

# Is it better to give information, receive it, or be ignorant in a two-player game?

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The standard approach in a biological two-player game is to assume both players choose their actions independently of one another, having no information about their opponent's action (simultaneous game). However, this approach is not realistic in some circumstances. In many cases, one player chooses his action first and then the second player chooses her action with information about his action (Stackelberg game). We compare these two games, which can be mathematically analyzed into two types, depending on the direction of the best response function (BRF) at the evolutionarily stable strategy in the simultaneous game ( $ESS_{sim}$ ). We subcategorize each type of game into two cases, depending on the change in payoff to one player, when both players are at the  $ESS_{sim}$ , and the other player increases his action. Our results show that in cases where the BRF is decreasing at the  $ESS_{sim}$ , the first player in the Stackelberg game receives the highest payoff, followed by both players in the simultaneous game, followed by the second player in the Stackelberg game. In these cases, it is best to be the first Stackelberg player. In cases where the BRF is increasing at the  $ESS_{sim}$ , both Stackelberg players receive a higher payoff than players in a simultaneous game. In these cases, it is better for both players to play a Stackelberg game rather than a simultaneous game. However, in some cases the first Stackelberg player receives a higher payoff than the second Stackelberg player, and in some cases the opposite is true. **Key words:** evolutionarily stable strategy, game, information, simultaneous solution, Stackelberg solution. [*Behav Ecol* 17:441–451 (2006)]

Evolutionary game theory has been used to model various biological interactions (for reviews see Dugatkin and Reeve, 1998; Maynard Smith, 1982). In general, the standard model involves a situation where neither player has any information about their opponent's action. We will refer to this as a simultaneous game. An example of a simultaneous game is the Houston and Davies (1985) parental effort model, where each parent chooses an effort to contribute to raising their young, with no information regarding the other parent's choice.

Another option is a Stackelberg game, named after its creator, Heinrich von Stackelberg (a German economist), who originally modeled a game with this structure in 1934. The game involves one player choosing first and the second player responding with full knowledge of the first player's action. In some biological situations, this may be more realistic than modeling the interaction as a simultaneous game. For example, consider the case of two females that produce offspring in the same location. In the absence of any previous interactions between them, the details of the biology will determine whether an approach based on a simultaneous game is realistic. If one female can assess how many eggs or young the other has produced, a Stackelberg game would be a more appropriate model than the simultaneous game. In both cases, there are still only two decisions made, the difference is whether the second player has information about what the first player has done.

McNamara et al. (2003) compare four types of parental effort game, including a Stackelberg game. The evolutionarily stable (ES) level of effort contributed to raising the young for the first parent in the Stackelberg game was less than the ES effort in the simultaneous game. The second parent's ES level

of effort in the Stackelberg game was more than in the simultaneous game. Consequently, in this case, the first player in a Stackelberg game receives a higher payoff than the second player in the same game and either player in the simultaneous game. (Note that, in a simultaneous game both parents contribute an identical effort.)

This result poses some interesting questions. Is it better to play a game with information (Stackelberg) or without (simultaneous)? If it is better to play a Stackelberg game, is it better to be the first or second player? Understanding which player is at an advantage in a game can give an insight into how selection acts on the decision process.

Sjerps and Haccou (1993) model the optimal clutch size of two female insects ovipositing on the same host. They consider three cases: in the first, no detection of another clutch is possible (simultaneous game); in the second, detection of another clutch is possible but not its size (also a simultaneous game); and in the third case, detection of another clutch and its size is possible (Stackelberg game). Their results show that in some cases the second female in the Stackelberg game does better to play the simultaneous game, and in other cases, the second female in the Stackelberg game does better to play the Stackelberg game. They note that whether the first Stackelberg female decreased or increased her clutch size, in comparison to her clutch size in a simultaneous game, was dependent on the shape of the fitness curve. They also point out that the first female will always get a better payoff in a Stackelberg game than in a simultaneous game; however, whether the second female gets a better payoff than in the simultaneous game will again depend on the shape of the fitness curve.

This paper aims to give a thorough analysis of modeling two-player evolutionary games using a Stackelberg model in comparison to a simultaneous model. In our analysis, we have assumed that there is no role asymmetry between the players in the simultaneous game, and both players have the same payoff function. The payoff function itself may be symmetric,  $W(x, y) = W(y, x)$ , where  $W(x, y)$  is the payoff to a player who plays  $x$ , given that his opponent plays  $y$ ; or asymmetric,

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Received 28 July 2005; revised 19 December 2005; accepted 15 January 2006.

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$W(x, y) \neq W(y, x)$ . For example, consider a game between two animals in which the payoff to an animal playing action  $x$  when its opponent plays  $y$  is

$$W(x, y) = B(x + y) - K(x),$$

and the payoff to its opponent is

$$W(y, x) = B(x + y) - K(y),$$

where  $B(x + y)$  is a joint benefit function derived from the actions of both players and  $K(\cdot)$  is the cost of the action to the focal player. In this example, there are no roles, and both players have an identical payoff function, which is asymmetric because  $W(x, y) \neq W(y, x)$ .

The two-player games we analyze below are of two types: those with an increasing best response function (BRF) and those with a decreasing BRF, at the evolutionarily stable strategy (ESS) in the simultaneous game. A BRF,  $b(x)$ , is the best action of an individual whose opponent played action  $x$ . We subcategorize each type of game into two further cases, which depends on the way the actions are labeled. This results in four different cases. We give an analysis of the actions and resulting payoffs obtained by each player in the Stackelberg game, in comparison to a simultaneous game, and then present a number of biological examples for each case.

## ANALYSIS OF SIMULTANEOUS AND STACKELBERG GAMES

Let  $W(y, x)$  be the payoff to a player playing action  $y$  whose opponent is playing action  $x$ , where  $x$  and  $y$  are continuous variables which may be interpreted differently in different games (see Table 1 for a summary of definitions). The BRF specifies the action of one player that maximizes their payoff, given a fixed action by their opponent. This can be found by differentiating the payoff function with respect to the first argument (we will use the notation  $u_1$  to represent this) and setting the result equal to zero,

$$\frac{\partial W}{\partial u_1}(b(x), x) = 0. \quad (1)$$

This gives us an equation for the BRF,  $b(x)$ , provided the following equation also holds (Eshel, 1983)

$$\frac{\partial^2 W}{\partial u_1^2}(b(x), x) < 0. \quad (2)$$

### Simultaneous game

When one player plays the ESS, their opponent can do no better than also play the ESS. Therefore, the ESS is a best response to itself, so

$$b(x^*) = x^*,$$

and the payoff to both players when using the simultaneous ESS is  $W(x^*, x^*)$ .

We will also assume that the condition below for convergence stability (Eshel, 1983) also holds to ensure that once at the ES solution, small perturbations in the strategy cannot cause a movement of the whole population away from the ESS,

$$\frac{\partial^2 W}{\partial u_1^2}(x^*, x^*) + \frac{\partial^2 W}{\partial u_1 \partial u_2}(x^*, x^*) < 0.$$

Therefore, all simultaneous ESS's,  $x^*$ , in the following analysis are continuously stable.

**Table 1**

**Table of terms**

Notation	Meaning
$W(y, x)$	Payoff to a player who plays $y$ , given that his opponent plays $x$
$b(x)$	Best response for a player, given that his opponent plays $x$
$x^*$	ES action in the simultaneous game
$x_s$	ES action for first player in the Stackelberg game
$y_s$	ES action for second player in the Stackelberg game
$x_c$	Action at the cooperative solution
$f(x^*)$	Payoff at the simultaneous ESS
$f(x_s)$	Payoff to the first player at the Stackelberg ESS
$g(x_s)$	Payoff to the second player at the Stackelberg ESS

### Stackelberg game: first player

Let player 1 choose first and player 2 choose second, without loss of generality. Player 1 knows the BRF of player 2. Therefore, the payoff,  $f(x)$ , to player 1, playing  $x$ , in the Stackelberg game can be defined as

$$f(x) = W(x, b(x)).$$

This function is maximized at  $x_s$  (the first player's Stackelberg ES action), where  $f'(x_s) = 0$ . If we evaluate  $f(x)$  at  $x^*$  (the ESS in the simultaneous game), we find that

$$f(x^*) = W(x^*, b(x^*)) = W(x^*, x^*). \quad (3)$$

However,  $x_s$  maximizes  $f(x)$ , hence

$$f(x_s) \geq f(x^*). \quad (4)$$

Thus, the payoff to player 1 in a Stackelberg game is always greater than, or equal to, the payoff to both players in the simultaneous game.

Assume that  $f(x)$  is a unimodal function (i.e., only one maximum). It follows from Equation 4 that:

$$f'(x^*) > 0 \Rightarrow x_s > x^*, \quad (5)$$

$$f'(x^*) < 0 \Rightarrow x_s < x^*, \quad (6)$$

$$f'(x^*) = 0 \Rightarrow x_s = x^*. \quad (7)$$

See Figures 1 and 2 for illustrations of  $x_s > x^*$  and  $x_s < x^*$ , respectively.

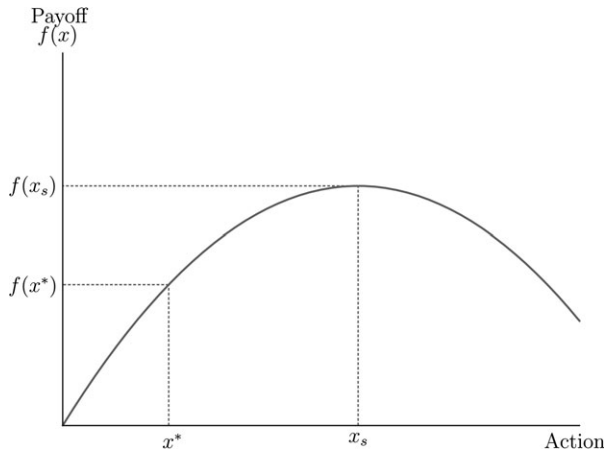
Differentiating  $f(x)$  gives

$$f'(x) = \frac{\partial W}{\partial u_1}(x, b(x)) + b'(x) \frac{\partial W}{\partial u_2}(x, b(x)),$$

where  $u_1$  and  $u_2$  represent differentiating with respect to the first and second arguments, respectively. By evaluating this at the simultaneous ESS, where  $x^* = b(x^*)$ , and then using Equation 1, we obtain

$$\begin{aligned} f'(x^*) &= \frac{\partial W}{\partial u_1}(x^*, x^*) + b'(x^*) \frac{\partial W}{\partial u_2}(x^*, x^*) \\ &= b'(x^*) \frac{\partial W}{\partial u_2}(x^*, x^*). \end{aligned} \quad (8)$$

Therefore, at the simultaneous ESS, whether the first Stackelberg player's payoff increases as his action increases depends on whether the BRF is increasing and whether an increase in the action of one player increases the payoff of the other.



**Figure 1**  
Payoff to the first player in the Stackelberg game, playing  $x_s$ , when  $f(x)$  is an increasing function at  $x^*$ .

### Stackelberg game: second player

Suppose player 1 has already chosen to play action  $x$ . Now, player 2 plays the best response to  $x$ , so the payoff to player 2 in the Stackelberg game  $g(x)$  can be defined as

$$g(x) = W(b(x), x).$$

Note that,

$$g(x^*) = W(x^*, x^*) = f(x^*). \quad (9)$$

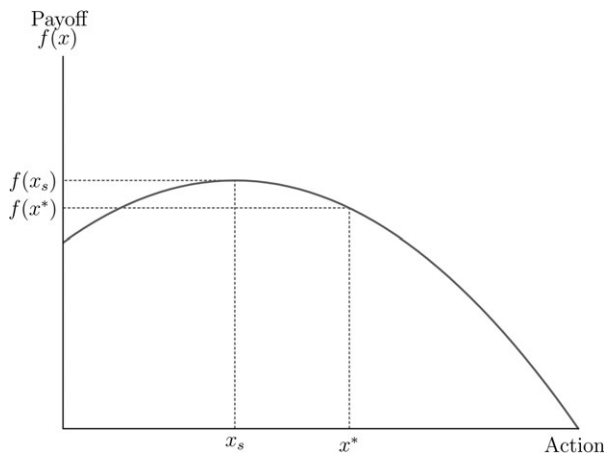
Differentiating  $g(x)$  gives

$$g'(x) = b'(x) \frac{\partial W}{\partial u_1}(b(x), x) + \frac{\partial W}{\partial u_2}(b(x), x).$$

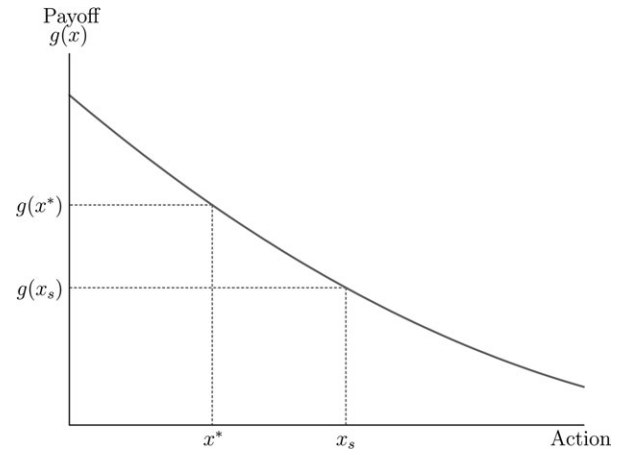
By evaluating this at  $x^* = b(x^*)$ , and then using Equation 1, we obtain

$$g'(x^*) = b'(x^*) \frac{\partial W}{\partial u_1}(x^*, x^*) + \frac{\partial W}{\partial u_2}(x^*, x^*) = \frac{\partial W}{\partial u_2}(x^*, x^*). \quad (10)$$

Therefore, at the simultaneous ESS, whether the second Stackelberg player's payoff increases as his action increases



**Figure 2**  
Payoff to the first player in the Stackelberg game, playing  $x_s$ , when  $f(x)$  is a decreasing function at  $x^*$ .



**Figure 3**  
Payoff to the second player in the Stackelberg game, when  $g(x)$  is a decreasing function at  $x^*$ .

depends on whether an increase in the action of one player increases the payoff of the other.

Substituting Equation 10 into Equation 8, we can obtain a formula connecting the direction of the payoff for player 1 in the Stackelberg game, at the simultaneous ESS, with the direction of the payoff for player 2 in the Stackelberg game, at the simultaneous ESS,

$$f'(x^*) = b'(x^*)g'(x^*).$$

### RESULTS

Evaluating  $f'(x^*)$  and  $g'(x^*)$ , using the Equations 8 and 10, gives the following four cases:

For Case A, let us assume that  $b'(x^*) < 0$  and  $\frac{\partial W}{\partial u_2}(x^*, x^*) < 0$ :

- From Equation 8, we find that  $f'(x^*) > 0$ . Therefore, from Equation 5, we know that the first Stackelberg player's action,  $x_s > x^*$ .
- From Equation 10, we find that  $g'(x^*) < 0$ . Therefore,  $g(x)$  is decreasing at  $x^*$ , and because  $x_s > x^*$ , this means  $g(x_s) < g(x^*)$  (see Figure 3).
- From Equations 4 and 9 and (ii) above, we find that  $g(x_s) < g(x^*) = f(x^*) < f(x_s)$ .
- We have assumed that  $b'(x^*) < 0$ . Therefore,  $b(x)$  is decreasing at  $x^*$  and, because  $x_s > x^*$ , this means the second Stackelberg player's action,  $y_s = b(x_s) < b(x^*) = x^* < x_s$ .

We will call the case illustrated above Case A. The results for Cases B–D can be explained similarly. See Table 2 for a complete mathematical categorization of all the cases.

The cases have been classified on a mathematical basis. However, examples of particular biological situations may fall into more than one case, depending on the assumptions made and therefore the payoff function used. For example, Sjerps and Haccou (1993) present various payoff functions to model two female insects ovipositing on the same host. In our categorization, some of their examples fall into Case A and some into Case C (depending on whether the BRP is decreasing or increasing, respectively, at the simultaneous ESS).

### Direction of best response

The BRP is just a property of the payoff function. Therefore, we can express  $b'(x^*)$  in terms of the payoff function. To find the best response equation, we maximize the payoff function,

**Table 2**  
Summary of the properties of Cases A–D and the symmetric case

Properties of the payoff function	$\frac{\partial W}{\partial u_2}(x^*, x^*) < 0$ or $x_c < x^*$	$\frac{\partial W}{\partial u_2}(x^*, x^*) = 0$ or $x_c = x^*$	$\frac{\partial W}{\partial u_2}(x^*, x^*) > 0$ or $x_c > x^*$
	Case A	Symmetric case	Case B
$\frac{\partial^2 W}{\partial u_1 \partial u_2}(x^*, x^*) < 0$ or $b'(x^*) < 0$	$g(x_s) < f(x^*) < f(x_s)$ $y_s < x^* < x_s$	$g(x_s) = f(x^*) = f(x_s)$ $y_s = x^* = x_s$	$g(x_s) < f(x^*) < f(x_s)$ $x_s < x^* < y_s$
$\frac{\partial^2 W}{\partial u_1 \partial u_2}(x^*, x^*) > 0$ or $b'(x^*) > 0$	Case C $f(x^*) < f(x_s), g(x_s)$ $x_s, y_s < x^*$	Case D $f(x^*) < f(x_s), g(x_s)$ $x^* < x_s, y_s$	

as shown in Equation 1. Differentiating this equation gives the direction of the BRF,

$$b'(x) \frac{\partial^2 W}{\partial u_1^2}(b(x), x) + \frac{\partial^2 W}{\partial u_1 \partial u_2}(b(x), x) = 0.$$

Evaluating this at the simultaneous ESS,  $x^*$ , gives us an equation for  $b'(x^*)$  in terms of the payoff function,

$$b'(x^*) = \frac{\frac{\partial^2 W}{\partial u_1 \partial u_2}(x^*, x^*)}{-\frac{\partial^2 W}{\partial u_1^2}(x^*, x^*)}.$$

The denominator is positive from Equation 2. Therefore, the direction of the BRF depends on the sign of

$$\frac{\partial^2 W}{\partial u_1 \partial u_2}(x^*, x^*), \quad (11)$$

which is how quickly the derivative  $\frac{\partial W}{\partial u_1}(x^*, x^*)$  (the slope of the payoff function, with respect to  $u_1$ , at the simultaneous ESS) is changing with  $u_2$  (see Table 2).

### Cooperative solution

We will now illustrate how the cases above can be reformulated in terms of the cooperative solution to a game. Assume that both players play the same action. The payoff to each is then

$$h(x) = W(x, x).$$

Let this function be maximized at  $x_c$ . Then we refer to  $x_c$  as the cooperative action. Using a similar method to the analysis for the “Stackelberg game: first player”, we find that:

$$\frac{\partial W}{\partial u_2}(x^*, x^*) > 0 \Leftrightarrow x_c > x^*,$$

$$\frac{\partial W}{\partial u_2}(x^*, x^*) < 0 \Leftrightarrow x_c < x^*,$$

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = 0 \Leftrightarrow x_c = x^*.$$

Therefore, as seen from Table 2, we may either categorize the cases in terms of whether the cooperative action is greater than or less than the simultaneous ES action; or in terms of the sign of  $\frac{\partial W}{\partial u_2}(x^*, x^*)$ .

### Labeling

From Table 2, we can see that the payoff function results are identical in Cases A and B:  $g(x_s) < f(x^*) < f(x_s)$ . However, the action results are different: for Case A,  $y_s < x^* < x_s$ , but for Case B,  $x_s < x^* < y_s$ . This is a consequence of how the actions are labeled.

For example, consider a vigilance game played between two birds. For a proportion of the time a bird forages for food and for the remainder of the time a bird is vigilant for attacks from predators. If we label “foraging” as the action we are interested in, then we find that in a Stackelberg game, the first bird to play will forage more ( $x_s > x^*$ ) and the second bird will forage less ( $y_s < x^*$ ), than in the simultaneous game (Case A). If we label “vigilance” as the action we are interested in, then we will find that in a Stackelberg game, the first bird to play will be less vigilant ( $x_s < x^*$ ) and the second bird will be more vigilant ( $y_s > x^*$ ), than in the simultaneous game (Case B). However, it is clear that the labeling will not affect the result that in the Stackelberg game, the first bird will always receive a higher payoff and the second bird will always receive a lower payoff, than in the simultaneous game. Cases C and D can be similarly compared.

Mathematically, it is very easy to switch the labels to move between Case A and B or between Case C and D. However, in a biological context, this is not always as easily understood as in the vigilance game. Therefore, we have retained four cases and have given examples for each.

In Table 2, we have also included the case where the payoff function is symmetric, so

$$W(x, y) = W(y, x)$$

$$\frac{\partial W}{\partial u_1}(x, y) = \frac{\partial W}{\partial u_2}(y, x),$$

with the result that

$$f'(x^*) = g'(x^*) = (1 + b'(x^*)) \frac{\partial W}{\partial u_1}(x^*, x^*) = 0. \quad (12)$$

Therefore, if the payoff function is symmetric, it makes no difference whether a simultaneous or Stackelberg game is played. The ESS and therefore the payoffs are identical for both players, for both games.

## EXAMPLES OF CASES A–D

The following biological examples illustrate four cases. However, if the same biological interaction were modeled using a different payoff function, it may not fit into the same case in our mathematical classification.

Case A:  $b'(x^*) < 0$ ,  $\frac{\partial W}{\partial u_2}(x^*, x^*) < 0$

*Example A1: model by Cant of two females producing young in the same location*

In the Cant (1998) model, two (possibly related) females are producing young in the same location. One example of animals which play this type of game would be acorn woodpeckers laying eggs in tree cavities (Koenig et al., 1995; Mumme et al., 1983). In the simultaneous game, the females can detect that other offspring are present, but not how many. In the Stackelberg game, the second female can detect the number of offspring the first female produced. Both females are assumed to remain and care for their combined brood.

Let  $x$  and  $y$  be the brood sizes of the first and second females, respectively. The general payoff function for the Cant (1998) model is

$$W(y, x) = \frac{y}{x+y} F(x+y) - K(y) + r \left( \frac{x}{x+y} F(x+y) - F(x) \right),$$

where  $F(x+y)$  is the fitness of the brood of size  $x+y$ ,  $K(x)$  is the cost of producing a brood of size  $x$ , and  $r$  is the relatedness of one female to the other (Equation 4 of Cant, 1998). However, depending on the specific functions chosen for  $F(x)$  and  $K(x)$ , the general payoff function may not always be classified into the same case in our analysis.

Cant (1998) presents a model using the specific fitness and cost functions:

$$F(x) = x(1 - kx), \quad (13)$$

$$K(x) = \mu x, \quad (14)$$

where  $k$  is a measure of the sensitivity of offspring fitness to crowding, and  $\mu$  scales  $x$  and represents the cost of producing a certain brood size. This results in the payoff function

$$W(y, x) = (1 - \mu - kx(1 + r))y - ky^2.$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = -\frac{(1 + r)}{2},$$

which is negative because  $r$  is positive. The change in payoff to one female at the simultaneous ES brood size when the other increases her brood size above the simultaneous ES brood size is

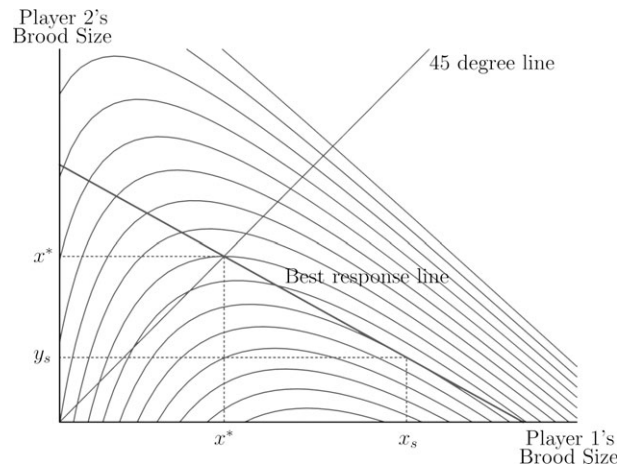
$$\frac{\partial W}{\partial u_2}(x^*, x^*) = -\frac{(1 - \mu)(1 + r)}{(3 + r)},$$

which is negative because  $r$  is positive and  $0 < \mu < 1$ . Therefore, this is an example of a Case A game.

*Results.* The ES brood sizes are

$$x^* = \frac{1 - \mu}{k(3 + r)}, \quad x_s = \frac{(1 - \mu)(1 - r)}{2k(1 - r(2 + r))},$$

$$y_s = \frac{(1 - \mu)(1 - r(4 + r))}{4k(1 - r(2 + r))},$$



**Figure 4**

Level payoff curves for player 1, in Case A, with payoff function  $W(x, y) = (1 - \mu - ky(1 + r))x - kx^2$ , where  $\mu = 0.2$ ,  $k = 0.4$ , and  $r = 0.1$ . Increasing payoff is in a downwards direction. The graph shows the simultaneous ESS,  $x^*$ , and Stackelberg ESS's,  $x_s$  and  $y_s$ , for the first and second players, respectively. The simultaneous ESS is at the point where the best response line crosses the maximum of a level payoff curve. The Stackelberg ESS's are at the point where the best response line forms a tangent with a level payoff curve.

therefore, it can be shown that  $y_s < x^* < x_s$ , as expected. The payoffs at the ES brood sizes are

$$f(x^*) = \frac{(1 - \mu)^2}{k(3 + r)^2},$$

$$f(x_s) = \frac{(1 - \mu)^2(1 - r)}{2k(1 - r(2 + r))} \times \left( 1 - \frac{(1 - r)}{2(1 - r(2 + r))} - \frac{(1 + r)(1 - r(4 + r))}{4(1 - r(2 + r))} \right),$$

$$g(x_s) = \frac{(1 - \mu)^2(1 - r(4 + r))}{4k(1 - r(2 + r))} \times \left( 1 - \frac{(1 - r^2)}{2(1 - r(2 + r))} - \frac{(1 - r(4 + r))}{4(1 - r(2 + r))} \right),$$

therefore, it can be shown that  $g(x_s) < f(x^*) < f(x_s)$ , as expected (see the Appendix for more detailed calculations of the ES brood sizes and payoffs). Figure 4 gives a graphical illustration of the simultaneous ESS and Stackelberg ESS brood sizes.

*Example A2: model by Sjerps and Haccou of optimal clutch sizes of competing insects*

Sjerps and Haccou (1993) modeled the optimal clutch size of two female insects ovipositing on the same host. Both females know that there will be another female ovipositing on the same host. The simultaneous game is when a female cannot detect the size of the other female's clutch. The Stackelberg game is when a female can detect the size.

Let  $x$  and  $y$  be the clutch sizes of the first and second females, respectively. The general payoff function for the Sjerps and Haccou (1993) model is

$$W(y, x) = yh(x + y),$$

where  $h(x + y)$  is the fitness gain per egg from a clutch of  $x + y$  eggs (Equation on page 475 of Sjerps and Haccou, 1993).

Depending on the shape of the fitness function,  $h(x + y)$ , the model may fall into Case A or Case C. For both Case A and Case C, an increase in the clutch size by one female results in a decrease in the payoff to the other female. However, in Case A, the best response to an increase in clutch size is to lay less eggs, whereas in Case C, the best response is to lay more eggs.

Sjerps and Haccou present a specific example (Equation (i), top of page 478 of Sjerps and Haccou, 1993) with payoff function

$$W(y, x) = y \left( 2 - 2^{\frac{x+y}{30}} \right).$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = -0.6.$$

The change in payoff to one female at the simultaneous ES clutch size when the other increases her clutch size above the simultaneous ES clutch size is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = -0.4.$$

Therefore, this is another example of a Case A game (see Example C1 below for an example of a Case C game using the same general model).

**Results.** Calculating  $x^*$  and taking  $x_s$  and  $y_s$  from Sjerps and Haccou (1993), the ES clutch sizes are

$$x^* = 10.4, \quad x_s = 15.9, \quad y_s = 7.3,$$

therefore,  $y_s < x^* < x_s$  as expected. The payoffs at the ES clutch sizes are

$$f(x^*) = 4.0, \quad f(x_s) = 4.6, \quad g(x_s) = 2.1,$$

therefore,  $g(x_s) < f(x^*) < f(x_s)$  as expected.

Case B:  $b'(x^*) < 0$ ,  $\frac{\partial W}{\partial u_2}(x^*, x^*) > 0$

**Example B1: model by McNamara et al. of parental effort raising offspring**

In the McNamara et al. (2003) model, two parents are contributing effort to raising their offspring. It is assumed that both parents remain to care for the young. (See Clutton-Brock, 1991, for a review of the occurrence of biparental care.) In the simultaneous game, both parents may be thought of as contributing their efforts simultaneously. In the Stackelberg game, the second parent can observe how much effort the first parent has contributed, before contributing his effort.

Let  $x$  and  $y$  be the efforts contributed by the first and second parent, respectively. The general payoff function for the McNamara et al. model (Equation 1 of McNamara et al., 2003) is

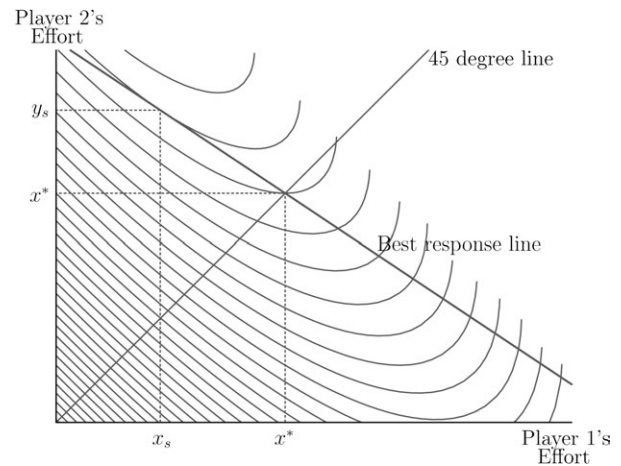
$$W(y, x) = B(x + y) - K(y),$$

where  $B(x + y)$  is the benefit to the offspring of the combined effort contributed (an increasing, decelerating function), and  $K(y)$  is the cost to the individual contributing effort  $y$  (an increasing, accelerating function).

McNamara et al. (2003) present a model using the specific benefit and cost functions

$$B(x + y) = 2(x + y) - (x + y)^2,$$

$$K(y) = ky^2,$$



**Figure 5**

Level payoff curves for player 1, in Case B, with payoff function  $W(x, y) = 2(x + y) - (x + y)^2 - x^2/2$ . Increasing payoff is in an upwards direction. The graph shows the simultaneous ESS,  $x^*$ , and Stackelberg ESS's,  $x_s$  and  $y_s$ , for the first and second players, respectively. The simultaneous ESS is at the point where the best response line crosses the minimum of a level payoff curve. The Stackelberg ESS's are at the point where the best response line forms a tangent with a level payoff curve.

where  $k$  is a positive parameter which scales the cost of the effort made by the parent. This results in the payoff function

$$W(y, x) = 2(x + y) - (x + y)^2 - ky^2.$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = -\frac{1}{1+k},$$

which is negative because  $k$  is positive. The change in payoff to one parent at the simultaneous ES effort when the other increases her effort above the simultaneous ES effort is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = 2 \left( 1 - \frac{2}{2+k} \right),$$

which is positive because  $k$  is a positive parameter. Therefore, this is an example of a Case B game.

**Results.** The ES efforts are

$$x^* = \frac{1}{2+k}, \quad x_s = \frac{k}{1+3k+k^2}, \quad y_s = \frac{1+k}{1+3k+k^2},$$

therefore, it can be shown that  $x_s < x^* < y_s$ , as expected. The payoffs at the ES efforts are:

$$f(x^*) = \frac{4+3k}{(2+k)^2}, \quad f(x_s) = \frac{1+3k}{1+3k+k^2},$$

$$g(x_s) = \frac{1+5k+8k^2+3k^3}{(1+3k+k^2)^2},$$

therefore, it can be shown that  $g(x_s) < f(x^*) < f(x_s)$ , as expected. Figure 5 gives a graphical illustration of the simultaneous ESS and Stackelberg ESS efforts.

**Example B2: model by Houston and McNamara of a vigilance game**

In the Houston and McNamara (1999) model, two animals are foraging. Both animals choose the proportion of time spent feeding as opposed to being vigilant for predators. This

type of behavior has been observed in various species of mammals and birds (Elgar, 1989), although vigilance may be less costly for some mammals (Fortin et al., 2004). In the simultaneous game, neither animal has any information about the vigilance of the other animal. In the Stackelberg game, the second animal can observe the vigilance of the first animal.

Let  $x$  and  $y$  be the proportion of time spent being vigilant by the first and second animal, respectively. (Note that,  $1 - x$  and  $1 - y$  are the proportions of time spent feeding for the first and second animal, respectively.) The payoff function for the Houston and McNamara (1999) model is

$$\begin{aligned} W(y, x) &= \theta \times \text{net intake rate} - \text{predation rate} \\ &= a\theta(1 - y) - \frac{\alpha}{2}(1 - x)^2(1 - y)^2, \end{aligned}$$

where  $a(1 - y)$  is the animal's net food intake rate (where  $a$  is a constant),  $\theta$  is the marginal rate of substitution of predation risk for energy gain, and  $\alpha$  is the rate at which attacks occur (Equation 7.2 of Houston and McNamara, 1999). The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = -2.$$

The change in payoff to one animal at the simultaneous ES vigilance level when the other increases its vigilance level above the simultaneous ES vigilance level is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = a\theta,$$

which is positive provided  $a > 0$ . Therefore, this is an example of a Case B game.

**Results.** The ES vigilance levels are

$$x^* = 1 - \sqrt[3]{\frac{a\theta}{\alpha}}, \quad x_s = 1 - \frac{a\theta}{\alpha}, \quad y_s = 1 - \frac{\alpha}{a\theta},$$

therefore, it can be shown that  $x_s < x^* < y_s$ , as expected. The payoffs at the ES vigilance levels are

$$f(x^*) = \frac{1}{2} \left( \sqrt[3]{\frac{a\theta}{\alpha}} \right)^4, \quad f(x_s) = \frac{(a\theta)^2}{\alpha} - \frac{\alpha}{2}, \quad g(x_s) = \frac{\alpha}{2},$$

therefore, it can be shown that  $g(x_s) < f(x^*) < f(x_s)$ , as expected.

Case C:  $b'(x^*) > 0$ ,  $\frac{\partial W}{\partial u_2}(x^*, x^*) < 0$

**Example C1: model by Sjerps and Haccou of optimal clutch sizes of competing insects**

See Example A2 for description of the model used by Sjerps and Haccou (1993). One example presented (Equation (ii), bottom of page 478 of Sjerps and Haccou, 1993) has the payoff function

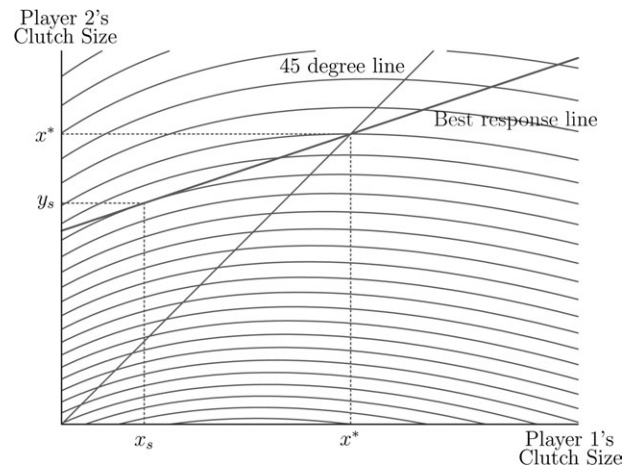
$$W(y, x) = \frac{158y}{25(1 + \frac{x+y}{30})^4}.$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = \frac{1}{3}.$$

The change in payoff to one female at the simultaneous ES clutch size when the other increases her clutch size above the simultaneous ES clutch size is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = -\frac{79}{200}.$$



**Figure 6**

Level payoff curves for player 1, in Case C, with payoff function  $W(x, y) = 158x/25(1 + \frac{x+y}{30})^4$ . Increasing payoff is in a downwards direction. The graph shows the simultaneous ESS,  $x^*$ , and Stackelberg ESS's,  $x_s$  and  $y_s$ , for the first and second players, respectively. The simultaneous ESS is at the point where the best response line crosses the maximum of a level payoff curve. The Stackelberg ESS's are at the point where the best response line forms a tangent with a level payoff curve.

Therefore, this is an example of a Case C game.

**Results.** The ES clutch sizes are

$$x^* = 15, \quad x_s = 10, \quad y_s = 13.3,$$

therefore, both  $x_s$  and  $y_s$  are less than  $x^*$ , as expected. The payoffs at the ES clutch sizes are

$$f(x^*) = 5.9, \quad f(x_s) = 6.3, \quad g(x_s) = 8.4,$$

therefore, both  $f(x_s)$  and  $g(x_s)$  are greater than  $f(x^*)$ , as expected. Note that in this case the second Stackelberg female does better than the first. However, this is not always the case. Both results are possible, depending on the specific payoff function involved. Figure 6 gives a graphical illustration of the simultaneous ESS and Stackelberg ESS clutch sizes.

Case D:  $b'(x^*) > 0$ ,  $\frac{\partial W}{\partial u_2}(x^*, x^*) > 0$

**Example D1: model of predator inspection by two fish**

Small fish inspect objects that might be predators. This is known as predator inspection. The inspection may provide information about whether the object represents danger (Pitcher, 1992). Sometimes fish inspect in pairs (Dugatkin, 1997). It is assumed that the benefit of inspection increases as the fish gets nearer to the predator, but the cost also increases. The advantage of inspecting as a pair is that the cost is reduced for both fish if there is another fish present.

In our model of predator inspection, the distance  $x$  and  $y$  of the fish A and fish B, respectively, is measured from a baseline point 0 toward the predator (at point 1). As  $x$  and  $y$  increase toward 1, the fish get closer to the predator. The survival probability,  $S(y, x)$ , depends on the distance from the baseline of the focal fish toward the predator and the position of the other fish. Survival of both fish decreases as they get closer to the predator, but if fish A is closer to the predator than fish B, then the survival probability of fish B is increased. In this model, the survival probability takes the form

$$S(y, x) = e^{-\frac{xy}{1+x}},$$

where  $\gamma$  is a positive constant. The benefit function depends only on the distance from the baseline of the focal fish and can take the form of a simple linear function, such as

$$B(y) = \alpha + \beta y.$$

This represents a fish obtaining benefit  $\alpha$  if it does not inspect the predator, but getting an increased benefit of  $\beta y$  if it gains some information about this unknown source.

Therefore, we have the following payoff function

$$W(y, x) = B(y)S(y, x) = (\alpha + \beta y)e^{-\frac{\gamma y}{1+x}}.$$

Setting  $\alpha = 1$ ,  $\beta = 4$ , and  $\gamma = 2$ , we have the following specific function

$$W(y, x) = (1 + 4y)e^{-\frac{2y}{1+x}}.$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = \frac{1}{2}.$$

The change in payoff to one fish at the simultaneous ES distance when the other fish increases its distance above the simultaneous ES distance is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = \frac{4}{9}.$$

Therefore, this is an example of a Case D game.

**Results.** The ES distances from the baseline are

$$x^* = 0.5, \quad x_s = 0.92, \quad y_s = 0.71,$$

therefore, both  $x_s$  and  $y_s$  are greater than  $x^*$ , as expected. The payoffs at the ES distances from the baseline are

$$f(x^*) = 1.540, \quad f(x_s) = 1.596, \quad g(x_s) = 1.833,$$

therefore, both  $f(x_s)$  and  $g(x_s)$  are greater than  $f(x^*)$ , as expected. Figure 7 gives a graphical illustration of the simultaneous ESS and Stackelberg ESS distances.

## SYMMETRIC PAYOFF FUNCTIONS

### Example S1: model of parental effort

In this parental effort game, the focal pair mates for life, and if one individual dies, the other will not remate (this is true monogamy as defined by Parker [1985]). This means the costs incurred by one parent in one breeding attempt will affect both parents in future breeding attempts. In effect, cooperation is imposed upon the pair.

We use the following general payoff function

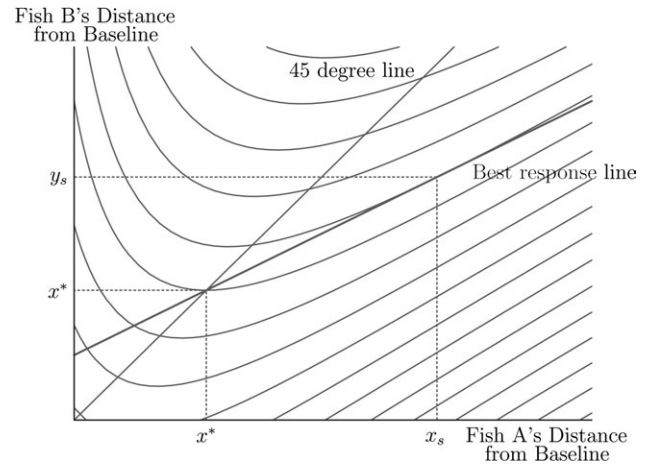
$$W(x, y) = B(x + y) + S(x)S(y)W(x, y),$$

where  $B(x + y)$  is the benefit to the offspring of the combined effort contributed to raising the young, and  $S(x)$  and  $S(y)$  are survival functions of the two parents, respectively; provided both parents survive the future payoff is  $W(x, y)$ . This can be rearranged to give

$$W(x, y) = \frac{B(x + y)}{1 - S(x)S(y)}.$$

We analyze a model using the specific benefit and survival functions

$$B(x + y) = 2(x + y) - (x + y)^2,$$



**Figure 7**

Level payoff curves for player 1, in Case D, with payoff function  $W(x, y) = (1 + 4x)e^{-\frac{2y}{1+x}}$ . Increasing payoff is in an upwards direction. The graph shows the simultaneous ESS,  $x^*$ , and Stackelberg ESS's,  $x_s$  and  $y_s$ , for the first and second players, respectively. The simultaneous ESS is at the point where the best response line crosses the minimum of a level payoff curve. The Stackelberg ESS's are at the point where the best response line forms a tangent with a level payoff curve.

$$S(x) = \frac{1}{2}(1 - x),$$

where  $0 < x, y < 1$ , and the resulting in the payoff function is

$$W(x, y) = \frac{4[2(x + y) - (x + y)^2]}{4 - (1 - x)(1 - y)}.$$

The differential of the BRF at the simultaneous ESS is

$$b'(x^*) = \frac{3(15\sqrt{3} - 26)}{2(26\sqrt{3} - 45)} = -0.866.$$

The change in payoff to one parent at the simultaneous ES effort when the other parent increases her effort above the simultaneous ES effort is

$$\frac{\partial W}{\partial u_2}(x^*, x^*) = 0.$$

### Results

The ES efforts are

$$x^* = x_s = y_s = 2\sqrt{3} - 3,$$

therefore, both  $x_s$  and  $y_s$  are identical to  $x^*$ , as expected. Therefore, the payoff at the ES effort is

$$f(x^*) = f(x_s) = g(x_s) = 4(2 - \sqrt{3}),$$

therefore, both  $f(x_s)$  and  $g(x_s)$  are identical to  $f(x^*)$ , as expected.

## DISCUSSION

We have shown that the form of the payoff function can give a general classification of two-player evolutionary games. The relevant aspects of the payoff function are:

- the direction of the BRF at the simultaneous ESS,  $x^*$ ; and
- when both players are at the simultaneous ESS,  $x^*$ , the change in an individual's payoff due to an increase of their opponent's action.



This results in the four cases mentioned above, and finally when the change in (b) is zero, we have the symmetric case.

We have presented a comparison of simultaneous and Stackelberg games for players with identical payoffs. Our results show that it is always better to go first in a Stackelberg game (where the second player has information about their opponent's action) rather than play a simultaneous game (no information). In other words, it is better to give information about one's action than to be in a game in which each player is ignorant about the other's action. However, it depends on (a) and (b) as to whether it is better to go second in a Stackelberg game rather than play a simultaneous game. In the Stackelberg game, in both Cases A and B, it is better to be the first player rather than the second. However, in the Stackelberg game, in both Cases C and D, whether it is better to go first or second depends on the shape of the payoff curves for the two players.

Our results show that an individual would prefer to play a Stackelberg game rather than a simultaneous game provided they were the first player in the Stackelberg game. Now assume an individual will not know which player they would be in the Stackelberg game. In this case, if the BRF is decreasing at the simultaneous ESS, they may do worse (if the second player) by playing a Stackelberg game. However, if the BRF is increasing at the simultaneous ESS, both players do better by playing a Stackelberg game. Therefore, we would expect selection to act on the decision process that determines the actions so that one of the players has information about the decision of the other player before it makes its own decision.

This analysis has gone beyond Sjerps and Haccou (1993) by categorizing two further mathematical cases. In their examples, the change in (b) was always negative (i.e., Cases A and C) because the model involved two female insects ovipositing on the same host, so if one female increased her clutch size, she would reduce the other female's payoff. We introduced the two cases where the change in (b) was positive, giving biological examples involving parental effort and predator inspection.

The games we have illustrated, using both the simultaneous and Stackelberg models, involve only two decisions, one by each player. However, this is not the only approach to modeling such interactions. Indeed, in some circumstances, this type of model may not be realistic. In many cases, a game in which the final efforts are negotiated, through a series of responses by one player to the other, may be more suitable. McNamara et al. (1999) give an example of a model using ES negotiation rules rather than ES actions, as in this paper. However, the Stackelberg game may still give a simple but accurate model for certain biological interactions.

Abe et al. (2003) compare a simultaneous game with a Stackelberg game to model the sex ratio of two female parasitoid wasps ovipositing sequentially on the same host. At first glance, this may appear to be very similar to Case A, which we illustrated using the Cant (1998) model of two females laying eggs in the same location and is also illustrated in Sjerps and Haccou (1993). However, in our Stackelberg games, both players have the same payoff function (i.e., the two players may be thought of as identical). In comparison, Abe et al. (2003) model a Stackelberg game where the players have different payoff functions (i.e., they are not identical players). In their model, there is a probability  $p$  that the second foundress will oviposit on the same host. Therefore, the payoff to the first foundress depends on this value  $p$ , whereas the payoff to the second foundress does not. Abe et al. (2003) have also introduced a factor  $C$ , the relative competitive ability of sons produced by the second foundress to those produced by the first, which further increases the asymmetry of the payoffs. Pen and Taylor (2005) compared the simultaneous and

Stackelberg (sequential) game in modeling the sex allocation conflict between queen and worker hymenopteran eusocial insects, which also have asymmetric payoffs because the preferred queen sex ratio is 1:1 male:female but the workers' is 1:3. Therefore, our analysis cannot be applied to either of these examples. However, an interesting extension of our analysis would be a similar analysis of games between individuals with different payoff functions.

Another example, in which the players have different payoff functions, is a sperm competition game between sneaks and guarders (Parker, 1990). This type of game is relevant in many types of animals such as insects, birds, rodents, and even humans (Birkhead and Møller, 1998). A guarder male is permanently paired with a mate, but the sneak male may obtain opportunistic matings with females that are already paired. Assuming the detection by a guarder of a sneak mating is rare (i.e., has probability much less than 1), the payoff functions for the sneak and guarder are different. However, if we assume a detection is made, the payoff functions become identical, and the game falls into Case C in our analysis.

There are parallels between continuous two-player games and discrete  $2 \times 2$  games. Rapoport (1967) describes the four archetypal  $2 \times 2$  games: "Game of Chicken," "Battle of the Sexes," "Apology," and "Prisoner's Dilemma." The  $2 \times 2$  games involve two players who can both choose one of two options. The simultaneous game solution is identical to the "natural outcome" in Rapoport's paper (the strategy that will minimize a player's loss were he to suffer one). In the Game of Chicken, two hooligans drive at each other down a narrow lane. The first to swerve loses face among his peers, but if neither swerves, both die. This is similar to Cases A and B in our categorization. If one player chooses first (i.e., not to swerve), then the other must swerve (to minimize his loss), so the first player in the Stackelberg game receives the highest payoff, followed by both players in the simultaneous game (both swerve), followed by the second player in the Stackelberg game. This means that it is advantageous to declare one's intentions in this game. It follows that an omniscient player that can perceive the intention of the other player is at a disadvantage (Brams, 1983). In the Battle of the Sexes, the husband wishes to go to a football match and the wife wishes to go to the opera, but both would prefer to be together rather than apart. In Apology, two neighbors have quarreled and both would benefit from going next door and apologizing. The one who apologized would pay for the gain with a "loss of face," but if both go to each other's house to apologize then both would lose out as neither would be at home. Battle of the Sexes and Apology are similar to Cases C and D because both Stackelberg players receive a higher payoff than players in a simultaneous game. The Prisoner's Dilemma does not fit into any of Cases A–D because the best response to an opponent does not depend on the opponent's action, consequently, the simultaneous and Stackelberg solution are the same.

This paper is mainly concerned with exposing the logic of when it is advantageous to give reliable information on intentions in an interaction and when it is disadvantageous to receive such information. Different mechanisms of information transfer are pertinent in different situations, and it is not our intention to review these in detail. Nevertheless, it is instructive to consider information transfer in the particular case of parental care and desertion decisions in birds. Suppose each parent must decide whether to care for the young or desert. Desertion is an advantage to a parent, provided the other parent cares for the current young, because it provides opportunities for further matings. Thus, there is a conflict of interest between the parents, with each preferring the other to care. In many species, the male has the opportunity to desert immediately after fertilization, whereas the female

must wait until young are born. The desertion game between the parents is then a Stackelberg game with the male choosing first. It may, however, be advantageous for the male to wait until eggs are laid so as to guard his paternity. If the male does wait and the female can hide the fact that the eggs have been laid, as in the Penduline Tit (Valera et al., 1997), the female may gain an advantage and be able to decide first. Theory also suggests that another strategy for the female may be to lose energy reserves before the male can desert (Barta et al., 2002). Provided that the male is able to observe this, and a lean female cannot care alone, the female has given him reliable information that she cannot care on her own and will desert if he deserts. This forces the male to care, allowing her to desert.

Our results enable us to interpret how animals should respond in biological situations when they have information about the action of their "opponent," and how they should respond when they do not.

## APPENDIX

The payoff for Example A1 is

$$W(y, x) = (1 - \mu - kx(1 + r))y - ky^2.$$

By maximizing  $W(y, x)$ , we find that the best response to  $x$  is given by

$$b(x) = \max\left(\frac{1 - \mu}{2k} - \frac{x(1 + r)}{2}, 0\right), \quad (15)$$

which takes account of the fact that neither female can lay less than zero eggs.

A Nash equilibrium requires that a strategy is a best response to itself. It is clear that laying zero eggs is not a best response to an opponent laying zero eggs, so therefore we can ignore  $b(x) = 0$ .

We now impose the Nash equilibrium condition,  $x^* = b(x^*)$ , on the BRF above, to give us the simultaneous ESS

$$x^* = \frac{1 - \mu}{k(3 + r)}.$$

Note that this is not the same as  $n^*$  in Cant (1998), which represents the optimal clutch size if only one female lays eggs in a location.

The payoff to both females using the simultaneous ESS is

$$\begin{aligned} f(x^*) &= W(x^*, x^*) = (1 - \mu - kx^*(1 + r))x^* - k(x^*)^2 \\ &= \frac{(1 - \mu)^2}{k(3 + r)^2}. \end{aligned}$$

The payoff to the first Stackelberg female is

$$f(x) = W(x, b(x)) = (1 - \mu - kb(x)(1 + r))x - kx^2.$$

Substituting  $b(x)$  into this equation and maximizing  $f(x)$  gives the best action of the first Stackelberg female

$$x_s = \frac{(1 - \mu)(1 - r)}{2k(1 - r(2 + r))}. \quad (16)$$

However, from Equation 15, the condition for  $b(x) > 0$  is

$$x < \frac{1 - \mu}{k(1 + r)}.$$

Therefore, for  $b(x) > 0$  and for Equation 16 to be an ESS, the following condition must hold

$$\frac{(1 - \mu)(1 - r)}{2k(1 - r(2 + r))} < \frac{1 - \mu}{k(1 + r)} \Rightarrow r < \sqrt{5} - 2.$$

When this condition is met, the numbers of eggs laid (the Stackelberg ES action) by the first female is

$$x_s = \frac{(1 - \mu)(1 - r)}{2k(1 - r(2 + r))},$$

and the response by the second female is

$$b(x_s) = y_s = \frac{(1 - \mu)(1 - r(4 + r))}{4k(1 - r(2 + r))}.$$

It can be shown that  $y_s < x^* < x_s$ , as expected.

The payoff to each female is as follows

$$\begin{aligned} f(x_s) &= W(x_s, y_s) \\ &= \frac{(1 - \mu)^2(1 - r)}{2k(1 - r(2 + r))} \\ &\quad \times \left(1 - \frac{(1 - r)}{2(1 - r(2 + r))} - \frac{(1 + r)(1 - r(4 + r))}{4(1 - r(2 + r))}\right), \end{aligned}$$

and

$$\begin{aligned} g(x_s) &= W(y_s, x_s) \\ &= \frac{(1 - \mu)^2(1 - r(4 + r))}{4k(1 - r(2 + r))} \\ &\quad \times \left(1 - \frac{(1 - r^2)}{2(1 - r(2 + r))} - \frac{(1 - r(4 + r))}{4(1 - r(2 + r))}\right). \end{aligned}$$

Therefore,  $g(x_s) < f(x^*) < f(x_s)$ , as expected.

## Error in Cant (1998)

The condition for  $r$  and the value for  $x_s$  when  $r < \sqrt{5} - 2$  is different from the result documented in the paper by Cant (1998). The condition Cant found was  $r < \sqrt{2} - 1$  and the value was  $x_s = (1 - \mu)/k(2 - r(1 + r))$ .

The result for when  $r > \sqrt{2} - 1$  found by Cant (1998) is identical to our result for  $r > \sqrt{5} - 2$ . However, this is found by using the best response  $b(x) = 0$ , which as discussed earlier, is not a Nash equilibrium, so it should be ignored.

We thank James Marshall and two anonymous referees for comments on previous versions of this paper. J.M.M. was supported by a Leverhulme Research Fellowship.

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