Animal Behaviour 89 (2014) 171–183

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

# Bourgeois versus anti-Bourgeois: a model of infinite regress

Mike Mesterton-Gibbons [a,*], Tom N. Sherratt [b,1]

[a] Department of Mathematics, Florida State University, Tallahassee, FL, U.S.A.
[b] Department of Biology, Carleton University, Ottawa, ON, Canada

ARTICLE INFO

*Article history:*
Received 21 September 2013
Initial acceptance 25 November 2013
Final acceptance 2 January 2014
Available online 7 February 2014
MS. number: A13-00796

*Keywords:*
animal contest
Bourgeois
evolutionarily stable strategy
game theory
Hawk–Dove model
infinite regress
ownership
private property
territoriality

One of the first applications of game theory in the field of animal behaviour was to show that respect for ownership (Bourgeois behaviour) can arise as an arbitrary convention to avoid costly disputes. However, this same theory indicated that a mirror-image dispute-avoiding convention in which owners concede their property to intruders (anti-Bourgeois) is also stable under the same conditions. It has since been shown repeatedly that the first individuals to find resources are frequently left unchallenged, while evidence for the alternative convention, according to which owners relinquish property to intruders without conflict, is rare at best. By far the most commonly invoked explanation for the rarity of anti-Bourgeois is that two individuals employing such behaviour over repeated rounds would be swapping roles continually, a potentially inefficient outcome known as 'infinite regress.' Here we set out to test the validity of this verbal reasoning by analysing a Hawk–Dove model with ownership asymmetry but introducing a fixed probability $w$ that two individuals meet again. While assuming that the resource has value to the winner (realized either at the end of the interaction, or after each round) and losers of fights pay costs, we also assume that individuals incur costs in taking ownership and relinquishing it. Contrary to expectation and despite the inefficiency of the anti-Bourgeois equilibrium, 'infinite regress' does not always render anti-Bourgeois unviable. Indeed if fighting is cheap, then repeated interactions can generate an anti-Bourgeois equilibrium where previously only obligate Hawk was a stable population strategy. Nevertheless, when probability $w$ exceeds thresholds determined by the costs of taking and relinquishing ownership, Bourgeois can become the only stable convention. Collectively, our model demonstrates that although infinite regress can facilitate the evolution of Bourgeois-like conventions, it is no panacea.


Individuals that are the first to find valuable resources are frequently left unchallenged by conspecifics, and are more likely to win contests if disputes arise (Gintis, 2007; Kokko, López-Sepulcre, & Morrell, 2006; Stake, 2004). Classically, our understanding of this respect for private property derives from an extension of the two-player Hawk–Dove game of animal conflict (Maynard Smith & Parker, 1976; Maynard Smith & Price, 1973), in which the status of owner is unambiguously perceived. Briefly, the model assumes that the resource has fixed value $V$. Should a fight arise, then the loser pays a cost $C$. Hawks are aggressive individuals prepared to fight to retain or gain a contested resource, while Doves are more passive individuals who display but retreat if their opponent escalates. When ownership is recognized by both parties, there are four possible role-dependent strategies. Obligate Hawk or H individuals are prepared to fight to retain or gain a contested resource, regardless of whether they are owners or intruders. By contrast, obligate Dove or D individuals always display, and retreat in either role if their opponent escalates. Bourgeois or B individuals are prepared to fight to retain a resource, but display in the role of intruder. Conversely, anti-Bourgeois or X individuals display as owners, but contest as intruders.

The simplest and most common variant of the above model (Maynard Smith, 1982) assumes that individuals encounter one another in pairs, with current ownership determined at random. Although the nature of the payoff structure depends on whether Dove-like (D or B) intruders are 'intrusive' or 'nonintrusive' (Mesterton-Gibbons, 1992), that is, whether or not they seek to obtain the property from Dove-like (D or X) owners, in both forms of the game, obligate Hawk (H) is the only evolutionarily stable strategy or ESS when $V > C$ (Maynard Smith, 1982). If, on the other hand, fighting is so costly that $V < C$, then Bourgeois (B) and anti-Bourgeois (X) are both ESSs in the classical (intrusive) game. Both B and X are competitively successful because they use the arbitrary convention of current ownership to settle disputes without incurring costly fighting.

* Correspondence: M. Mesterton-Gibbons, Department of Mathematics, Florida State University, 1017 Academic Way, Tallahassee, FL 32306-4510, U.S.A.
*E-mail address:* mesterto@math.fsu.edu (M. Mesterton-Gibbons).
[1] *E-mail address:* sherratt@connect.carleton.ca.

0003-3472/$38.00 © 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2014.01.002

The Hawk–Dove game with ownership asymmetry is remarkable in allowing for entirely peaceful ESSs based on convention if $V < C$, when there would always be at least a proportion of individuals playing Hawk in a population of obligate Hawks and Doves. Moreover, the observation that Bourgeois is an ESS has helped to explain a wide variety of empirical observations, beginning with early accounts of resident butterflies consistently winning territorial disputes without significant contests (Davies, 1978; Maynard Smith & Parker, 1976). Indeed the possibility that such a simple model might strategically explain a wide variety of empirical observations has continued to excite researchers for decades (e.g., Wenseleers et al., 2013).

Nevertheless, there is a well-known problem with the above model, namely, that anti-Bourgeois is also an ESS. While conflict-avoiding Bourgeois is seen as a 'common sense' convention, the alternative convention of giving property away to individuals that challenge for it appears so counterintuitive that it has been labelled 'paradoxical' (Maynard Smith, 1982). Indeed plausible examples of anti-Bourgeois are few and far between (Kokko et al., 2006). Even those rare examples of anti-Bourgeois reported in the literature may have arisen from a misunderstanding of what anti-Bourgeois behaviour actually entails (Hernández & Benson, 1998, see Field & Hardy, 2000) as well as through additional confounding asymmetries (Goubault, Batchelor, Linforth, Taylor, & Hardy, 2006; see Bentley, Hull, Hardy, & Goubault, 2009).

One reason why the paradoxical anti-Bourgeois strategy may be rare is that there exists a 'correlated asymmetry', in that owners tend to have higher resource holding potential (RHP) than intruders (e.g. Fayed, Jennions, & Backwell, 2008; Kemp & Wiklund, 2004) or tend to value the resource more than intruders (for example, when the owner has engaged in 'nontransferable work'; Kokko, 2013). However, even when such correlated asymmetries exist, anti-Bourgeois can remain an ESS, albeit under a more restricted set of conditions (Hammerstein, 1981; Maynard Smith, 1982). Instead, perhaps the most commonly invoked explanation for why the anti-Bourgeois strategy is so rare, and appears so paradoxical, is that two individuals employing anti-Bourgeois behaviour over repeated rounds would be swapping roles continually. Maynard Smith (1982, p. 96) highlighted this obvious deficiency noting that: 'The difficulty with strategy X is that it leads to a kind of infinite regress, because as soon as an owner loses a contest it becomes an intruder, and hence able to win its next contest. We are unlikely, therefore, to meet strategy X when the contested resource is of value only if it can be held for a long time'. This view has since been reinforced, not only by Maynard Smith and Harper (2003), but also by many other authors. For example, Yee (2003) noted that 'In an AP (anti-Possessor = anti-Bourgeois) culture, citizens are forced to alternate as owners and intruders in an unending tag-team match. Due to relocation costs, AP is not as viable as P (Bourgeois)'. Likewise, McElreath and Boyd (2007, p. 58) proposed that 'since an Anarchist (anti-Bourgeois) would be displaced by another, or even by the one it had just displaced, this strategy seems unlikely to be stable in even a slightly more realistic model'. Echoing Maynard Smith (1982), Krier (2009) argued that 'Animals behaving in anti-Bourgeois fashion would end up constantly moving around, looking for territory and occupying it, only to be quickly displaced. There would be no time for breeding'.

Of course, anti-Bourgeois does appear to be an extremely inefficient way of deciding ultimate ownership when repeated interactions are possible, especially in cases that involve significant opportunity costs (time spent role swapping is time not spent on other activities) or 'conveyance' (entry and departure) costs. Note, however, that efficiency in itself is not a prerequisite for stability. Thus, even if anti-Bourgeois have low payoffs against one another, by definition, X would remain an ESS if alternative strategies played against X had even lower payoffs. Maynard Smith (1982, p. 101) chose not to present a model involving infinite regress, and to our knowledge the consequences of repeated interactions have never been elucidated in the type of strategic model for which Maynard Smith has been justly acclaimed. Without such a model we should be cautious in accepting the widespread notion that continued role swapping will in itself render anti-Bourgeois unviable. Indeed, in ecologically motivated models involving repeated interactions of conspecifics over multiple resources, the anti-Bourgeois strategy either has been found a common outcome of natural selection (Mesterton-Gibbons, 1992), or has at least turned up as an occasional stable equilibrium (Kokko et al., 2006).

The aim of this paper is to develop and characterize a strategic model of conflict based on the classical Hawk–Dove model with ownership asymmetry, this time allowing for repeated interactions between players and introducing a transaction cost for transfer of ownership. Arguably, models incorporating infinite regress have already been presented by Mesterton-Gibbons (1992) and Kokko et al. (2006) in the context of territorial behaviour and by Broom, Luther, and Ruxton (2004) in that of kleptoparasitism, but these models were detail-rich, making it difficult to isolate the effects of repeated role swapping from other aspects of the models, such as the tendency for good fighters to become owners. Yet game-theoretic models are often most valuable when used to expose the logic of verbal arguments cleanly and unambiguously. Accordingly, here we trade ecological realism for enhanced transparency and analytical tractability by developing a classical Hawk–Dove model in which pairs of individuals repeatedly interact over a single indivisible resource in the roles of owner and intruder, using only strategies H, B, D or X in the absence of any advantage to an owner in the event of a fight. Thus both Bourgeois and anti-Bourgeois, when evolutionarily stable, are purely arbitrary conventions. As with Maynard Smith and Parker (1976, p. 159), it is not part of our argument that owners and intruders do not differ in RHP or in the value they place on a contested resource. Instead, we simply wish to establish the conditions under which ownership itself is capable of settling contests without fighting, were such correlated asymmetries absent. If respect for ownership is shown to be a widespread stable convention under these conditions, then clearly one would not need to invoke additional factors such as correlated asymmetries to understand it.

## METHODS AND RESULTS

We use the methods of evolutionary game theory (see, e.g. Broom & Rychtář, 2013) to develop a model that captures what we think Maynard Smith (1982, p. 96) most likely meant by infinite regress.

### *Mathematical Model*

Consider a pair of animals, drawn at random from a large population containing many such pairs, contesting an indivisible resource through repeated rounds of interaction of indeterminate duration. Each round is followed by a subsequent round with constant probability $w$, where $w < 1$. At each round, one of the animals is an owner and the other is an intruder. We denote these roles by O and I, respectively. There are thus four possible transitions between roles, from O to O, from O to I, from I to O and from I to I. When the interaction ceases, so do all transitions: the current owner remains an owner and the current intruder remains a nonowner.

We consider two versions of our model. In the first version, which we call Model 1, the resource yields no value until the interaction ceases. It is then worth $V$ to its ultimate owner. In the