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Evolutionary Game Auctions

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The War of Attrition and the Scotch Auction are instances of a general type of evolutionary game, here referred to as an evolutionary auction. Evolutionary auctions are symmetric, without injury, settled by a single scalar variable ("the bid"), and subject to an overshoot cost function which depends on the difference between the bids. For what appears to be the general class of biologically tenable overshoot cost functions we show that (with the single pathological exception of the Scotch Auction) there is a unique ESS, whose density function is defined on an interval $[0, b)$. Examples are given, and general methods of finding the ESS discussed. Implications for the evolution of animal display behaviour and morphological characters are discussed.

1. Introduction

Among the simplest types of evolutionary game are those which are confined to play definable by one scalar variable, without asymmetry or injury. Two such evolutionary games are well-known; the War of Attrition, put forward in Maynard Smith & Price (1973), and the Scotch Auction, due to Parker (1979). The present article analyses a generalized evolutionary game which has these two games as special cases.

Contests like the War of Attrition have long been studied as part of the theory of auctions in economics (Hirshleifer & Riley, 1978). But they are of little practical economic interest, because all bids by losers must be paid in full. This is almost never the case in commercial transactions. Thus "auctions" like the War of Attrition and the Scotch Auction are of importance solely in biological evolution. To set them aside from commercial auctions, they will be referred to as evolutionary game auctions.

In such an auction, two (or more) players are contesting for a prize, which will go to the highest bidder. In Rose (1978), the Scotch Auction was shown

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to be evolutionarily transient if there were mutants whose bidding depended on the bid of the opponent. One such class of mutants consists of those which use a "reserve-bid" strategy. Such a bidding strategist has in mind a bid, M, which he will never exceed; once his opponent's bid exceeds M, he will drop out. But, if his opponent drops out before M is reached, the mutant will exceed his opponent's bid, but not necessarily as far as M. Such a cheating mutant will be able to invade rule-obeying populations. As discussed in Rose (1978), the reserve-bid strategy would then itself become subject to selection tending to reduce the extent to which the opponent's bid is exceeded.

In the limit, such a reserve-bid strategist would stop bidding at precisely the level of the opponent's reserve bid, whenever it was lower than its own reserve bid. This establishes the War of Attrition, analysed in Maynard Smith (1974). However, for actual organisms, some degree of overshoot may be unavoidable. In particular, if a large scale physiological investment is involved in bidding, for example bids which entail the development of special plumage among courting male birds, then bid increments ceasing at precisely the level of the opponent's final bid seems a practical impossibility.

Therefore, there are good reasons for regarding the Scotch Auction and the War of Attrition as limiting cases of evolutionary auctions which are, in general, subject to bid overshoot costs.

Below, evolutionary auctions subject to a class of overshoot cost functions are examined. General results are found for this class of functions. These results are then applied to cases of animal display contests and evolutionary game contests with fixed investments.

2. The Two-player Evolutionary Game Auction

We suppose that auctions are contested between two opponents, without asymmetries in prize value, contest frequency, side-benefits and so on. The entire prize, value V, will go to the player who makes the larger bid. Otherwise, let x and $y (x > y \geq 0)$ represent the values the contestants are prepared to bid. Then the potential x-player gains V, and pays the amount $y + f(x - y)$, where $f(.)$ is the *overshoot cost function.*

The demands of the biology impose certain constraints on f. Since f is a cost, it will be non-negative, but we may suppose that $f(u) \leq u$, because otherwise the winner of the contest would be paying more than his potential bid. Further, we assume that $f'(u) \geq 0$ and $f''(u) \leq 0$; the first condition ensures that the more you are initially prepared to pay, the more you actually pay (for any given opponent's bid) and the second condition corresponds to the idea that it will be harder to tell that an opponent has desisted immediately after the event, and that it gets relatively easier to hold back your own bid, the more you exceed his.

Figure 1 gives simple examples of overshoot cost functions meeting these conditions; these examples are discussed further in section 5 below.

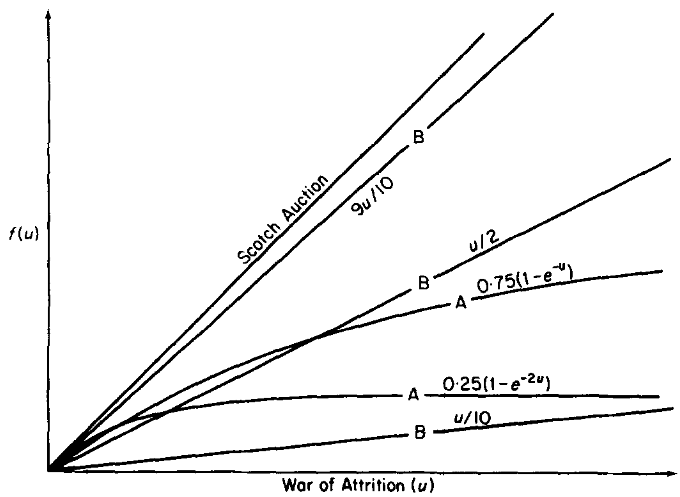

FIG. 1. Examples of overshoot cost functions $f(u)$ meeting the assumptions made in the text. The extreme points, namely the War of Attrition $f(u)=0$ and the Scotch Auction $f(u)=u$ are also shown.

3. ESS Theorems

An *evolutionary stable strategy*, or ESS, was defined by Maynard Smith (1974), and is a strategy which, if played by a population, protects the population from invasion by mutant strategies. In our context, a strategy corresponds to a probability density function; the amount a player is prepared to bid is a random variable with that probability density.

Given an overshoot cost function f, defined on $[0, \infty)$, we write $g(u) = f'(u) - 1$. The conditions on f imply the assumptions (i) $-1 \leq g(.) \leq 0$ and (ii) $g'(.) \geq 0$, which we assume without further comment. It will be shown below that the Scotch Auction, corresponding to $g(u) \equiv 0$, shown by Rose (1978) to have no ESS, is thereby exceptional amongst the auctions which are defined by these functions g.

We seek ESSs. Given strategies I, J with density functions p, q, we shall write $E(p, q)$ to denote the mean payoff to the player of I when his opponent plays J: for a pure strategy x, we shall write $E(x, q)$ to denote the mean payoff to a player playing x against an opponent who uses q. Following the notation of Bishop & Cannings (1978), we write

$R(I) \equiv R(p) = \{x : x$ is a point of increase of $P(x)$, the distribution function of $p(x)\}$

$S(I) \equiv S(p) = \{x : E(x, p) = E(p, p)\}$.

Theorem 1 of Bishop & Cannings (1978) is that $R(I) \subset S(I)$, and thus says that, if $x \in R(I)$, then

$$E(x, p) = \int_0^x [V - y - f(x-y)]p(y)\,\mathrm{d}y - \int_x^\infty xp(y)\,\mathrm{d}y = \text{const.} \quad (3.1)$$

Upon differentiationg with respect to x and re-arranging, we obtain the key equation

$$Vp(x) - 1 - \int_0^x g(x-y)p(y)\,\mathrm{d}y = 0. \quad (3.2)$$

It is easy to adapt the proof of theorem 6 of Bishop & Cannings (1978) to see that no ESS can have an atom of probability at any point, so any ESS I has a density p which satisfies (3.2) over the set $R(I)$. Our principal result is:

Theorem 1. For all functions g such that $-1 \leq g(\,.\,) \leq 0$ and $g'(\,.\,) \geq 0$ there is an interval $[0, b)$ (possibly with $b = \infty$) over which equation (3.2) has a solution $p(x)$ which is the probability density function corresponding to some strategy I. Further

(i) $p(0) = 1/V$,

(ii) $p(x)$ is non-increasing over $[0, b)$,

(iii) $p(x) > 0$ for $0 \leq x < b$.

Finally, except in the Scotch Auction case where no ESS exists, this strategy I is the unique ESS of the evolutionary game defined by g.

The proof of this theorem is given in the Appendix.

It is of some interest to know the conditions under which $b < \infty$ or $b = \infty$. A partial result in this direction is:

Theorem 2. With the notation of theorem 1, if $\exists \varepsilon, c > 0$ such that $g(x) \geq -1 + \varepsilon$ for $x \geq c$, then b is finite.

Proof: If b is not finite, we can choose K such that $\int_K^\infty p(y)\,\mathrm{d}y < \varepsilon/2$, and consider $x \geq K + c$. For such x, from (3.2)

$$\begin{aligned} Vp(x) &= 1 + \int_0^K g(x-y)p(y)\,\mathrm{d}y + \int_K^x g(x-y)p(y)\,\mathrm{d}y \\ &\geq 1 + (\varepsilon - 1)\int_0^K p(y)\,\mathrm{d}y + R \end{aligned}$$

where

$$|R| \leq \int_K^\infty p(y)\,\mathrm{d}y < \varepsilon/2$$

Hence $Vp(x) \geq \varepsilon(1-\varepsilon/2)+\varepsilon/2+R \geq \varepsilon/4$ (by taking ε sufficiently small). We have shown that, if $x \geq K+c$, then $p(x) \geq \varepsilon/(4K)$, which is clearly impossible since p is a density function. Hence b is finite.

4. Methods of Analysis

(A) COST FUNCTION KNOWN

When f is known, so is g, and we seek a solution to

$$Vp(x) = 1 + \int_0^x g(x-y)p(y)\,\mathrm{d}y \tag{3.2}$$

over $[0, b)$, where $p(x) \geq 0$ over $[0, b)$ and $P(b) = 1$.

It is clear from (3.2) that $p(x)$ over $[0, b)$ depends only on $g(x)$ over $[0, b)$, so we may assume, if we like, that (3.2) holds for all x and, having obtained $p(x)$ over $[0, \infty)$, we can then find the first b for which $P(b) = 1$, and truncate our solution at this point. Since, in advance of finding $p(.)$, b is unknown, this is a particular convenience. Taking formal Laplace transforms in (3.2), and using * to denote Laplace transformation, we have

$$Vp^* = 1/s + g^*p^*$$

and hence

$$p^* = 1/[s(V-g^*)] = 1/(sV - 1 - s^2 f^*). \tag{4.1}$$

Equation (4.1) is easily solved in the important cases $f(u) = cu$ $(0 \leqslant c \leqslant 1)$ and $f(u) = c\alpha[1-\exp(-u/\alpha)]$ $(0 < c \leq 1,\ 0 < \alpha)$ treated in section 5 below.

Another method of solving (3.2) is to define the operator K by

$$K\psi(x) = \int_0^x \frac{g(x-y)}{V}\psi(y)\,\mathrm{d}y.$$

Equation (3.2) can then be written

$$p(x) = \frac{1}{V} + Kp(x) \tag{4.2}$$

which is a Volterra Integral Equation with formal solution

$$p(x) = \sum_{n=0}^{\infty} K^n\left(\frac{1}{V}\right);$$

again, truncation of $p(.)$ at b will be necessary, but the iterates $K^n(1/V)$ will generally be difficult to calculate.

A third approach is to differentiate (3.2) successively in order to find the McLaurin Series for $p(x)$. It is easy to see that

$$Vp^{(n)}(0) = \sum_{r=0}^{n-1} g^{(r)}(0)p^{(n-r-1)}(0), \tag{4.3}$$

and so from the recurrence relation (4.3), the terms $p^{(n)}(0)$ can be obtained from the values of the derivatives of f at 0.

(B) ESS KNOWN

Theorem 1 puts certain restrictions on the density function p of an ESS, and we may wish to know the form of the cost function that could correspond to a given ESS p. However, not all functions p that satisfy these restrictions can arise, as the example $p(x) = A/(B+x)^n$ shows. For a p of this form, it is easy to see that $p(x) = V^{n-1}(n-1)^n/(Vn-V+x)^n$; from (4.3), $g(0) = V^2p'(0)$, so $g(0) = -n/(n-1)$, and this contradicts assumption (i) about g. Hence no function p of this form can be an ESS. Similarly, for a function of the form $p(x) = (1-Ax)/V$ over the finite range $[0, b)$, a suitable re-parametrization is $b = cV$, $A = 2(c-1)/(c^2V)$, and $1 \le c \le 2$. The corresponding function g, from (4.1) or (4.3), is $g(x) = -AV\exp(Ax)$, and our constraint on g, that $g(b) \ge -1$, implies that $2(c-1)/c \le \log[c^2/[2(c-1)]]$, i.e. $1 < c \le 1{\cdot}6065$ approx. Note that, even for such c, it is irrelevant that there are (large) values of x for which $g(x) < -1$, since p is determined by $g(x)$ for $0 \le x \le b$, and so we can replace $g(x)$ by $g^*(x) = \max[-AV\exp(Ax), -1]$ *without alteration to p*, so long as $1 < c \le 1{\cdot}6065$. Thus, ESSs of the form $p(x) = (1-Ax)/V$ over $[0, b]$ do exist if $AV < 0{\cdot}470$, but not for all possible values of A that correspond to density functions.

(C) THE AMOUNTS ACTUALLY PLAYED

Consider a contest between two players with reward V, overshoot cost function f, both using the unique ESS $p(t)$ of Theorem 1. Then X, Y, the random variables representing the time the players are prepared to wait are independent, each having density function p. Suppose $Z = \min.(X, Y)$ and $T = \max.(X, Y)$; then the values actually *used* by the two players are Z and $W = Z + f(T-Z)$. Thus

$$\begin{aligned} H(z, w) &= P(Z \le z, W \le w) \\ &= 2P[X \le Y, X \le z, X + f(Y-X) \le w] \\ &= 2P[X \le z, X \le Y \le X + f^{-1}(w-X)] \end{aligned}$$

where f^{-1} needs careful interpretation when its argument is outside the range of f. Subject to this interpretation,

$$H(z, w) = 2\int_0^z p(x)\int_x^{x+f^{-1}(w-x)} p(y)\,dy\,dx.$$

For the single random variable Z, the simple result

$$p_Z(z) = 2p(z)[1-P(z)]$$

always holds, but the expression for p_W is more complicated. Some special cases are considered in the next section.

5. Examples

Until this point, discussion has been confined to the abstract ESS bid distributions depending on overshoot cost functions in a wide range of evolutionary game auctions. The general results which have been obtained are difficult to interpret biologically as they stand. Accordingly, this section will apply these results to particular, simplified, evolutionary situations which illustrate their significance.

(A) ANIMAL DISPLAY AUCTIONS

Here the term "display" is used in the sense defined in Maynard Smith (1974). Bird displays provide the best examples of this kind of auction. Two things may be considered typical of such display behaviour. Firstly, it will not always be immediately apparent to the animal with the highest reserve bid that its opponent has ceased to contest the disputed fitness unit. Secondly, after some "noticing period", in which overshoot costs increase with the difference between the higher reserve bid and the losing bid, overshoot costs will not increase further. From these two features, overshoot cost functions which approach an asymptotic plateau seem to be required, as in curves A of Fig. 1.

The overshoot cost function given by

$$f(u) = c\alpha[1-\exp(-u/\alpha)], \quad 1 \geq c > 0 \quad \text{and} \quad \alpha > 0,$$

has the necessary features and is fairly simple in form. ESS results for it should suggest what the results for similar functions would be like. We also take $V = 1$, without loss of generality. The Laplace transform of p, assuming equation 3.2 is defined over $[0, \infty)$, is

$$p^*(s) = \frac{s + \beta + \left(\frac{1}{\alpha} - \beta\right)}{(s+\beta)^2 + \frac{1}{\alpha} - \beta^2}$$

where

$$\beta = \frac{1 + \alpha d}{2\alpha}, \quad d = 1 - c.$$

Let $\alpha_1 = (1 + \sqrt{c})^{-2}$, $\alpha_2 = (1 - \sqrt{c})^{-2}$; if $\alpha = \alpha_1$ or $\alpha = \alpha_2$ then $(1/\alpha) - \beta^2 = 0$.

For $0 < \alpha < \alpha_1$, or $\alpha > \alpha_2$, the quantity $\beta^2 - (1/\alpha) = k^2$, say, is positive, and the corresponding ESS is

$$p(t) = \frac{1}{2k} e^{-\beta t}\left[\left(k - \beta + \frac{1}{\alpha}\right) e^{kt} + \left(k + \beta - \frac{1}{\alpha}\right) e^{-kt}\right];$$

for $0 < \alpha < \alpha_1$, this is a density function over $[0, \infty)$, but for $\alpha > \alpha_2$ it is a density function over $[0, b)$, where

$$\exp(2kb) = (1 + k - \beta)/(1 - k - \beta).$$

For $\alpha = \alpha_1$ or $\alpha = \alpha_2$, the corresponding ESS has density

$$p(t) = [1 + (\beta^2 - \beta)t] \exp(-\beta t);$$

the range is $[0, \infty)$ for $\alpha = \alpha_1$, but $[0, 1/\sqrt{c})$ for $\alpha = \alpha_2$.

For $\alpha_1 < \alpha < \alpha_2$, write $\omega^2 = \alpha^{-1} - \beta^2$. Then $\omega^2 > 0$, and the ESS is

$$p(t) = \left[\cos \omega t + \frac{1}{\omega}\left(\frac{1}{\alpha} - \beta\right) \sin \omega t\right] \exp(-\beta t)$$

over $[0, b)$, where $\cos \omega b = (1 - \beta)/\sqrt{c}$.

We note in passing that, given c, as α increases from 0^+ to ∞, so the ESS adopts the forms shown in turn. The reader may care to verify algebraically that b, the maximum possible play, infinite for $0 < \alpha \leq \alpha_1$, is a decreasing function of α in the range (α_1, ∞).

It is also easy to check that the means of these probability densities vary continuously as α, c change, and, after some tedious integrations, the following results can be obtained.

Range	*Mean*
$0<\alpha\leq\alpha_1$	$1-\alpha c$
$\alpha_1\leq\alpha\leq\alpha_2$	$1-\alpha c+\alpha\sqrt{c}\,e^{-\beta b}$, where $\cos\omega b=(1-\beta)/\sqrt{c}$
$\alpha\geq\alpha_2$	$1-\alpha c+\dfrac{\alpha c}{1-k-\beta}\exp[-(k+\beta)b]$, where $\exp(2kb)=(1-\beta+k)/(1-\beta-k)$.

These properties refer to the amounts players are prepared to play, but the actual amounts played will have a different distribution, as described in section 4.C. Concise analytic answers seem impossible in this case, even in the special case $c=1$. Suppose that $4\alpha<1$, so that the ESS is over $[0,\infty)$. Then

$$p_W(w)=\begin{cases}2\alpha\displaystyle\int_0^w p(x)p\left(x-\alpha\log\frac{\alpha-w+x}{\alpha}\right)\frac{dx}{\alpha-w+x} & \text{if } w\leq\alpha\\ 2p(w-\alpha)P(w-\alpha) & \\ \qquad+2\alpha\displaystyle\int_{w-\alpha}^w p(x)p\left(x-\alpha\log\frac{\alpha-w+x}{\alpha}\right)\frac{dx}{\alpha-w+x} & \text{if } w>\alpha.\end{cases}$$

A reasonable approximation to pW can be obtained from the fact that $W\simeq Z+(1-\varepsilon)\alpha$, for some small ε. This arises because the density $p(t)$ has a comparatively large variance, so X and Y are quite likely to differ considerably; hence, although $f(W-Z)$ cannot exceed α, it is likely to be close to α.

When $4\alpha>1$, the formal expression for $p_W(w)$ is further complicated by the upper bound, b, on its density. For α very large, the game is close to the Scotch Auction, and since the winner plays very nearly the full amount of his bid, the distribution of bids played is close to the ESS itself.

From these results, the bidding distribution found in Maynard Smith (1974) can be seen as but the simplest possible case for the evolution of animal display behaviour. When the further complications outlined in the discussion section are also considered, it becomes apparent that evolutionary game theory does not yet offer simple, and therefore particularly useful, predictions for the evolution of animal display behaviour.

(B) LINEAR OVERSHOOT COST FUNCTIONS

A contrasting case is provided by a strictly linear overshoot cost function, as illustrated by curves B of Fig. 1. This might arise when an animal had the capability to make a very high reserve bid, but was able, when the contest was over, to re-allocate a fixed proportion of these energies to other ends.

In this case let $f(u) = cu$, with $1 \geq c \geq 0$. Let $d = 1 - c$ and $V = 1$, as before. The special case with $c = 1$ is the Scotch Auction, which has no ESS (Rose, 1978). This auction will arise only if it is entirely impossible to forestall or reallocate a morphological investment. In the face of strong selection pressure to escape this limitation, it seems unlikely that it would persist (Rose, 1978). The other special case is that with $c = 0$, analysed in Maynard Smith (1974) and Bishop & Cannings (1978). This case is a boundary asymptote for the general ESS given by

$$p(x) = \exp(-dx) \text{ over } [0, b),$$

where $b = -(1/d)\log(c)$, which is a truncated negative exponential, declining from $p(0) = 1$ to $p(b) = c$, so that the implications for c approaching zero or unity are clear.

In the notation of section 4.C, the distributions of actual plays are

$$p_X(x) = e^{-dx}$$

$$p_Z(z) = 2\,e^{-dz}(e^{-dz} - c)/d$$

and

$$p_W(w) = \begin{cases} \dfrac{2}{d(1-2c)}(e^{-2dw} - e^{-dw/c}), & \text{if } 0 \leq w \leq bc, \\[2ex] \dfrac{2}{d(1-2c)}(e^{-2dw} - c\,e^{bc-w}), & \text{if } bc \leq w \leq b, \end{cases}$$

except that, when $c = \frac{1}{2}$,

$$p_W(w) = \begin{cases} 4we^{-w}, & \text{if } w \leq \log 2 \\ 4\,e^{-w}(2\log 2 - w), & \text{if } \log 2 \leq w \leq 2\log 2. \end{cases}$$

The respective means are

$$\mu_X = (d + c\log c)/d^2$$

$$\mu_Z = (d - 3cd - 2c^2\log c)/(2d^3)$$

$$\mu_W = 1 - \mu Z.$$

Table 1 compares the means of the bids played for various c values. Figures 2, 3, 4, 5 show the bid distributions that arise for three different values of c.

These results show that the distribution of bids actually played can be quite different between winner and loser. In the case of the fixed investment

TABLE 1

Mean values of the ESS (μ_X), and amounts played by the winner of a contest (μ_W) when $f(u) = cu$

	$c=0$	0·1	0·2	0·3	0·4	0·5	0·6	0·7	0·8	0·9	1^-
μ_X	1	0·83	0·75	0·69	0·65	0·61	0·58	0·56	0·54	0·52	0·50
$1-\mu_Z=\mu_W$	0·5	0·54	0·56	0·58	0·60	0·61	0·63	0·64	0·65	0·66	0·67

auction, such ESS bid distributions would be reflected in the distribution of use made of a morphological character for intra-specific competition. The use of the character for all fitness-enhancing purposes would reflect the underlying reserve-bid distribution. In all likelihood, such distributions would have to be realised by genetic polymorphism, rather than ontogenetic randomisation. Because of overall ontogenetic failures and genetic load arising from mutation and/or segregation, the hypothetical reserve bid distribution boundaries will be subject to blurring, especially at the lower end of the distribution.

As was noted at the end of section 4.B, it may be possible to modify f for large values of its argument without change to the ESS. Thus, in this example, provided $m \geq b = -(1/\mathrm{d}) \log c$, if $f(u) = cu$ on $[0, m]$, and is constant for $u \geq m$, the ESS remains as $\exp(-\mathrm{d}x)$ over $[0, b)$.

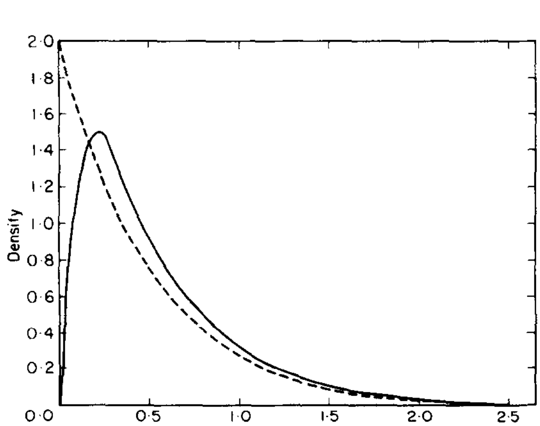

FIG. 2. For the case of $f(u) = cu$, with $c = 0{\cdot}1$, the density functions of the strategies played by the winner (———) and the loser (------).

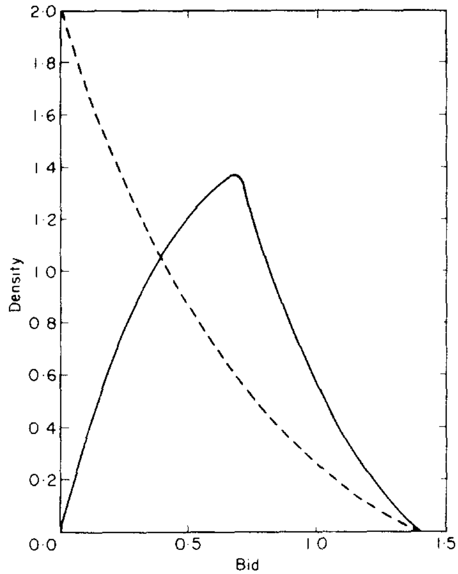

FIG. 3. For the cases of $f(u) = cu$, with $c = 0{\cdot}5$, the density functions of the strategies played by the winner (———) and the loser (– – – – – –).

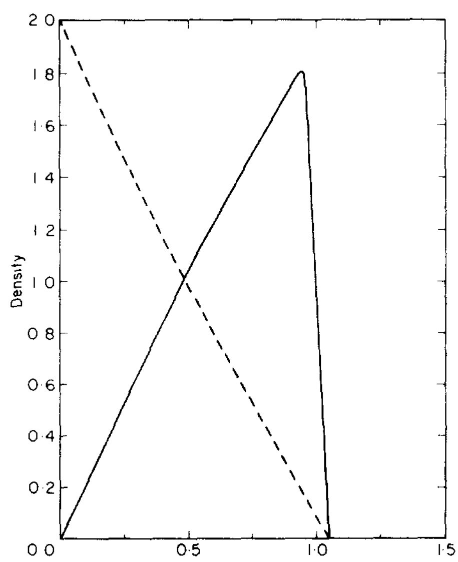

FIG. 4. For the cases of $f(u) = cu$, with $c = 0{\cdot}9$, the density functions of the strategies played by the winner (———) and the loser (– – – – – –).

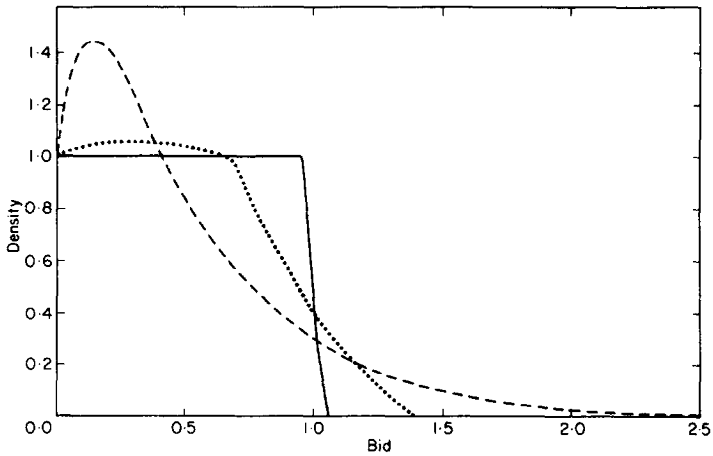

FIG. 5. Density functions of the strategies observed in the population (i.e. average of winner and loser) for the cases $f(u) = cu$, with $c = 0{\cdot}1$ (------), $c = 0{\cdot}5$ (......) and $c = 0{\cdot}9$ (———).

6. Discussion

In general, the analysis given here reveals some of the complexity of auction strategy evolution. However, further complicatoins may also arise for particular auctions.

In the case of behavioural bidding, such as bird display, it is reasonable to assume that there is variation in the value of the contested prize for each player, as in Bishop, Canning & Maynard Smith (1978). That analysis has shown that the ESSs for such cases are radically different from those with fixed prize value. On the other hand, morphological bidding in "life-long" auctions probably depends on prize values which do not vary that much within breeding and interacting populations.

Another complications is that of variation in bid and overshoot costs between individuals. To some extent, this problem can be simply re-expressed in terms of variation in prize-value, as in Bishop, Canning & Maynard Smith (1978), since playing cost and prize-value are relative to one another. However, non-linear changes in bid costs cannot be accommodated by this device.

In the case of life-long auctions, but probably not most behavioural auctions, n-player bidding occurs for single prizes. From the form of the equations involved in the present analysis, it seems unlikely that n-player auctions give rise to a radically different sort of ESS compared with those for two-player auctions.

Finally, like all ESS analyses, the problem of genetic specification remains untouched. Given the complexities which genetics can impose on the evolution of the most straightforward characters, general formulae for the evolutionary dynamics of Mendelian populations subject to evolutionary game auctions may be unobtainable.

REFERENCES

BISHOP, D. T. & CANNINGS, C. (1978). *J. theor. Biol.* **70**, 85.
BISHOP, D. T., CANNINGS, C., & MAYNARD SMITH, J. (1978). *J. theor. Biol.* **74**, 377.
HIRSCHLEIFER, J. & RILEY, J. (1978). *Elements of the Theory of Auctions and Contests.* UCLA Economics Department Working Paper 118B.
MAYNARD SMITH, J. (1974). *J. theor. Biol.* **47**, 209.
MAYNARD SMITH, J. & PRICE, G. R. (1973). *Nature* **246**, 15.
PARKER, G. A. (1979). In *Sexual Selection and Reproductive Competition* (M. A. Blum & N.. A. Blum, eds). London: Academic Press.
ROSE, M. R. (1978). *J. theor. Biol.* **75**, 21.

APPENDIX

Proof of Theorem 1

The structure of this proof is as follows:

(1) Prove that necessary conditions for p to be an ESS are that $0 \in R(p)$ and then that $R(p)$ is some interval $[0, b)$.

(2) For such a function p, show (i), (ii) and (iii).

(3) Show that such a function p is an ESS by showing

(a) if q is a function with $R(q) \not\subset R(p)$, then $E(q, p) < E(p, p)$

(*b*) if $R(q) \subset R(p)$, then $E(q, p) = E(p, p)$, but $E(p, q) > E(q, q)$ unless $q = p$(a.s.). This will conclude the proof.

Suppose first that p satisfies (3.1) and that, if $c = \inf\{x : x \in R(p)\}$, then $c > 0$. By (3.1), $E(c, p) = -c$, since $\int_0^c p(y)\,dy = 0$; but now

$$E(0, p) = 0 > -c = E(c, p) = E(p, p),$$

so p cannot be an ESS since it is susceptible to invasion by the point strategy "play 0". Hence $0 \in R(p)$.

Suppose now that $R(p)$ is not connected, and define $\alpha = \{\inf x : x \notin R(p)\}$ and choose $\beta > \alpha$ so that $\beta \in R(p)$ and $P(\beta) = P(\alpha)$. Then

$$E(\alpha, p) = \int_0^{\alpha} [V - y - f(\alpha - y)]p(y)\,dy - \int_{\alpha}^{\infty} \alpha p(y)\,dy$$

$$E(\beta, p) = \int_0^{\beta} [V - y - f(\beta - y)]p(y)\,dy - \int_{\beta}^{\infty} \beta p(y)\,dy$$

and

$$\int_\alpha^\beta p(y)\,dy = 0.$$

Hence

$$E(\alpha, p) - E(\beta, p) = \int_0^\alpha [f(\beta - y) - f(\alpha - y)]p(y)\,dy + (\beta - \alpha)\int_\beta^\infty p(y)\,dy \geq 0$$

with equality if and only if $f(\beta - y) = f(\alpha - y)$ for $0 \leq y \leq \alpha$ and $\int_\beta^\infty p(y)\,dy = 0$. The condition on f implies that f is constant, and hence zero, over $[0, \beta]$, and so $g = -1$ in this range. Thus $p(y) = (1/V)\exp(-y/V)$ for $0 \leq y \leq \beta$, which contradicts $\int_\beta^\infty p(y)\,dy = 0$. Thus $R(p)$ is connected, and is hence of the form $[0, b)$.

Since (3.2) holds over $[0, b)$ for some $b > 0$, (i) is trivial. Differentiating (3.2) we obtain

$$Vp'(x) = g(0)p(x) + \int_0^x g'(x - y)p(y)\,dy$$

over $[0, b)$, and hence, so long as $p(y) \geq 0$ for $0 \leq y \leq x$, the conditions on g imply that $p'(x) \leq 0$, so $p(.)$ is non-increasing. So long as $p(y) \geq 0$ in $[0, x]$, since $g \geq -1$ we have

$$V_p(x) \geq 1 - \int_0^x p(y)\,dy = 1 - P(x),$$

so

$$P(x) \geq 1 - V_p(x). \qquad (*)$$

Since $p(.)$ is a density function, there is no $\varepsilon > 0$ with $p(x) \geq \varepsilon$ for all $x > 0$, so either $p(x) = 0$ for some finite x, or $p(x) \to 0$ as $x \to \infty$. If the former, write $b_1 = \inf\{x : p(x) = 0\}$, and see from (*) that $P(b_1) \geq 1$; hence $\exists b \leq b_1$ such that $P(b) = 1$. If the latter, either $\exists b$ such that $P(b) = 1$, or $P(x) \to 1$ as $x \to \infty$. Whatever alternatives hold, (ii) and (iii) follow.

So far we have shown that the conditions on the function p described in the theorem are necessary for p to be an ESS. To prove the sufficiency, note first that, if $x > b$, as in the argument above

$$E(b, p) - E(x, p) = \int_0^b [f(x - y) - f(b - y)]p(y)\,dy \geq 0$$

with equality only if f is zero over $[0, x)$; but then $p(y) = (1/V)\exp(-y/V)$ over $[0, b)$, so $b = \infty$ and $x > b$ cannot arise. Hence $E(b, p) > E(x, p)$ if $x > b$.

Thus, if q is any density function with $R(p)\cap R(q)$ non-empty, since $E(q,p)$ is a weighted average (with weights according to the density q) of quantities equal to $E(p,p)$ and quantities strictly less than this, $E(q,p) < E(p,p)$.

Thus to prove p is an ESS, we need only consider its performance against strategies q with $R(q)\subset R(p)$. For such a q, $E(q,p)=E(p,p)$, so we shall show that $E(p,q) > E(q,q)$ unless $q=p$(a.s.).

For any two density functions r and s,

$$E(r,s)=\int_0^\infty r(x)\left[\int_0^x [V-y-f(x-y)]s(y)\,\mathrm{d}y-\int_x^\infty x\,s(y)\,\mathrm{d}y\right]\mathrm{d}x$$

$$=\int_0^\infty r(x)\left[VS(x)-x+\int_0^x S(y)\,\mathrm{d}y-\int_0^x f(x-y)s(y)\,\mathrm{d}y\right]\mathrm{d}x \tag{A1}$$

Using (A1) for $E(p,q)$ and $E(q,q)$, we find, after re-arrangement

$$E(p,q)-E(q,q)=-\frac{V}{2}+\int_0^\infty H(x,Q)\,\mathrm{d}x \tag{A2}$$

where

$$H(x,Q)=Vp(x)Q(x)+[P(x)-Q(x)][1+g(0)Q(x)+\int_0^x Q(y)f''(x-y)\,\mathrm{d}y]$$

Hence

$$\frac{\partial H}{\partial Q}=Vp(x)-1+[P(x)-Q(x)]g(x)-\int_0^x g(x-y)q(y)\,\mathrm{d}y$$

For p satisfying equation (3.2), and $\dfrac{\partial H}{\partial Q}=0$, we find, on subtraction that

$$[P(x)-Q(x)]g(x)-\int_0^x g(x-y)[q(y)-p(y)]\,\mathrm{d}y=0$$

which can be re-arranged as

$$T\phi(x)=0 \tag{A3}$$

where $\phi(x)=P(x)-Q(x)$, and T is the linear operator defined by

$$T\phi(x)=[g(x)+g(0)]\phi(x)+\int_0^x g'(x-y)\phi(y)\,\mathrm{d}y.$$

From our assumptions about g, $g(x)+g(0)\le 0$ and $g'\le 0$, with equality only in the Scotch Auction case. Since $\phi(0) = 0$, the only solution to (A3) in the non-Scotch Auction case is $\phi \equiv 0$.

We have shown that, if p is as described, the only solution to $(\partial H/\partial Q) = 0$ is $Q = P$, so $Q = P$ is a turning point of $\int_0^\infty H(x, Q)\,\mathrm{d}x$. It is not a maximum, since then $E(p, q) < E(q, q)$ for all $q \neq p$, which is clearly contradicted by choice of q to correspond to the pure strategy "play 0". Hence $Q = P$ minimises $\int_0^\infty H(x, Q)\,\mathrm{d}x$, and, unless $Q = P$, $E(p, q) > E(q, q)$. This is what we set out to prove, so p is the unique ESS.