

Co-operation and Defection: Playing the Field and the ESS

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If food is patchily dispersed, food clumps being very rich, but rare and hard to find, each individual in a foraging flock then faces an evident dilemma: whether to co-operate and participate in the search, thus enhancing the rate by which rich patches are discovered, or to defect and let others do the searching, thus avoiding any possible expenditures and risks involved in the search (but enjoying the abundant resources once a rich patch is discovered).

This conflict (and its possible solution) is treated as an example in the analysis of the synergistic n -player game presented in this paper. After deriving conditions for the existence of a mixed ESS in such games, the evolutionary stability of the mixed strategy against invasions by pure strategists, in particular against invasions by recognizable defectors, is analyzed. Whereas in any “degenerating” mixed-strategy model a recognizable defector can invade and spread, a “non-degenerating” model can sometimes yield a mixed ESS which is immune to such invasions.

Introduction

A certain class of evolutionary games consists of n -player games in which two pure strategies are possible, namely co-operation and defection. While co-operation confers a common benefit to all group members, it imposes a personal cost on the individuals that adopt this strategy. An interesting question is what kind of behavior is favored by natural selection, or at least what are the evolutionarily stable strategies (ESS) in such games. Clearly, if the personal cost due to co-operation is too high, defection is the only ESS. If, on the other hand, the cost of co-operation is small enough, we can expect co-operation to be evolutionarily stable. But what happens if the cost of co-operation has an “intermediate” value? In many cases it results in a mixed ESS, characterized by a positive probability of choosing to co-operate. A few biological examples of such n -player games having a mixed ESS are the vigilance game (Pulliam *et al.*, 1982; Parker & Hammerstein, 1985; Motro & Cohen, 1989, 1990), the root game among desert plants (Riechert & Hammerstein, 1983), kin selection with more than one potential helper (Eshel & Motro, 1988; Motro & Eshel, 1988) and more.

One objective of this work is to outline conditions under which a synergistic n -player game will have a mixed ESS, thus extending the results already obtained by Maynard Smith (1982) for pairwise contests. The stability of the mixed ESS against invasions by pure strategists, in particular against invasions by recognizable defectors (see Motro & Cohen, 1989), will then be considered, thereby supplementing contributions by Thomas (1984) and by Vickery (1987).

The analysis is accompanied by a theoretical example which examines the foraging behavior in a flock feeding in an uncertain, patchy environment.

The ESS in the Synergistic n -Player Game

Consider a group of n unrelated individuals. For each, either one of two actions is possible, that is, either "co-operation" or "defection". By choosing to co-operate, the individual contributes a common benefit to all group members (including itself), while incurring a personal cost c ($c > 0$).

If m ($m = 0, 1, \dots, n$) individuals in the group co-operate, the personal benefit to each of the n group members is b_m , and the assumption of synergism implies that b_m is an increasing function of m (i.e. $b_0 \leq b_1 \leq \dots \leq b_n$, with $b_0 = 0$ and $b_n > 0$). Let $\delta_m = b_{m+1} - b_m$. Since b_m is monotonically increasing, it follows that $\delta_m \geq 0$ (with $\sum_{m=0}^{n-1} \delta_m > 0$).

For ego, if m out of the other $n-1$ group members co-operate, its payoff is $b_{m+1} - c$ (if ego co-operates) or b_m (if ego defects). Denote by y ($0 \leq y \leq 1$) the probability for ego to choose co-operation. Hence, the conditional payoff to ego (given that among the other $n-1$ group members there are exactly m individuals that co-operate) is

$$W_m = y(b_{m+1} - c) + (1 - y)b_m = b_m + y(\delta_m - c). \quad (1)$$

In order to find the evolutionarily stable strategies, assume that the prevailing strategy in the population is x , that is, each individual has the same probability x ($0 \leq x \leq 1$) of choosing to co-operate (and probability $1 - x$ of choosing to defect), and consider the payoff to a rare mutant having a different strategy y , $y \neq x$. If each individual draws its own action independently of the others, then m in eqn (1) has the binomial distribution, with the parameters $n-1$ and x . Hence, the (unconditional) payoff to the mutant is

$$\begin{aligned} W(y, x) &= \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} W_m \\ &= \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} b_m + y \left[\sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m - c \right], \end{aligned} \quad (2)$$

and is a linear function of y .

Denote

$$\sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m,$$

which is the expected contribution (increase in benefit) if ego co-operates (given the other $n-1$ group members all adopt the same strategy x), by $E(\delta; n-1, x)$. Thus, if $E(\delta; n-1, x) > c$, the mutant's best reply is $y = 1$; if $E(\delta; n-1, x) < c$, its best reply is $y = 0$; whereas if $E(\delta; n-1, x) = c$, the payoff to the mutant does not depend on y .

Three different forms of the monotonically increasing benefit function will be considered: linear, convex and concave.

(i) Linear benefit function (i.e. additivity of benefit, $\delta_m = \delta > 0$ for all $m, m = 0, 1, \dots, n-1$): In this case, the contribution due to one's co-operation is constant, independent of the actual number of other co-operators. Here $E(\delta; n-1, x) = \delta$, and the best reply does not depend on the strategy adopted by the others. It is either $y = 1$ (if $c < \delta$) or $y = 0$ (if $c > \delta$). Hence, the ESS is

$$x^* = \begin{cases} 1 & \text{if } c < \delta \\ 0 & \text{if } c > \delta, \end{cases} \tag{3}$$

and the payoff in an evolutionarily stable (ES) population is

$$W^* \equiv W(x^*, x^*) = \begin{cases} n\delta - c & \text{if } c < \delta \\ 0 & \text{if } c > \delta. \end{cases} \tag{4}$$

(ii) Convex benefit function (i.e. δ_m is an increasing function of $m, m = 0, 1, \dots, n-1$): This is a case of superadditivity of benefit—the contribution due to one's co-operation is greater if more individuals in the group choose to co-operate (see, e.g. the case of the fig wasps: Galil & Eisikowitch, 1968; Cohen & Eshel, 1976). Here $E(\delta; n-1, x)$ is an increasing function of x (see Appendix), with $\delta_0 \leq E(\delta; n-1, x) \leq \delta_{n-1}$. Hence, if $c \leq \delta_0$, the mutant's best reply is $y = 1$ (irrespective of the value of x), and if $c \geq \delta_{n-1}$, the best reply is $y = 0$ (irrespective of the value of x). If $\delta_0 < c < \delta_{n-1}$, the equation $E(\delta; n-1, x) = c$ has a single solution in the interval $0 < x < 1$, which will be denoted by \tilde{x} . Thus, for $x < \tilde{x}$, $E(\delta; n-1, x) < E(\delta; n-1, \tilde{x}) = c$, the payoff to the mutant is then a decreasing function of y , and the mutant's best reply is $y = 0$, whereas for $x > \tilde{x}$, the best reply is $y = 1$. Hence, there are two ESSs in this situation, namely the two pure strategies (while \tilde{x} , though a Nash solution of the game, is not an ESS).

To summarize the convex case, the ESS are

$$x^* = \begin{cases} 1 & \text{if } c \leq \delta_0 \\ 0 \text{ and } 1 & \text{if } \delta_0 < c < \delta_{n-1} \\ 0 & \text{if } c \geq \delta_{n-1}, \end{cases} \tag{5}$$

and the payoff in an ES population is

$$W^* = \begin{cases} b_n - c & \text{if } c \leq \delta_0, \text{ or if } \delta_0 < c < \delta_{n-1} \text{ and } x^* = 1 \\ 0 & \text{if } c \geq \delta_{n-1}, \text{ or if } \delta_0 < c < \delta_{n-1} \text{ and } x^* = 0. \end{cases} \tag{6}$$

(iii) Concave benefit function (i.e. δ_m is a decreasing function of $m, m = 0, 1, \dots, n-1$): in this case we have a subadditive benefit function, which indicates diminishing returns from co-operation—while the benefit to each individual increases as a function of the number of co-operators, the contribution of each co-operator decreases as a function of that number. Here $E(\delta; n-1, x)$ is a decreasing function of x (see Appendix), with $\delta_{n-1} \leq E(\delta; n-1, x) \leq \delta_0$. Hence, if $c \leq \delta_{n-1}$, the mutant's best reply is $y = 1$ (irrespective of the value of x), and if $c \geq \delta_0$, the best reply is $y = 0$ (irrespective of the value of x). If $\delta_{n-1} < c < \delta_0$, then for x smaller than \hat{x} (which is the single solution of $E(\delta; n-1, x) = c$ in the interval $0 < x < 1$),

the mutant's best reply is $y = 1$, whereas for $x > \hat{x}$, the best reply is $y = 0$. Therefore, the mixed strategy \hat{x} is the only ESS in this situation.

To summarize the concave case, the ESS is

$$x^* = \begin{cases} 1 & \text{if } c \leq \delta_{n-1} \\ \hat{x} & \text{if } \delta_{n-1} < c < \delta_0 \\ 0 & \text{if } c \geq \delta_0, \end{cases} \quad (7)$$

where \hat{x} ($0 < \hat{x} < 1$) is the single solution of $E(\delta; n-1, \hat{x}) = c$. Since for a concave benefit function, $E(\delta; n-1, x)$ decreases both as a function of x and as a function of n (see Appendix), it follows that \hat{x} is a decreasing function of n .

The expected payoff in an ES population is

$$W^* = \begin{cases} b_n - c & \text{if } c \leq \delta_{n-1} \\ E(\mathbf{b}; n-1, \hat{x}) & \text{if } \delta_{n-1} < c < \delta_0 \\ 0 & \text{if } c \geq \delta_0, \end{cases} \quad (8)$$

where

$$E(\mathbf{b}; n-1, \hat{x}) = \sum_{m=0}^{n-1} \binom{n-1}{m} \hat{x}^m (1-\hat{x})^{n-1-m} b_m$$

is the expected benefit to an individual in a group of size $n-1$, all adopting the same strategy \hat{x} .

Thus, in the concave case, if the contribution (i.e. the additional benefit) due to co-operation is always larger than the cost of co-operation, absolute co-operation is the only ESS. If, on the other hand, the contribution is always smaller than the cost of co-operation, absolute defection is the only ESS, while in any other situation the ESS is a mixed strategy of co-operation and defection, bringing the expected contribution due to co-operation to be equal to the cost of co-operation. (Note that of the three different forms considered for the benefit function, only the concave case yields the possibility of a mixed ESS.)

For the special case $n=2$, the results obtained here coincide with the results already obtained by Maynard Smith (1982) for pairwise encounters.

Since the payoff to a mixed strategy is assumed to be a linear combination of the payoffs to the respective pure strategies, our model is a "degenerating" one (using the terminology of Thomas, 1984). Thus, one cannot predict whether an ES population will be monomorphic, consisting exclusively of mixed strategists (all adopting the same strategy \hat{x}), or will be polymorphic, either consisting of a mixture of pure strategists (with a proportion \hat{x} of pure co-operators and $1-\hat{x}$ of pure defectors), or consisting of any other mixture of types, such that the expected number of actual co-operators in a random group of size n will be $n\hat{x}$ (Maynard Smith, 1982; Thomas, 1984).

An Example—Foraging in a Patchy Environment

Consider a flock foraging in a patchy environment, which is characterized by a clumped dispersion of food. Examples are quite common—herons searching over

mudflat areas for suitable feeding pools (Krebs, 1974), chickadees looking for aggregates of worms (Krebs, 1979), corssbills searching among pine trees for trees richer in seeds (Benkman, 1988), and more. (For reviews see Krebs, 1979; Barnard & Thompson 1985; also Benkman 1988 and references therein.)

Suppose that the distribution of patches is such that at any given time unit a searching individual has a probability p of finding a good patch (i.e. a patch rich in food). Once an individual locates a good patch, the others will join and share the patch's resources. The assumption is that a good patch contains enough food to eliminate the possibility of exploitative competition among flock members.

If m individuals search independently of each other, the probability of finding a good patch (during any given time unit) is $1 - (1 - p)^m$, and the benefit to each individual in the flock is proportional to this probability. Searching, however, imposes a cost on the searcher, such as the extra energy involved in the sampling and the higher risk of predation during the search, whereas defectors can use the time for selfish activities like grooming [or defending their hierarchial position, as may be suggested by the aggressive behavior observed among idle crossbills during group foraging (Benkman, 1988)].

At any moment, each individual can choose either to co-operate (i.e. to search) or to defect (refrain from searching) during that time unit. Hence for each time unit this foraging game can be regarded as a special case of the synergistic n -player game with a concave benefit function, where (by appropriately choosing the units of cost and benefit) c is the cost of search per unit of time, $\delta_m = p(1 - p)^m$ and n is the flock size. (The assumption is that the decision to search bears the same cost whether or not a good patch is found during that time unit.) Substituting in eqn (7), we obtain the ESS

$$x^* = \begin{cases} 1 & \text{if } c \leq p(1-p)^{n-1} \\ \hat{x} & \text{if } p(1-p)^{n-1} < c < p \\ 0 & \text{if } c \geq p, \end{cases} \quad (9)$$

where $\hat{x} = [1 - (c/p)^{1/(n-1)}]/p$, and is a decreasing function of n .

For an ES flock, the probability of finding a good patch during any given time unit is

$$E(\mathbf{b}; n, x^*) = 1 - (1 - px^*)^n = \begin{cases} 1 - (1 - p)^n & \text{if } c \leq p(1-p)^{n-1} \\ 1 + c\hat{x} - c/p & \text{if } p(1-p)^{n-1} < c < p \\ 0 & \text{if } c \geq p. \end{cases}$$

If decisions at distinct time units are independent, the expected time until an ES flock finds a good patch (provided, of course, that $c < p$) is

$$T^* = \begin{cases} 1/[1 - (1 - p)^n] & \text{if } c \leq p(1-p)^{n-1} \\ 1/[1 + c\hat{x} - c/p] & \text{if } c > p(1-p)^{n-1}. \end{cases} \quad (10)$$

Hence, for small flocks [i.e. if $n \leq 1 + \log(c/p)/\log(1-p)$], the expected finding time decreases as a function of n , while for larger flocks [$n > 1 + \log(c/p)/\log(1-p)$], the expected finding time becomes an increasing function of

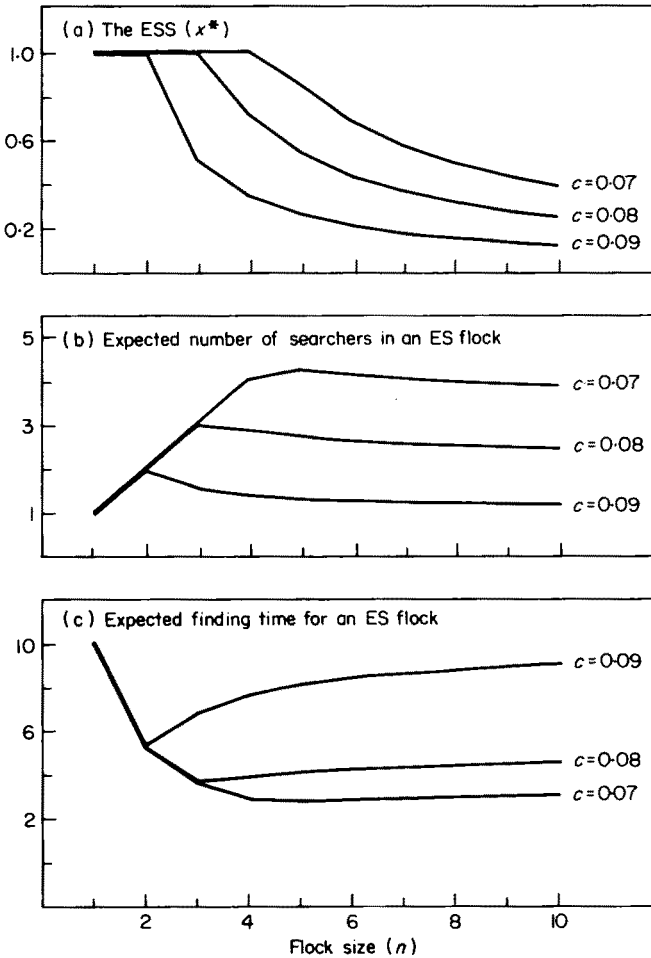


FIG. 1. The foraging game: (a) the ES probability x^* , (b) the expected number of simultaneous searchers in an ES flock (i.e., nx^*), and (c) the expected time it takes an ES flock to find a good patch, all as a function of flock size (n). The probability that a searcher will find a good patch during any time unit is $p=0.10$, and three different cost values are considered: $c=0.07$, $c=0.08$ and $c=0.09$.

n (see also Fig. 1). This theoretical prediction is in good accordance with Benkman's observations on the foraging behavior of crossbills (Benkman, 1988).

More on the Stability of the Mixed ESS

In the case of a mixed ESS (\hat{x}), an ES population can consist of any composition of types, as long as the mean value of the strategy in the population is equal to \hat{x} . If, however, individuals adopting the pure strategy of defection can be recognized as such by other group members, any composition of types other than that of pure strategists is no longer stable. This is because if a group is known to contain a

defector, the ESS is not the best reply for the non-defectors, and another strategy, which is the solution of $E(\delta; n-2, x) = c$, is then the best reply. Since in the case of a concave benefit function the expectation of δ satisfies $E(\delta; n-2, x) > E(\delta; n-1, x)$ and is also a decreasing function of x (see Appendix), this best reply determines an increased level of co-operation. Thus, the presence of a recognizable defector creates a situation favoring increased co-operation by non-defectors, and this in turn endows the defector with a selective advantage. This potential advantage is, of course, frequency dependent—it exists as long as the frequency of the defectors in the population is smaller than $1 - \hat{x}$ (reflecting the fact that while in any mixed group the defectors enjoy a larger benefit than do the co-operators, being a defector in an all-defector group is a disadvantage indeed). An evolutionary process can thus be envisaged, leading eventually to a stable polymorphism, in which pure co-operators and pure defectors coexist together (in proportions \hat{x} and $1 - \hat{x}$, respectively).

It should be noted that recognizability of pure strategists is not the only mechanism preventing the establishment of the mixed strategy. Since in a finite population encounter rates are not exactly equal to the frequencies of the strategists in the population (because an individual will never encounter itself), the mixed strategy of a “degenerating” model played in any finite population will always be unstable against invasions by pure strategists (Vickery, 1987). Although Vickery dealt only with pairwise encounters, his argument can nevertheless be applied also to the n -player game.

The mixed strategy can be stable, however, if we break the conventional assumption that the payoff to the mixed strategy is the linear combination of the payoffs to the corresponding pure strategies. If we assume, for example, that the cost of co-operation is not constant, but depends on the strategy adopted by the player, our model then changes into a “non-degenerating” one. A strategy-dependent cost can arise, for example, if the game is repeatedly played by an individual over a large, more or less fixed, number of times (not necessarily always against the same players, and without any further assumptions pertaining to reciprocation and retaliation, individual recognition or non-random encounters). An x -strategist is then expected to co-operate a proportion x of the times (and defect a proportion $1 - x$ of the times). If the player’s gains from repeated defection are not additive but, rather, subadditive; that is, if its total gain from defection is a concave function of the number of times the player defects (reflecting diminishing returns from defection), then c , the cost of co-operation, is an increasing function of x . Thus, in the vigilance models, for example, the game is repeatedly played at each time unit, and the cumulative gain from defection (i.e. the gains from feeding) is considered to have this diminishing returns property (Pulliam *et al.*, 1982; Parker & Hammerstein, 1985; Motro & Cohen, 1989). A similar assumption can as well be applied to the foraging game presented in this paper. The payoff to any mutant occurring in a population of x -strategists will then be smaller than the payoff to the conforming x -strategist, and the mixed ESS will thus be stable. Yet, as demonstrated by Fig. 2, if the groups are large enough, a *recognizable* defector can still invade and spread (compare also with Motro & Cohen, 1989).

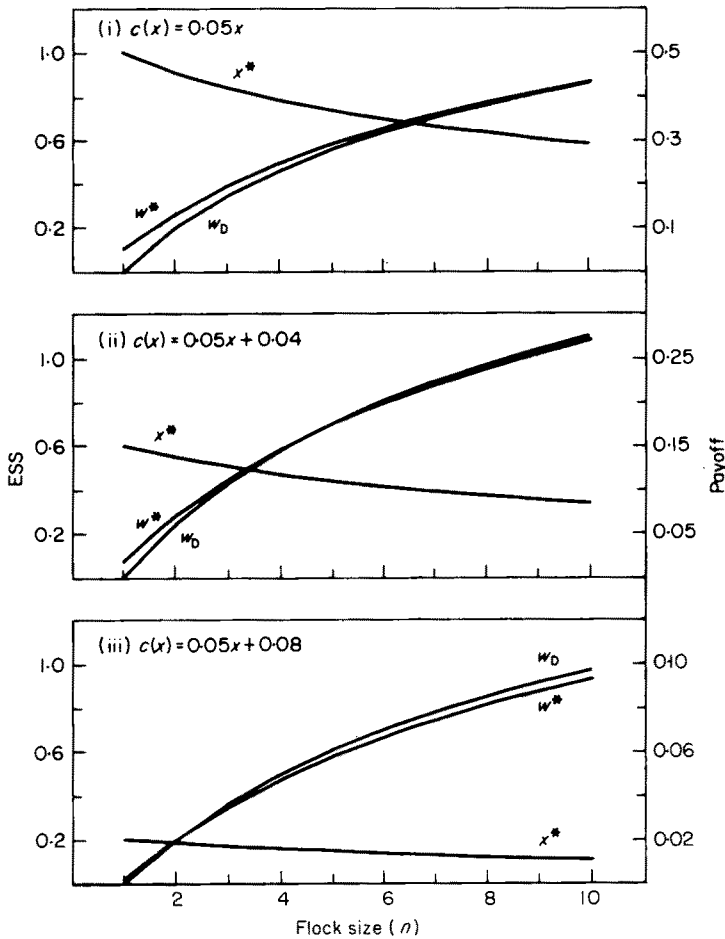


FIG. 2. The foraging game with a strategy-dependent cost: x^* = the ESS, W^* = the payoff in an ES flock, and W_D = the payoff to a recognizable defector (if the other $n-1$ flock members adopt their best-reply). Three different linear functions for the strategy-dependent cost are considered (in each case, $p = 0.10$). Note that for large enough flocks, W_D is larger than W^* .

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REFERENCES

- BARNARD, C. J. & THOMPSON, D. B. A. (1985). *Gulls and Plovers*. New York: Columbia University Press.
- BENKMAN, C. W. (1988). Flock size, food dispersion, and the feeding behavior of crossbills. *Behav. Ecol. Sociobiol.* **23**, 167-175.
- COHEN, D. & ESHEL, I. (1976). On the founder effect and the evolution of altruistic traits. *Theor. Pop. Biol.* **10**, 276-302.
- ESHEL, I. & MOTRO, U. (1988). The three brothers' problem: kin selection with more than one potential helper. 1. The case of immediate help. *Am. Nat.* **132**, 550-566.

- GALIL, J. & EISIKOWITCH, D. (1968). Pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* **49**, 259-269.
- KREBS, J. R. (1974). Colonial nesting and social feeding as strategies of exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour* **51**, 99-134.
- KREBS, J. R. (1979). Foraging strategies and their social significance. In: *Social Behavior and Communication* (Marler, P., & Vandenbergh, J. G., eds) New York: Plenum Press.
- MAYNARD SMITH, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- MOTRO, U. & COHEN, D. (1989). A note on vigilance behavior and stability against recognizable social parasites. *J. theor. Biol.* **136**, 21-25.
- MOTRO, U. & COHEN, D. (1990). Selfish cooperation in social roles: the vigilance game in continuous time. In: *The Sociobiology of Conflict* (van der Dennen, H., Falger, V. S. E., Hopp, M. & Irwin, C. J., eds) London: Chapman & Hall, in press.
- MOTRO, U. & ESHEL, I. (1988). The three brothers' problem: kin selection with more than one potential helper. 2. The case of delayed help. *Am. Nat.* **132**, 567-575.
- PARKER, G. A. & HAMMERSTEIN, P. (1985). Game theory and animal behaviour. In: *Evolution: Essays in Honour of John Maynard Smith* (Greenwood, P. J., Harvey, P. & Slatkin, M., eds) pp. 73-94. New York: Cambridge University Press.
- PULLIAM, H. R., PYKE, G. H. & CARACO, T. (1982). The scanning behaviour of juncos: a game theoretical approach. *J. theor. Biol.* **95**, 89-103.
- RIECHERT, S. E. & HAMMERSTEIN, P. (1983). Game theory in the ecological context. *Ann. Rev. Ecol. Syst.* **14**, 377-409.
- THOMAS, B. (1984). Evolutionary stability: states and strategies. *Theor. Pop. Biol.* **26**, 49-67.
- VICKERY, W. L. (1987). How to cheat against a simple mixed strategy ESS. *J. theor. Biol.* **127**, 133-139.

APPENDIX

Proposition: If δ_m is an increasing (a decreasing) function of m , then $E(\delta; n-1, x)$ is

- (i) an increasing (a decreasing) function of x .
- (ii) an increasing (a decreasing) function of n .

Proof:

$$\begin{aligned}
 & \text{(i) } \frac{\partial}{\partial x} E(\delta; n-1, x) \\
 &= \frac{\partial}{\partial x} \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m \\
 &= \sum_{m=0}^{n-1} \binom{n-1}{m} [m x^{m-1} (1-x)^{n-1-m} - (n-1-m) x^m (1-x)^{n-2-m}] \delta_m \\
 &= (n-1) \sum_{m=0}^{n-2} \binom{n-2}{m} x^m (1-x)^{n-2-m} \delta_{m+1} \\
 &\quad - (n-1) \sum_{m=0}^{n-2} \binom{n-2}{m} x^m (1-x)^{n-2-m} \delta_m \\
 &= (n-1) \sum_{m=0}^{n-2} \binom{n-2}{m} x^m (1-x)^{n-2-m} (\delta_{m+1} - \delta_m).
 \end{aligned}$$

Hence, if δ_m is an increasing (a decreasing) function of m , the derivative of $E(\delta; n-1, x)$ with respect to x is positive (negative), thus $E(\delta; n-1, x)$ is an increasing (a decreasing) function of x .

$$\begin{aligned}
& \text{(ii) } E(\delta; n, x) - E(\delta; n-1, x) \\
&= \sum_{m=0}^n \binom{n}{m} x^m (1-x)^{n-m} \delta_m - \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m \\
&= \sum_{m=0}^n \left[\binom{n-1}{m-1} + \binom{n-1}{m} \right] x^m (1-x)^{n-m} \delta_m - \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m \\
&= \sum_{m=1}^n \binom{n-1}{m-1} x^m (1-x)^{n-m} \delta_m + \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-m} \delta_m \\
&\quad - \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m \\
&= \sum_{m=0}^{n-1} \binom{n-1}{m} x^{m+1} (1-x)^{n-1-m} \delta_{m+1} - x \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} \delta_m \\
&= x \sum_{m=0}^{n-1} \binom{n-1}{m} x^m (1-x)^{n-1-m} (\delta_{m+1} - \delta_m).
\end{aligned}$$

Hence, if δ_m is an increasing (a decreasing) function of m , $E(\delta; n, x)$ is larger (smaller) than $E(\delta; n-1, x)$.