexual characters. Alternatively, males may avoid making such investment and instead specialize in obtaining direct access to female gametes without claiming a monopoly on females, and irrespective of female interests (Taborsky 1994). These two alternatives are very widespread and appear to be distributed throughout most animal taxa (Gross 1996).

If we are interested in the adaptive value of such behavioural tactics, we should refer to them with functional terms. This facilitates comparisons of these phenomena between taxa and the search for essential, functional characteristics. In animal behaviour research, both descriptive terms (tail wagging, ramming, biting) and functional terms (courting, defending, ingesting) are

used. The former indicate the form of behaviour, while the latter are often collective terms describing functional units that may serve similar purposes, or result from similar selection regimes. We may speak of a “head shake” if we are interested in the form of the behaviour or in the morphological and physiological mechanisms involved, whereas we may call it a “submissive display” if we refer to its functional context.

Often, males exploiting the reproductive investment of other males have been referred to by descriptive terms such as sneakers, streakers, hidlers, stunted males, supernumerary males, small outlier males or interference spawners, just to give some examples from the fish literature. These terms are also applied sometimes as collective, functional terms in a metaphorical sense (e.g. ‘sneaking’ is also used to describe very conspicuous, parasitic behaviour of males), which is misleading. The common characteristic of this tactic is that the effort of others is exploited; therefore, I proposed to call males pursuing this tactic ‘parasitic males’ or ‘male reproductive parasites’ (Taborsky 1994).

Males trying to monopolize females have been referred to by a variety of descriptive and functional terms, for example, guarders, large males, fighting or courting males, owners, pair males, territorial males, primary males, parentals, Type I males or cuckolds. Usually, these terms have been adopted to describe a specific situation in a particular example. The common characteristic of this tactic is that males invest in special features with the aim of gaining privileged access to females. This investment may be behavioural (e.g. defence, courtship), physiological or morphological (e.g. secondary sexual characters). This does not preclude, however, that a male pursuing this tactic may also exploit the investment of conspecific neighbours if the opportunity arises. To meet the demands for a uniform term representing the functional essence of this reproductive tactic, I proposed to call these males ‘bourgeois’ (Taborsky 1994). In the behavioural context this term has been used mainly in biological game theory to des-

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cribe a strategy characterized by behaving as “owner” in a territory, i.e. with a high tendency to fight if challenged, while behaving as “intruder” in others’ territories, i.e. with an increased likelihood of retreat if challenged (e.g. Maynard Smith 1982, Parker 1984, Gerard and Quenette 1992; see McFarland 1993, pp 101–102, for a discussion of examples). Even though the context in which I use this term is reproductive rather than agonistic, I think the term bourgeois exactly matches the connotation of this behavioural strategy (see e.g. Taborsky 1994, Wedekind 1996, Martin and Taborsky 1997).

A number of alternative functional terms have been used to describe parasitic and bourgeois male reproductive behaviours. There are several problems with these terms, however:

1. Some of them reveal little about the functional role of these tactics; for example, the terms Type II males, males pursuing secondary tactics, or accessory males standing for reproductive parasites; Type I males or primary males for bourgeois males.

2. Other terms may represent only one particular functional aspect of the respective tactic, e.g. for parasitic males: female mimics, pseudofemales, transvestite males, opportunist males, outsiders of fertilization, cuckolders, or satellites; for males pursuing the bourgeois tactic: pair males, territorial males, cuckolds or parentals.

3. The pairs of terms with the most general, functional meaning are producer-scrunner and owner-intruder. The first pair of terms is perhaps too general to be correctly understood in this context and may be misleading (males in the bourgeois position do not necessarily “produce” anything, e.g. they may monopolize a female merely following an earlier or quicker approach to her). The second pair of terms is adequate for a territorial situation but less so in numerous species that lack territorial behaviour (see Taborsky 1994 for a review in fish).

The term “bourgeois” is not as commonly used in the behavioural literature as is its counterpart “parasite”, perhaps because of its sociological roots. This may call for a substitution of this term. The most adequate alternative to the term bourgeois in this context might be “males investing in primary access to females”, or “primary access males” as an abbreviation. I prefer bourgeois to this alternative, however, because:

1. “Primary access males” does not imply that a male investing in primary access to females (e.g. a defender of a reproductive territory) may also exploit the investment of others (e.g. territorial neighbours); “bourgeois” does strongly imply this possibility because of its meaning in biological game theory.

2. This alternative term is more cumbersome, even if abbreviated, and the abbreviated form does not stress an important constituent of this tactic, which is the investment necessary to obtain primary access.

In conclusion, I argue that functional terms are needed to address alternative reproductive tactics. I regard the pair of terms “bourgeois – parasitic” as most adequate for a general description of these functionally opposing male reproductive behaviours, because of their connotation in other fields of biology (parasitic: field, zoology; context, alimentary behaviour; bourgeois: field, biological game theory; context, spacing behaviour). Even though this pair of terms has only been used to address male reproductive tactics as yet, I propose its application to female reproductive tactics as well (see Taborsky 1994 for a discussion). In this context, bourgeois would denote females investing in, for example, territory maintenance, nest building and brood care, while a parasitic female would dump her eggs in the nest of bourgeois conspecifics. As in the case of their male counterparts, bourgeois females may also exploit the investment of other bourgeois females if the opportunity arises.

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