



Contents lists available at ScienceDirect

Journal of Theoretical Biology

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

Contract theory for the evolution of cooperation: The right incentives attract the right partners

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ARTICLE INFO

Article history:

Received 30 September 2010

Received in revised form

15 October 2010

Accepted 20 October 2010

Available online 28 October 2010

Keywords:

Mutualism

Symbiosis

Screening

Game theory

ABSTRACT

Partner choice is a critical stage of many biological interactions, from mating to cooperation. When the quality of the potential partners is unknown, one way to choose is to rely on signaling: costly signals can reveal the quality of the sender and allow the receiver to choose. In some cases, however, signaling (or an active choice based on signals) is not possible, for example in the initiation of the symbiosis between the squid *Euprymna scolopes* and the bioluminescent bacterium *Vibrio fischeri*. How is partner choice possible in this and other similar cases? I show that in a game with asymmetric information without signaling, imposing a deliberate cost for establishing the interaction allows the non-informed individual to attract the right partner if the cost induces only high quality individuals to accept the interaction. Furthermore, imposing different costs and rewards may induce the informed individuals to screen themselves according to their types, and therefore allow the non-informed individual to establish an association with the correct partners in the absence of signaling.

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1. The problem

1.1. Partner choice

How to choose among potential partners when their quality is unknown? In many pairwise interactions one party has relevant information (for example about his own quality) that the other party does not have. Consider mate choice: in many species females choose males (Andersson, 1995), but they cannot observe their quality directly. While females prefer males of good quality, males would find it profitable to mate irrespective of their quality, therefore they have an incentive to reveal their real quality only if they are good, and to pretend they are good if they are not. How can a female tell a good quality male from a bad quality one? The problem of partner choice (Bull and Rice, 1991; Noë and Hammerstein, 1994; Sachs et al., 2004) is not restricted to sexual selection; it is relevant in any situation in which information is asymmetric.

1.2. Signaling

One way to solve the problem of asymmetric information is by signaling: if the signal has a cost, only good quality individuals will find it profitable to advertise their quality, therefore the signal will be honest. Signaling theory is well known in the context of mate

choice and is relevant to other cases of partner choice. In fact it was introduced initially in economics by Spence (1973) and verbal arguments had been put forward already by Veblen (1899). It was introduced in evolutionary biology by verbal arguments by Zahavi (1975) and formal models by Grafen (1990) and others, and a vast literature on signaling exists (Searcy and Nowicki, 2005; Maynard Smith and Harper, 2003). But what happens when signaling is not possible?

1.3. Partner choice without signaling?

Consider the mutualism between the bioluminescent bacteria *Vibrio fischeri* and the squid *Euprymna scolopes*, one of the most well studied symbioses (Ruby and McFall-Ngai, 1999; Small and McFall-Ngai, 1999; Visick and Mcfall-Ngai, 2000; Visick et al., 2000): the bacteria produce light for the squid while the squid provides shelter for the bacteria. Both luminescent and non-luminescent bacteria exist, and bacteria cannot signal their quality (they are not visible and luminescence occurs only inside the squid), therefore squids are not able to tell good (luminescent) from bad (non-luminescent) bacteria in advance. And yet only luminescent bacteria are normally found in the light organs of the squid. How does a squid manage to interact only with the luminescent bacteria and avoid the non-luminescent ones? Other examples exist in which the informed individual cannot signal or the non-informed individual cannot choose. For example, how do ant-plants recruit only mutualistic ants? In general, is partner choice possible in the absence of signaling?

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1.4. A cost for entry

The idea of this paper is that there is a solution to the problem of partner choice that does not require signaling. The non-informed individual (the squid for example) can impose a cost for entering the interaction that will lead the possible partners (the bacteria) to screen themselves according to their own interest: if entering the interaction is too costly for low quality individuals (non-luminescent) but not for good quality (luminescent) individuals, then only high quality individuals will find it profitable to enter. This strategy, imposing a cost for establishing the interaction, can induce partners of unknown quality to screen themselves according to their own quality, even though the non-informed individual neither observes quality nor any signal.

2. The contract game

Consider the following game. One individual (the principal) invites another (the agent) to carry out an action; the action requires a cost by the agent and produces a benefit for the principal; the principal pays a reward to the agent. Agents can be of two types x : high ($x=Q$) or low ($x=q$) quality, chosen by nature, known to the agent but unknown to the principal. Agents cannot signal their type. Principals cannot choose the reward based upon the quality or the actions of the agent; instead, the principal can only set up certain fixed conditions (a reward offered and an effort required) that agents of unknown quality can only accept or reject. Our question is: is it possible for a principal to design the right costs and rewards to attract only Q agents?

Agents can choose to remain free-living or engage in the interaction, based on their own quality. Agent strategy \mathbf{a}_i is defined by the vector $\mathbf{a}_i=[a_i(Q), a_i(q)]$, where $a_i(x)$ is the probability that when the agent is of quality x , he enters an interaction with the principal. The four possible pure strategies \mathbf{a}_i are as follows:

- $\mathbf{a}_1=[0, 0]$ (never enter).
- $\mathbf{a}_2=[1, 0]$ (enter only if Q).
- $\mathbf{a}_3=[0, 1]$ (enter only if q).
- $\mathbf{a}_4=[1, 1]$ (always enter).

Principals can be demanding or non-demanding. Principal strategy p_j is defined by the probability that the principal imposes a cost on the agent to enter the interaction. The two pure strategies are as follows:

- $p_1=1$ (demanding).
- $p_2=0$ (non-demanding).

The fitness of agent strategy \mathbf{a}_i is

$$W(\mathbf{a}_i) = \sum_{j=1,2} f_{p_j} \sum_{x=q,Q} f_x \{ a_i(x)[p_j(1-\alpha_x) + (1-p_j)(1)] + [1-a_i(x)]\phi_A \}$$

The fitness of principal strategy p_j is

$$W(p_j) = \sum_{i=1,4} f_{\mathbf{a}_i} \sum_{x=q,Q} f_x \{ a_i(x)[(1-\pi_x)] + [1-a_i(x)]\phi_p - \delta p_j \}$$

where f_{p_j} is the frequency of principal strategy p_j , $f_{\mathbf{a}_i}$ is the frequency of agent strategy \mathbf{a}_i , f_x is the frequency of agents of quality x , α_x is the cost paid by an agent of quality x interacting with a demanding (p_1) principal ($\alpha_q > \alpha_Q$), π_x is the cost for any principal interacting with an agent of quality x ($\pi_q > \pi_Q$), δ is the cost for being demanding for a principal (p_1), and ϕ_p and ϕ_A are the reservation utilities (the payoffs for free-living) for principals and agents, respectively. A principal prefers to interact with a Q agent than being free-living

($1-\pi_Q > \phi_p$) and prefers to be free-living than interacting with a q agent ($1-\pi_q < \phi_p$).

2.1. The simultaneous game

Consider first the game in which agent and principal move at the same time (or at different times without observing each other's moves). With $f_{p1}=1$,

$$\begin{aligned} W(\mathbf{a}_1) &= \phi_A \\ W(\mathbf{a}_2) &= f_Q(1-\alpha_Q) + f_q(\phi_A) \\ W(\mathbf{a}_3) &= f_Q(A) + f_q(1-\alpha_q) \\ W(\mathbf{a}_4) &= f_Q(1-\alpha_Q) + f_q(1-\alpha_q) \end{aligned}$$

therefore it is easy to see that \mathbf{a}_2 (enter if Q) is a dominant strategy when $1-\alpha_Q > \phi_A$ and $1-\alpha_q < \phi_A$. With $f_{p2}=1$

$$\begin{aligned} W(\mathbf{a}_1) &= \phi_A \\ W(\mathbf{a}_2) &= f_Q(1) + f_q(\phi_A) \\ W(\mathbf{a}_3) &= f_Q(\phi_A) + f_q(1) \\ W(\mathbf{a}_4) &= 1 \end{aligned}$$

therefore it is easy to see that \mathbf{a}_2 (always enter) is a dominant strategy if $\phi_A < 1$.

If $\delta=0$ (there is no cost for being demanding), principal strategies are neutral, irrespective of the type of agents. If $\delta > 0$ (there is a cost for being demanding), however, principal strategy p_2 (non-demanding) dominates p_1 . Therefore (\mathbf{a}_4, p_2) ("always enter", "non-demanding") is stable if $\delta \geq 0$, while (\mathbf{a}_2, p_1) ("enter if Q ", "demanding") is stable only if $\delta=0$. In summary, mutualism can be stable in the simultaneous game only if there is no cost for being demanding for the principal; even in this case whether this (\mathbf{a}_2, p_1) or the alternative (\mathbf{a}_4, p_2) equilibrium will evolve depends on the initial conditions of the system. Fig. 1 shows a simplified version of this game with only two agent strategies.

2.2. The sequential game

Consider now the sequential version of the same game, in which the principal moves first (Fig. 2). As before, if the principal is demanding (p_1) agent strategy \mathbf{a}_2 ("enter only if Q ") is stable if

$$1-\alpha_q < \phi_A < 1-\alpha_Q \tag{1}$$

while if the principal is non-demanding (p_2) agent strategy \mathbf{a}_4 ("always enter") is always stable (if $\phi_A < 1$). Now, since with agent strategy \mathbf{a}_4 $W(p_2)=f_q[1-\pi_q]+f_Q[1-\pi_Q]$ and with agent strategy \mathbf{a}_2 $W(p_1)=f_q[\phi_p]+f_Q[1-\pi_Q]-\delta$, we can reason by backward induction that p_1 ("demanding") is the best strategy for the principal when $W(p_1) > W(p_2)$, that is when

$$\delta < f_q[\phi_p - (1-\pi_q)] \tag{2}$$

Therefore (1) and (2) are the conditions for the stability of the following strategy in a sequential game in which the principal moves first: the agent plays "enter only if Q " if the principal is demanding ($\mathbf{a}_2|p_1$) and "always enter" if the principal is non-demanding ($\mathbf{a}_4|p_2$); the principal plays "demanding" (p_1). We can define an agent strategy using the matrix $\mathbf{s}_{i1,i2}=[\mathbf{a}_{i1}|p_1, \mathbf{a}_{i2}|p_2]$; the conditional agent strategy described above corresponds to $\mathbf{s}_{2,4}=[[1,0][1,1]]$; the strategy "never enter" corresponds to $\mathbf{s}_{1,1}=[[0,0][0,0]]$, and "always enter" corresponds to $\mathbf{s}_{4,4}=[[1,1][1,1]]$ (while this notation is useful to define conditional strategies, with one principal strategy j fixed in the population the game reduces to the four-strategy game described so far).

The replicator dynamics (Figs. 3 and 4) of the system suggest that mutualism can evolve easily from a state of free-living (\mathbf{a}_1, p_2 ; "never enter", "non-demanding"). If the system originates from parasitism (\mathbf{a}_4, p_2 ; "always enter", "non-demanding"), it can initially drift to an intermediate frequency of conditional agents and all

	p_2		p_1	
a_2	$\frac{1}{2} + \frac{1}{2}\phi_A$	$\frac{1}{2}\phi_p + \frac{1}{2}(1 - \pi_Q)$	$\frac{1}{2}(1 - \alpha_Q) + \frac{1}{2}\phi_A$	$\frac{1}{2}\phi_p + \frac{1}{2}(1 - \pi_Q) - \delta$
a_4	1	$\frac{1}{2}(1 - \pi_q) + \frac{1}{2}(1 - \pi_Q)$	$\frac{1}{2}(1 - \alpha_Q) + \frac{1}{2}(1 - \alpha_q)$	$\frac{1}{2}(1 - \pi_q) + \frac{1}{2}(1 - \pi_Q) - \delta$

$\delta=0$	p_2	p_1
a_2	0.9	0.9
a_4	1	0.7

$\delta=0.05$	p_2	p_1
a_2	0.9	0.9
a_4	1	0.7

Fig. 1. Simplified simultaneous contract game. Payoffs of the contract game with the two principal strategies p_1 (“demanding”) and p_2 (“non-demanding”) and only the two agent strategies a_2 (“enter only if Q”) and a_4 (“always enter”); $f_Q = \frac{1}{2}$. Each cell shows the payoffs to agent, principal. **Top:** The payoff for agent a_4 is [1] when the principal is p_2 : the agent always accepts the interaction and does not pay any cost; and $[\frac{1}{2}(1 - \alpha_Q) + \frac{1}{2}(1 - \alpha_q)]$ when the principal is p_1 : the agent always accepts the interaction and pays a cost α_x . The payoff for agent a_2 is $[\frac{1}{2} + \frac{1}{2}\phi_A]$ when the principal is p_2 : the agent enters the interaction when Q and does not pay any cost, but he does not enter the interaction when q; and $[\frac{1}{2}(1 - \alpha_Q) + \frac{1}{2}\phi_A]$ when the principal is p_1 : the agent enters the interaction when Q and pays a cost α_Q but he does not enter the interaction when q. The payoff for the principal is $[\frac{1}{2}\phi_p + \frac{1}{2}(1 - \pi_Q)]$ when the agent is a_2 because the principal gets $1 - \pi_Q$ when the agent is Q and ϕ_p when the agent is q; the payoff for the principal is $[\frac{1}{2}(1 - \pi_q) + \frac{1}{2}(1 - \pi_Q)]$ when the agent is a_4 because the principal gets $1 - \pi_Q$ when the agent is Q and $1 - \pi_q$ when the agent is q; in addition the principal pays a cost δ when he is demanding (p_1). **Bottom:** Examples with $\phi_A=0.8$; $\phi_p=0.8$; $\pi_Q=0$; $\pi_q=0.6$; $\alpha_Q=0.1$; $\alpha_q=0.8$ and $\delta=0$ (left) or $\delta=0.05$ (right). The arrows show the direction of increase of payoffs.

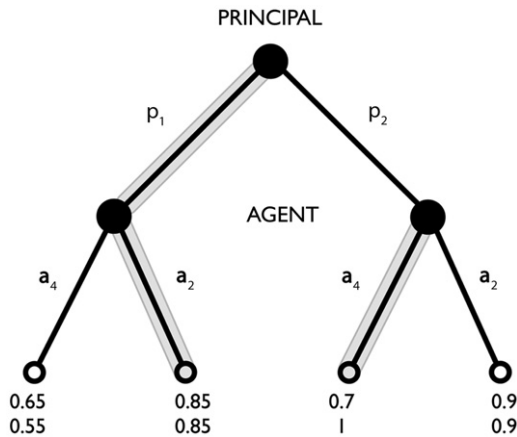


Fig. 2. Simplified sequential contract game. An example of the sequential contract game with the two principal strategies (p_1 : “demanding”; p_2 : “non-demanding”) and only two agent strategies (a_2 : “enter only if Q”; a_4 : “always enter”). Black circles: player’s move; open circles: payoffs to principal (top) and agent (bottom); $\phi_A=0.8$; $\phi_p=0.8$; $\pi_Q=0$; $\pi_q=0.6$; $\delta=0.05$; $\alpha_Q=0.1$; $\alpha_q=0.8$; $f_Q = \frac{1}{2}$. The gray branches show the dominant strategies for each subgame. The best strategy for the agent is to play “enter only if Q” if the principal plays “demanding” (because $0.85 > 0.55$) and to play “always enter” if the principal plays “non-demanding” (because $1 > 0.9$); therefore the best strategy for the principal is to play “demanding” (because $0.85 > 0.7$).

non-demanding principals (the right end of the series of neutral equilibria in Fig. 3) and from there evolve to mutualism.

2.3. Rationale of the contract game

In summary, the contract game illustrates how partner choice is possible when agents cannot signal. The principal imposes a strategic cost that the agent has to pay if he wants to enter the interaction. The cost to enter the interaction must be greater than the cost of remaining free-living for low quality agents but smaller than the cost of remaining free-living for high quality agents

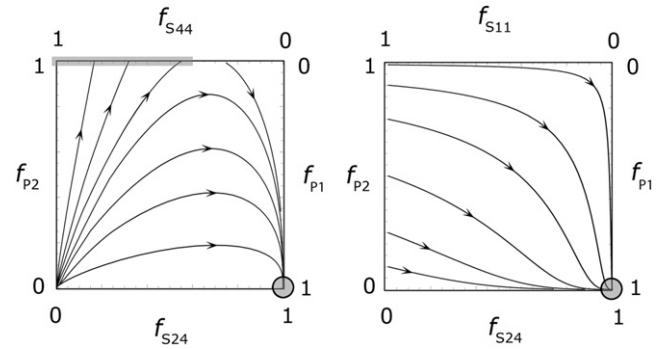


Fig. 3. Replicator dynamics of a simplified sequential game with two agent strategies. Replicator dynamics of agent strategy $s_{2,4}$ (“enter only if Q when the principal is demanding”, “always enter when the principal is not demanding”), the two principal strategies p_2 (“non-demanding”) and p_1 (“demanding”) and one other agent strategy; the frequency of agent strategy $s_{11,12}$ is $f_{s11,12}$. The payoffs for $s_{2,4}$ can be derived from Fig. 1. $\phi_A=0.8$; $\phi_p=0.8$; $\pi_Q=0$; $\pi_q=0.6$; $\delta=0.05$; $\alpha_Q=0.1$; $\alpha_q=0.8$; $f_Q = \frac{1}{2}$. Arrows show the direction of change over generations along the trajectories shown; gray circles show stable equilibria; the gray line is a series of neutral equilibria. **Left:** with agent strategy $s_{1,1}$ (“never enter”); the payoffs with $s_{1,1}$ are ϕ_A for the agent and ϕ_p for the principal (no interaction is established). **Right:** with agent strategy $s_{4,4}$ (“always enter”) the payoffs are the same as the payoffs for a_4 (see Fig. 1).

(condition 1). This is the screening mechanism that allows the principal to induce only Q agents to accept the interaction. The cost imposed on the agent makes the interaction less efficient, but it is necessary to prevent invasion from q agents. It is implicit in the model that the cost imposed by the principal is correlated with the quality of the agent that is relevant for the principal, not with any quality that may help the agent bear the cost (a condition analogous to the single-crossing condition of signaling models). Note that the cost paid by the agent is not transformed into any direct benefit for the principal (aside from that resulting from screening). Finally, the principal must not pay too large a cost for being demanding (condition 2).

What exact costs and rewards must the principal impose? The simple model described above is not enough and we must use a model with continuous variables and resort to constrained optimization techniques.

3. The optimal incentives

Let us assume now that a principal can propose reward w_x and effort e_x (chosen from continuous levels of effort and reward) to the agents. The subscript x denotes the type of agent for which the cost and reward are designed, but the principal cannot assess the quality of the agent, therefore there is no way, a priori, for the principal to assign actively the task (w_x, e_x) to the correct agent type. The principal simply proposes efforts and rewards (w_x, e_x) and lets the agent (who know their own type x) choose whether to accept or not. Designing the correct effort and reward in a way that attracts only the right type of agent is exactly the problem that the principal must solve.

The fitness of an agent depends on the utility $u(w_x)$ he gets from the reward w_x obtained from the principal, and from the disutility $v(e_x)$ of the effort required e_x , that is $u(w_x) - v(e_x)$ for Q agents and $u(w_x) - kv(e_x)$ for q agents, with $k > 1$ (a q agent has a larger disutility than a Q agent for the same effort level). A is the reservation utility (the payoff for free-living) for the agent. The fitness of the principal depends on the benefit $b(e_x)$ he receives from the effort e_x made by the agent and on the cost $c(w_x)$ of the reward w_x paid to the agent. If g is the frequency of Q agents

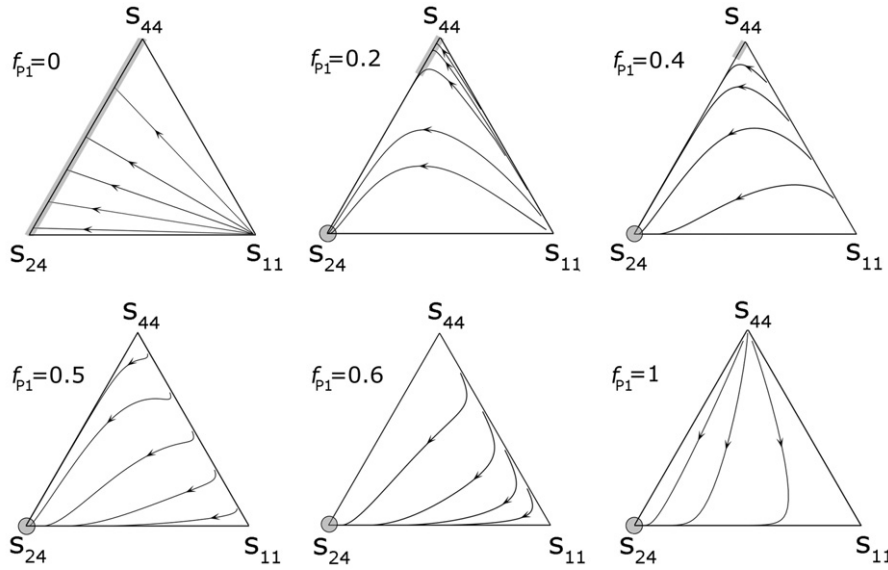


Fig. 4. Replicator dynamics of a simplified sequential game with three agent strategies. Same as in Fig. 3, but showing only the dynamics of the agent strategies (the frequency of a strategy is proportional to its distance from the opposite side); f_{p1} is the initial frequency of principal strategy p_1 (“demanding”).

recruited by the principal, his fitness is $g[b(e_Q) - c(w_Q)] + (1 - g)[b(e_q) - c(w_q)]$. P is the reservation utility (the payoff for free-living) for the principal.

A principal must set up the right conditions (w_x^* and e_x^*) to attract agents of the desired quality, minimizing the reward paid to the agent and maximizing the effort required. An agent will accept the conditions if and only if his net utility from entering the interaction it is at least as large as his reservation utility (the payoff for free-living).

3.1. One contract

If a principal wants to accept only Q agents, her problem is to maximize

$$b(e_Q) - c(w_Q)$$

subject to the constraint that only the good agent will accept the task, that is

$$u(w_Q) - v(e_Q) \geq A$$

$$u(w_q) - kv(e_q) < A$$

It can be shown that a general solution exists (see Appendix A) and exact values can be found for different functions. For example, with $b(e) = \beta e$, $v(e) = e^2$, $c(w) = w$, $u(w) = w$ the optimal effort required is

$$e^* = \beta/2$$

and the optimal reward is

$$w^* = A + e^{*2}$$

The reward paid to the agent must be higher if his reservation utility is high, and if the effort required is high; therefore the reward paid at equilibrium increases with A and β . At equilibrium a Q agent has fitness

$$w^* - e^{*2} = A$$

A q agent, if he accepted the interaction, would have fitness $w^* - ke^{*2} < A$, therefore he does not accept; the principal has fitness

$$g(\beta e^* - w^*) + (1 - g)P$$

3.2. Two contracts

If the principal decides to offer two different sets of conditions (costs and rewards) to the two types of agents, her problem is to maximize

$$g[b(e_Q) - c(w_Q)] + (1 - g)[b(e_q) - c(w_q)]$$

subject to two kinds of constraints; first, both types of agent must find the conditions of the interaction more profitable than free-living:

$$u(w_Q) - v(e_Q) \geq A$$

$$u(w_q) - kv(e_q) \geq A$$

Second, each type must prefer the conditions designed for that type to the ones designed for the other type:

$$u(w_Q) - v(e_Q) \geq u(w_q) - v(e_q)$$

$$u(w_q) - kv(e_q) \geq u(w_Q) - kv(e_Q)$$

To achieve separation of the two agent types, the task designed for the Q agent must give a higher reward and demand more effort than the task designed for the q agent. If these values are set correctly, the Q agent will find the more difficult (but more rewarding) task more profitable than the low-effort/low-reward task, and the q agent will only find the second type of task profitable, and thus choose that.

For example (the solution for the general case is in the appendix) with $b(e) = \beta e$, $v(e) = e^2$, $c(w) = w$, $u(w) = w$ at equilibrium the effort required of the Q agent is still

$$e_Q^* = \beta/2$$

but the reward is now increased to

$$w_Q^* = A + e_Q^{*2} + (k-1)e_q^{*2}$$

to dissuade the Q agent from choosing the task designed for q agents, which requires a lower effort. The reward is increased by $(k-1)e_q^{*2}$ as the result of the principal's inability to tell apart agent types a priori. The effort required of q agent is

$$e_q^* = \beta(g-1)/[2(g-k)]$$

and their reward is

$$w_q^* = A + ke_q^{*2}$$

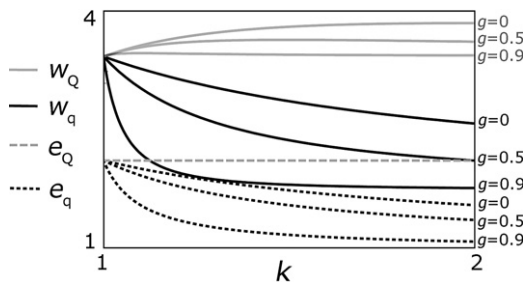


Fig. 5. Equilibrium values of efforts and rewards with two tasks. The optimal contract (w_Q, w_q, e_Q, e_q) as a function of the disutility ratio (k) for low quality agents when costs and benefits are $b(e)=\beta e, v(e)=e^2, c(w)=u(w)=w$, with $\beta=3, A=1$, for different frequencies (g) of the high quality agents; e_Q is the same for any g .

(note that both effort required and reward granted are lower for the q than for the Q agent) (Fig. 5). With these values, Q agents have fitness

$$w_Q^* - e_Q^{*2} = A + (k-1)e_q^{*2} > A$$

and q agents have fitness

$$w_q^* - ke_q^{*2} = A$$

The principal has fitness

$$g(\beta e_Q^* - w_Q^*) + (1-g)(\beta e_q^* - w_q^*)$$

Remember that the principal has fitness $g(\beta e^* - w^*) + (1-g)P$ if she offers only one task; therefore for the principal offering one task is better than offering two if $g(\beta e_Q^* - w_Q^*) + (1-g)(\beta e_q^* - w_q^*) > g(\beta e^* - w^*) + (1-g)P$, that is if $P > \beta^2(g-1)/[4(g-k)]$, that is the reservation utility P for the principal must be large enough. If this is not the case the principal will prefer to contract low quality agents too.

4. Discussion

In summary, imposing the right costs and rewards allows a principal with no information on the quality of her possible partners to induce the possible partners (agents) to screen themselves according to their quality. There is no need of signaling, and the principal never chooses the agents; it is the agents that accept or reject the principal based on the balance of costs and rewards. A rational principal could calculate these optimal costs and rewards to impose on the agents; in fact this mechanism of screening is one of the two standard ways of dealing with asymmetric information in microeconomics (Mussa and Rosen, 1978; Archetti et al., in press). Clearly, however, there is no need to assume rationality in order to play the optimal strategy; natural selection will lead to the optimal costs and rewards. As Noë and Hammerstein (1994) noticed, biological markets are similar in many respects to real markets.

4.1. An example: bioluminescent squids

The bioluminescent bacteria *V. fischeri* and the sepiolid squid *E. scolopes* form a well studied symbiosis (Ruby and McFall-Ngai, 1999; Small and McFall-Ngai, 1999; Visick and Mcfall-Ngai, 2000; Visick et al., 2000) in which the bacteria produce light that the squid uses for hunting and hiding, while the squid provides shelter for the bacteria that reproduce at a much higher rate than free-living ones. In spite of the existence of non-luminescent varieties, which have a net advantage in growth rates (because luminescence is costly), mutant bacteria unable to induce normal

luminescence seem incapable to establish an association with the squid (Visick and Mcfall-Ngai, 2000; Visick et al., 2000). The bacteria cannot signal their quality; therefore squids are not able to tell good from bad bacteria in advance. How does a squid manage to choose the luminescent bacteria and avoid the non-luminescent ones? A strategy the squid could adopt is to impose a cost on the bacteria that only the luminescent ones would be willing to accept. In the contract model, the squid is the principal, and the bacteria are the agents. What kind of cost can induce the bacteria to screen themselves according to their ability to produce light?

The squid seems to have found the right solution: producing radical oxygen species (ROS). The light organ of the squid is rich in ROS that are toxic for many bacteria, including *V. fischeri*. Luminescent bacteria have an active enzyme called luciferase which is able to consume ROS, thereby detoxifying the environment and in this way they are able to live inside the squid; in the reaction the enzyme emits light (Ruby and McFall-Ngai, 1999; Small and McFall-Ngai, 1999). Non-luminescent bacteria, instead, cannot afford to live in an environment so rich in ROS. Therefore, although luminescence per se is not necessary for entering the interaction, and although the squid cannot select bacteria based on their emission of light, the squid has found a strategy to make only the luminescent bacteria accept the interaction: generating ROS making the light organ oxidatively stressful.

Naturally, it is also possible that both types (luminescent and non-luminescent) of bacteria enter the squid and the non-luminescent ones are killed afterwards by the presence of ROS. However the bacteria must actively swim (using a dedicate flagellum) inside the squid to reach the light organ, and it seems reasonable to expect that natural selection would lead non-luminescent strains to avoid entering the squid altogether.

5. Conclusions

Imposing a strategic cost for an establishing and maintaining an interaction can allow an individual to find the right partner among individuals of unknown quality by inducing them to screen themselves according to their type. Like in signaling theory, a strategic cost allows the screening; in this case however, the informed individual does not need to signal and the non-informed individual does not need to choose. This can help explain cases of partner choice in the absence of signaling, like the symbiosis between squids and bioluminescent bacteria. Other species of fish, mollusks, insects, worms and cnidarians that support cooperative bacterial associations produce ROS (Ruby and McFall-Ngai, 1999) and are therefore good candidates for a similar screening mechanism. Plants that must establish an association with mutualistic ants face the same problem of asymmetric information faced by a squid that must interact with bioluminescent bacteria, and a similar screening mechanism may be operating in these cases (Yu and Davidson, 1997). These and other examples are discussed at length elsewhere (Archetti et al. forthcoming).

Acknowledgments

Douglas Yu first noticed the similarity between my model and principal-agent models and suggested using the terminology of contract theory. This work started while I was supported by a Junior Research Fellowship at St. John's College, Oxford and continued while I was supported by NSF Grant SES-0750480 at Harvard University.

Appendix A. Constrained maximization

An individual (principal) is considering recruiting another (agent) for performing a task in a mutualistic interaction; there are two types of agent, good ($x=Q$) and bad ($x=q$); a principal cannot tell Q and q apart, and an agent cannot signal his quality. A principal can propose a certain effort and reward to the agent, who can accept or reject.

The fitness of an agent depends on his own quality x , on the utility $u(w_x)$ of the reward w_x and on the disutility $v(e_x)$ of the effort e_x for performing the task:

$$u(w_Q) - v(e_Q) \quad \text{for a } Q \text{ agent}$$

$$u(w_q) - kv(e_q) \quad \text{for a } q \text{ agent}$$

Assuming $k > 1$, the low quality agents have a larger disutility than the good quality agent for the same effort level. A_Q and A_q are the reservation utilities (the payoffs for free-living) for Q and q agents.

The fitness of the principal depends on the benefit $b(e_x)$ due to the effort e_x made by the agent and by the cost $c(w_x)$ due to the reward w_x paid to the agent. If g is the frequency of Q agents recruited by the principal and $(1-g)$ the frequency of q agents, the fitness of the principal is

$$g[hb(e_Q) - c(w_Q)] + (1-g)[b(e_q) - c(w_q)]$$

We can assume that $h \geq 1$, that is Q agents confer at least the same benefit as bad agents to the principal. The important point is that q agents suffer greater disutility for the same level of effort ($k > 1$). We can assume that both fitness functions are increasing and concave, that is $u'(w_x) > 0$, $u''(w_x) \leq 0$, $v'(e_x) > 0$, $v''(e_x) \geq 0$, $b'(e_x) > 0$, $b''(e_x) \leq 0$, $c'(w_x) > 0$, $c''(w_x) \geq 0$.

An agent will accept the task if and only if his net utility from performing it is at least as large as he could get by not accepting the task that is his reservation utility.

A.1. One contract

The principal can decide to set up only one task (for Q agents); the problem is (using $e=e_Q$ and $w=w_Q$ to simplify the notation):

$$\text{Max}_{\{e,w\}} [hb(e) - c(w)] \tag{A.1}$$

subject to

$$u(w) - v(e) \geq A_Q \quad \text{(constraint for } Q \text{ to accept)} \tag{C1.1}$$

$$u(w) - kv(e) < A_q \quad \text{(constraint for } q \text{ to reject)} \tag{C1.2}$$

The Lagrangian is

$$\mathcal{L}(e,w,\lambda_1,\lambda_2) = hb(e) - c(w) - \lambda_1[v(e) - u(w)] - \lambda_2[u(w) - kv(e)]$$

(where λ_1 and λ_2 are the Lagrange multipliers). The first order conditions for w and e are, respectively:

$$\partial \mathcal{L} / \partial w = -c'(w) + \lambda_1 u'(w) - \lambda_2 u'(w) = 0 \tag{1}$$

$$\partial \mathcal{L} / \partial e = hb'(e) - \lambda_1 v'(e) + \lambda_2 kv'(e) = 0 \tag{2}$$

The constraints are

$$-u(w) + v(e) \leq -A_Q \tag{3}$$

$$u(w) - kv(e) < A_q \tag{4}$$

The multipliers must be non-negative:

$$\lambda_1 \geq 0 \tag{5}$$

$$\lambda_2 \geq 0 \tag{6}$$

The two complementary slackness conditions are

$$\lambda_1 [u(w) - v(e) - A_Q] = 0 \tag{7}$$

$$\lambda_2 [u(w) - kv(e) - A_q] = 0 \tag{8}$$

We look for a solution in (w,e) and λ_1, λ_2 to all the equations and inequalities above. The first two conditions can be rewritten as follows:

$$-c'(w) + [\lambda_1 - \lambda_2]u'(w) = 0$$

$$hb'(e) + [k\lambda_2 - \lambda_1]v'(e) = 0$$

From which we get

$$\lambda_1 - \lambda_2 = c'(w) / u'(w)$$

$$\lambda_1 - k\lambda_2 = hb'(e) / v'(e)$$

λ_1 must be > 0 because Kuhn–Tucker conditions require the Lagrangean multipliers to be non-negative and $\lambda_1 = 0$ would imply, by (1) that $\lambda_2 < 0$, which is impossible. Therefore, from (7):

$$u(w) - v(e) = A_Q \tag{S1.1}$$

(the total payoff for agent must be the same he would get by not accepting the task) and from (8) $\lambda_2 = 0$, which implies, from (2):

$$hb'(e) / c'(w) = v'(e) / u'(w) \tag{S1.2}$$

(same marginal rates of substitution of effort and wages for both players)

$$u(w) - kv(e) < A_q \tag{S1.3}$$

(S1.3) is binding if k is small enough, because $A_q \leq A_Q$.

Note that if the principal needs N partners and there are only N agents in the population, her fitness will be $(1-g)[hb(e) - c(w)] + gP$, where P is her reservation utility. This will only be convenient for a principal (as opposed to offering two tasks) if g and P are not too low (see below).

A.2. Two contracts

If the principal decides to offer two different tasks to the two types of agent, an agent must find the conditions profitable enough to accept the interaction (that is prefer the interaction to being free-living) and must prefer the task designed for his type than the one designed for the other type. The problem is the following:

$$\text{Max}_{\{(e_Q,w_Q),(e_q,w_q)\}} g[hb(e_Q) - c(w_Q)] + (1-g)[b(e_q) - c(w_q)] \tag{A.2}$$

subject to

$$u(w_Q) - v(e_Q) \geq A_Q \tag{C2.1}$$

$$u(w_q) - kv(e_q) \geq A_q \tag{C2.2}$$

$$u(w_Q) - v(e_Q) \geq u(w_q) - v(e_q) \tag{C2.3}$$

$$u(w_q) - kv(e_q) \geq u(w_Q) - kv(e_Q) \tag{C2.4}$$

The first two conditions (C2.1) and (C2.2) ensure that agent accepts the task. The second two conditions (C2.3) and (C2.4) ensure that agent prefers the task designed for his type rather the one designed for the other type.

(C2.3) and (C2.4) imply that greater effort is demanded of the Q agents because

$$kv(e_Q) - kv(e_q) \geq u(w_Q) - u(w_q) \geq v(e_Q) - v(e_q)$$

which implies that $v(e_Q) \geq v(e_q)$ if $k > 1$. Note that (C2.1) is implied in (C2.2) and (C2.3) if $A_Q = A_q$. Let us assume for the moment, in what follows, that $A_Q = A_q$. The Lagrangian is

$$\begin{aligned} \mathcal{L}(e,w,\lambda_2,\lambda_3,\lambda_4) = & g[hb(e_Q) - c(w_Q)] + (1-g)[b(e_q) - c(w_q)] \\ & + \lambda_2 [kv(e_q) - u(w_q)] + \lambda_3 [u(w_Q) \\ & - u(w_q) + v(e_q) - v(e_Q)] \\ & + \lambda_4 [u(w_q) - u(w_Q) + kv(e_Q) - kv(e_q)] \end{aligned}$$

(where $\lambda_2, \lambda_3, \lambda_4$ are the Lagrange multipliers for the second to fourth constraint). The first order conditions for w_Q, w_q, e_Q, e_q are, respectively,

$$\partial \mathcal{L} / \partial w_Q = g[-c'(w_Q)] - \lambda_3[u'(w_Q)] - \lambda_4[-u'(w_Q)] = 0 \quad (9)$$

$$\partial \mathcal{L} / \partial w_q = (1-g)[-c'(w_q)] - \lambda_2[u'(w_q)] - \lambda_3[u'(w_q)] + \lambda_4[u'(w_q)] = 0 \quad (10)$$

$$\partial \mathcal{L} / \partial e_Q = g[hb'(e_Q)] - \lambda_3[v'(e_Q)] + \lambda_4[kv'(e_Q)] = 0 \quad (11)$$

$$\partial \mathcal{L} / \partial e_q = (1-g)[b'(e_q)] + \lambda_2[kv'(e_q)] + \lambda_3[v'(e_q)] - \lambda_4[kv'(e_q)] = 0 \quad (12)$$

That is, respectively,

$$\lambda_3 - \lambda_4 = gc'(w_Q)/u'(w_Q)$$

$$\lambda_2 - \lambda_3 + \lambda_4 = (1-g)c'(w_q)/u'(w_q)$$

$$\lambda_3 - k\lambda_4 = ghb'(e_Q)/v'(e_Q)$$

$$k\lambda_2 - \lambda_3 + k\lambda_4 = (1-g)b'(e_q)/v'(e_q)$$

From (9), because Kuhn–Tucker conditions require the Lagrangean multipliers to be non-negative, we know that $\lambda_3 > 0$ because $\lambda_3 = 0$ would require $\lambda_4 < 0$, which is impossible. Now (9) and (10) imply that

$$\lambda_2 = (1-g)c'(w_q)/u'(w_q) + gc'(w_Q)/u'(w_Q),$$

and (11) and (12) imply that

$$k\lambda_2 = ghb'(e_Q)/v'(e_Q) + (1-g)b'(e_q)/v'(e_q)$$

If it was the case that $e_Q = e_q$ this would imply also $w_Q = w_q$ from (11) and (12) and the previous two equations (with $Q = q$) would be

$$\lambda_2 = c'(w)/u'(w)$$

$$k\lambda_2 = [1 + gh - g]b'(e_Q)/v'(e_Q)$$

From (9) and (11) we would have

$$\lambda_3 = \lambda_4 + gc'(w)/u'(w) = g\lambda_2 + \lambda_4$$

$$\lambda_3 = k\lambda_4 + ghb'(e)/v'(e) = k(g\lambda_2 + \lambda_4)/[1 + gh - g]$$

which is impossible unless $k = 1 + gh - g$; therefore it must be the case that $e_Q > e_q$ (if $k = 1 + gh - g$ then $e_Q = e_q$ and we have only one contract, see above). Now because $e_Q > e_q$ one of the two conditions (C2.3) and (C2.4) must not bind, since $k > 1$; and since $\lambda_3 > 0$ condition (C2.3) binds and (C2.4) does not, which implies that

$\lambda_4 = 0$. Therefore, from (C2.3),

$$u(w_Q) - v(e_Q) = A + (k-1)v(e_q) \quad (S2.1)$$

$$u(w_q) - kv(e_q) = A \quad (S2.2)$$

From (9) and (11),

$$hb'(e_Q)/c'(w_Q) = v'(e_Q)/u'(w_Q) \quad (S2.3)$$

From (10) and (12),

$$b'(e_q)/c'(w_q) = kv'(e_q)/u'(w_q) + g(k-1)v'(e_q)/(1-g)u'(w_Q) \quad (S2.4)$$

the conditions for Q are distorted to avoid Q agents to be tempted by the task designed for the q agents; in this way the interaction is less efficient for the principal. The magnitude of the distortion depends on the frequency g of the Q types.

References

- Andersson, M., 1995. Sexual Selection. Princeton University Press, Princeton.
- Archetti, M., Ubeda, F., Fudenberg, D., Green, J., Pierce, N.E., Yu, D.W., in press. Let the right one in: a microeconomic approach to partner choice in mutualisms. *American Naturalist*.
- Bull, J.J., Rice, W.R., 1991. Distinguishing mechanisms for the evolution of co-operation. *J. Theor. Biol.* 149, 63–74.
- Grafen, A., 1990. Biological signals as handicaps. *J. Theor. Biol.* 144, 517–546.
- Maynard Smith, J., Harper, D., 2003. *Animal Signals*. Oxford University Press, Oxford.
- Mussa, M., Rosen, S., 1978. Monopoly and product quality. *J. Econ. Theory* 18, 301–317.
- Noë, R., Hammerstein, P., 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* 35, 1–11.
- Ruby, E.G., McFall-Ngai, M.J., 1999. Oxygen-utilizing reactions and symbiotic colonization of the squid light organ by *Vibrio fischeri*. *Trends Microbiol.* 7, 414–420.
- Sachs, J.L., Mueller, U.G., Wilcox, T.P., Bull, J.J., 2004. The evolution of cooperation. *Q. Rev. Biol.* 79, 135–160.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton.
- Small, A.L., McFall-Ngai, M.J., 1999. Halide peroxidase in tissues that interact with bacteria in the host squid *Euprymna scolopes*. *Cell Biochem.* 72, 445–457.
- Spence, M., 1973. Job market signaling. *Q. J. Econ.* 87, 355–374.
- Veblen, T., 1899. *The Theory of the Leisure Class*. Houghton Mifflin, Boston.
- Visick, K.L., Foster, J., Doino, J., Mcfall-Ngai, M.J., Ruby, E.G., 2000. *Vibrio fischeri* lux genes play an important role in colonization and development of the host light organ. *J. Bacteriol.* 182, 4578–4586.
- Visick, K.L., Mcfall-Ngai, M.J., 2000. An exclusive contract: specificity in the *Vibrio fischeri*–*Euprymna scolopes* partnership. *J. Bacteriol.* 182, 1779–1787.
- Yu, D.W., Davidson, D.W., 1997. Experimental studies of species-specificity in *Cecropia*–ant relationships. *Ecol. Monogr.* 67, 273–294.
- Zahavi, A., 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* 53, 205–214.