Animal Behaviour 78 (2009) 949–959

Contents lists available at ScienceDirect

Animal Behaviour

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

Honest and cheating strategies in a simple model of aggressive communication

Ferenc Szalai [a,1], Szabolcs Számadó [b,*]

[a] Research Institute for Solid State Physics and Optics, Hungarian Academy of Sciences
[b] Department of Plant Taxonomy and Ecology, HAS Research Group of Ecology and Theoretical Biology, Eötvös Loránd University

ARTICLE INFO

Article history:
Received 3 August 2007
Initial acceptance 12 November 2007
Final acceptance 22 June 2009
Published online 27 August 2009
MS. number: 9479R

Keywords:
cheating
communication
honesty
mixed equilibrium
value of information

The honesty of communication in competitive situations has long been debated. We investigated the coexistence of a diverse set of strategies in a simple model of aggressive communication by means of individual-based computer simulations. The game is an extended Hawk–Dove game in which there are two types of individual, weak and strong, and in which individual can communicate by means of cost-free signals before deciding whether to attack. The available strategies can be classified into three categories: honest, cheaters and those that ignore the signalling system. We found a diverse set of equilibria, most of them consisting of a mixture of honest and cheating individuals. We found that when starting populations consist of all strategies (1) the honest equilibrium can evolve, (2) communication is almost always present when signals are informative, and (3) strategies that ignore signalling are generally rare. Honest individuals need not be the majority in these populations yet communication will be present and stable in the long run. In contrast, the pure honest equilibrium is unlikely to evolve when the starting populations consist of strategies that ignore signals. Strategies that ignore signals are more frequent in these types of run however, signalling strategies are still present in the most frequently evolved equilibria. Even in this simple system two different kinds of use of signals can evolve: the first when signals refer to resource-holding potential and a second where signals are used to create a payoff-irrelevant asymmetry. In general, regardless of the starting conditions, a low resource value favours weak individuals, both honest and cheaters, and cowards, medium values favour strong individuals that use and listen to signals, and a high resource value favours strong individuals that ignore the signalling system and attack under all conditions. Although it is possible to find parameter combinations with a negative value of information, the value of information is positive in the overwhelming majority of equilibria. Thus one can conclude that for the majority of parameter combinations an equilibrium evolved that might not be honest, not even on average, but communication is present and signals are worth listening to.

Conflict of interest is a major obstacle in the way of honest communication. It follows that honest communication in competitive situations always demands special explanation, as by definition conflict of interest exists between competitors. Accordingly, some early investigators claimed that honest communication is not possible under such circumstances (Maynard Smith 1974). Enquist (1985) was able to show with the help of a simple game-theoretical model that honest communication of relevant states can be evolutionarily stable in such a competitive situation provided that some conditions are met. It turned out, however, that it is possible to find a mixed equilibrium in Enquist's model in which honest and cheating strategies can coexist and where the frequency of cheaters can be arbitrarily high (i.e. close to one; Számadó 2000). There is also a growing literature on the use of honest and cheating signals in nature. Examples include Batesian mimicry in butterflies (Wiley 1983); reproductive strategies of bluegill sunfish, *Lepomis macrochirus* (Dominey 1980; Gross & Charnov 1980) and damselflies, *Ischnura ramburi* (Robertson 1985); aggressive communication in stomatopods (Caldwell & Dingle 1975; Adams & Caldwell 1990), fiddler crabs, *Uca annulipes* (Backwell et al. 2000), snapping shrimps, *Alpheus heterochaelis* (Hughes 2000), hermit crabs, *Pagurus bernhardus* (Elwood et al. 2006) and American goldfinches *Carduelis tristis* (Popp 1987); and finally signalling in cleaner–client systems (with the cleaner *Labroides dimidiatus*; (Bshary & Grutter 2002). In parallel with these observations there are a growing number of theoretical models that try to explain the existence of these signalling systems (Johnstone & Grafen 1993; Adams & Mesterton-Gibbons 1995; Viljugrein 1997; Számadó 2000; Freckleton & Cote 2003). Although these models established that

* Correspondence: S. Számadó, Department of Plant Taxonomy and Ecology, HAS Research Group of Ecology and Theoretical Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c., H-1117 Budapest, Hungary.
E-mail address: szamszab@ludens.elte.hu (S. Számadó).
[1] F. Szalal is at the Research Institute for Solid State Physics and Optics, Hunagrian Academy of Sciences, P. O. Box 49, H-1525 Budapest, Hungary.

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.06.025

cheating strategies can coexist with honest strategies under some conditions, they mostly focused on only one kind of cheating, namely when weak individuals pretend to be strong. However, there can be different kinds of cheating strategies, as well as strategies that ignore the signalling system as opposed to the simple scenario described above. Although the existence of these strategies is known and the stability of the honest equilibrium against these strategies has been investigated by several authors (Owens & Hartley 1991; Johnstone & Norris 1993; Hurd 1997; Számadó 2000), the interactions of these strategies and the emerging signalling equilibria have not yet been investigated. We ran a series of computer simulations to investigate the interactions of eight different strategies. Two of these strategies can be considered as honest, two of them as cheaters, and finally four of them ignore the signalling system but each behaves in a different way. These strategies could interact according to a simple symmetric game of communication introduced by Enquist (1985). We asked the following questions (1) What kinds of equilibria evolve out of random and honest starting populations as opposed to starting populations that consist of strategies that ignore signals? (2) What is the frequency of the honest equilibrium at these equilibria? (3) What kinds of equilibria are possible? (4) What is the relation between the value of information (as defined by Lachmann & Bergstrom 2004) and honesty? (5) Is it possible to get equilibria with a negative value of information?

THE MODEL

We used Enquist's (1985) model of aggressive communication. Consider a modified version of the Hawk–Dove game (Maynard Smith 1982), where each player can be weak or strong, with a probability q and $1-q$, respectively, and knows its own level of strength but not that of the opponent. The contest consists of two steps. In the first step, each player can choose between two cost-free signals A or B; in the second step, each animal can give up (flee), attack unconditionally (fight) or attack if the opponent does not withdraw (conditional attack). Let V denote the value of the contested resource, C_{ww} and C_{ss} the expected cost of a fight between weak and strong individuals, respectively. We assume that the expected benefit of a contest between weak individuals is always greater than zero, $0.5V-C_{ww}>0$. In contrast, we assume that the expected payoff of a fight between strong individuals is smaller than zero, $0.5V-C_{ss}<0$. The reason behind this assumption is that weak individuals are expected to settle the contest in a less violent manner (thus probably suffering few or no injuries) than strong individuals. We further assume that a strong animal can always beat a weak one with a cost C_{sw}, and C_{ws} is the expected cost that a weak animal should suffer on this occasion. The following relation holds between these costs: $C_{ss}>C_{ws}>C_{ww}$, and $C_{ss}>C_{sw}>C_{ww}$. In addition, there is a cost of attacking a fleeing opponent (F_A), and of waiting if the opponent attacks unconditionally (F_P). It is biologically realistic, but not necessary, to assume that $C_{sw}>F_A$ and F_P (Hurd 1997). Finally, a fleeing player does not have to pay the full cost of the fight, that is, it gets a fixed reduction (F_F) in the fighting cost. We have chosen the payoffs $0.5V-C_{ss}$ and $0.5V-C_{ww}$ when equal opponents decide to flee instead of the original $0.5V$. Then the payoffs for weak and strong contestants can be written as shown in Table 1.

Introduction of the Possible Strategies

A strategy is a specification of three things. (1) What kind of signal should a player give: A or B? (2) How should it react to signal A: flee, attack or conditional attack? (3) Finally, how should it react to signal B? Here the options are the same as before. The strategy set (**S**), which consists of eight strategies ($N_s=8$) is as follows.

(1) Honest–strong (Shs): give signal A; if opponent gives signal A then attack. If it gives signal B then wait until it flees. If it does not flee then attack (that is, after signal B use conditional attack).

(2) Honest–weak (Shw): give signal B; if opponent gives signal A then flee. If it gives signal B then attack.

(3) Liar–strong (strong) (Sls): give signal B; if opponent gives signal A then flee. If it gives signal B then attack.

(4) Liar–weak (weak) (Slw): give signal A; if opponent gives signal A then flee; if it gives signal B then use conditional attack.

(5) Coward A (weak) (ScA): give signal A; flee regardless of the opponent's signal.

(6) Coward B (weak) (ScB): give signal B; flee regardless of the opponent's signal.

(7) All-attack A (strong) (SaaA): give signal A; attack regardless of the opponent's signal.

(8) All-attack B (strong) (SaaB): give signal B; attack regardless of the opponent's signal.

The strategy set is described in Table 2. Table 3 shows how the strategies map ($b:\mathbf{S}\times\mathbf{S}\rightarrow\mathbf{B}$) to behaviours. We call this mapping the behaviour map.

SIMULATION TECHNIQUE

We investigated the model by means of computer simulation because of the complexity of the problem, which makes analytical solutions hard to obtain (for a simple three-strategy interaction and investigation of cheating as a mixed strategy see Számadó, 2000) The simulation is an individual-based representation of the model. We assume a well-mixed, asexual population of N individuals. Individuals have four genes represented by four bits. These genes

Table 1
The payoff matrix (after Számadó 2000)

	SA	ScA	SF	WA	WcA	WF
SA	$0.5V-C_{ss}$	$0.5V-C_{ss}$	$V-F_A$	$V-C_{sw}$	$V-C_{sw}$	$V-F_A$
ScA	$0.5V-C_{ss}-F_P$	$V-C_{ss}$	V	$V-C_{sw}-F_P$	$V-C_{sw}$	V
SF	$-C_{ss}+F_F$	0	$0.5V-C_{ss}$	$-C_{sw}+F_F$	0	$0.5V$
WA	$-C_{ws}$	$-C_{ws}$	$V-F_A$	$0.5V-C_{ww}$	$0.5V-C_{ww}$	$V-F_A$
WcA	$-C_{ws}-F_P$	$-C_{ws}$	V	$0.5V-C_{ww}-F_P$	$0.5V-C_{ww}$	V
WF	$-C_{ws}+F_F$	0	$0.5V$	$-C_{ww}+F_F$	0	$0.5V-C_{ww}$

S and W denote strong and weak individuals, respectively, and A, cA and F denote attack, conditional attack and flee behaviours. V denotes the value of the contested resource, C_{**} denotes the expected cost of a fight between given pairs of individuals where * can be weak (w) or strong (s). In addition, there is a cost of attacking a fleeing opponent (F_A), and of waiting if the opponent attacks unconditionally (F_P), and finally, a fleeing player does not have to pay the full cost of the fight, that is, it gets a fixed reduction (F_F) of the fighting cost.

Table 2
Definition of strategies

Strategies	Strong	Use signal?	Signal	Behaviour against opponent that signals	
				A	B
Honest–strong (Shs)	Yes	Yes	A	Fight	Conditional attack
Honest–weak (Shw)	No	Yes	B	Flee	Fight
Liar–strong (Sls)	Yes	Yes	B	Flee	Fight
Liar–weak (Slw)	No	Yes	A	Flee	Conditional attack
Coward A (ScA)	No	No	A	Flee	Flee
Coward B (ScB)	No	No	B	Flee	Flee
All-attack A (SaaA)	Yes	No	A	Fight	Fight
All-attack B (SaaB)	Yes	No	B	Fight	Fight

The table shows the various strategies, whether they use signals or not, and what behaviour they select in response to signals A and B. The columns give the name of the strategy, its strength, whether the given strategy listens to signals or not, which signal the animal should give, and the following behaviour as a function of the opponent's signal.