

Stable Equilibrium Strategies and Penalty Functions in a Game of Attrition

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(Received 30 March 1976, and in revised form 28 July 1976)

Maynard-Smith (1974) has presented a game of attrition model for animal conflict. He assumed that the penalty function, giving the cost in terms of fitness, of displaying for a given time period, is a linear function of the time of display. Under this assumption he shows that an evolutionary stable strategy (ESS) always exists: one such is a mixed strategy for which display times have a negative exponential distribution. Given the diversity of reproductive strategies and patterns of agonistic behavior in nature, it is reasonable to consider games with different types of cost functions. In this paper it is shown that if more general cost functions are allowed (not necessarily linear), then ESS's still exist and give a great variety of distributions of display time. Supporting data are presented to suggest that these distributions may be found in nature. It is suggested that the interrelations between an animal's fitness budget and the game's penalty function will determine the nature of an ESS for different kinds of games.

1. Introduction

Maynard-Smith & Price (1973) and Maynard-Smith (1974) formulated a game theory for agonistic contests and demonstrated an evolutionary stable strategy (ESS) in which players display conventionally unless an opponent escalates, in which case they retaliate. Contests lacking escalation are defined as a "war of attrition", and the winner is the contestant that displays the longest. In the war of attrition the ESS is not a pure strategy, but a mixed strategy having a negative exponential distribution of display times. Maynard-Smith (1974) pointed out that his model could not account for the behavioural complexity of conventional displays. However, Parker (1974) has introduced a rigorous theoretical framework that models

conventional displaying as a method of assessing an opponent's resource holding power (RHP).

A game for us will be a symmetric contest between two animals (symmetric means that the same set of strategies are available to each contestant, and the same payoffs apply). Each contestant can choose from a number of pure strategies, or he may employ a mixed strategy, which plays different pure strategies according to some probability function. A strategy for us will be a mixed strategy (of which the pure strategies are special cases corresponding to trivial probability functions). The outcome of the game is determined by the pair of strategies chosen by the contestants. We denote by $E_i(j)$ the expected payoff to a contestant using strategy j against strategy i . A strategy i is called an equilibrium strategy if $E_i(i) \geq E_i(j)$. An equilibrium strategy i is called (evolutionarily) stable (or an ESS for short) if whenever $E_i(i) = E_i(j)$ for some j then $E_j(i) > E_j(j)$. This definition is from Maynard-Smith (1974). It guarantees that in a population consisting entirely of individuals adopting strategy i , rare mutants employing strategy j would not increase in frequency. Hence the population is in this sense stable.

2. Existence of ESS's in a Game of Attrition

In Maynard-Smith's (1974) model for a "war of attrition" contestants display for a certain length of time, and the winner is the contestant who displays the longest. The pure strategies are the lengths of time x for which a contestant displays. Thus, in general, if the two contestants choose pure strategies x and y where $y > x$ then the game lasts for time x and the payoff to the winner is $E_x(y) = v - q(x)$ where v is the value of the win and $q(x)$ is the penalty incurred (lost time or energy will reduce fitness) in displaying for time x . The payoff to the loser is $E_y(x) = -q(x)$.

In Maynard-Smith's model it is tacitly assumed that the penalty function q is the linear function $q(x) = x$. In this case he shows that an ESS exists and has a negative exponential distribution: if $p(x)$ is the probability density of displaying for time x then

$$p(x) = \frac{1}{v} \exp(-x/v). \quad (1)$$

Let us consider more general penalty functions. It is reasonable to put a few conditions on $q(x)$: it should be positive, differentiable, non-decreasing ($q'(x) > 0$), and satisfy

$$q(0) = 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} q(x) = \infty.$$

The condition that q be non-decreasing simply says that longer display times

correspond to greater penalties. The condition

$$\lim_{x \rightarrow \infty} q(x) = \infty$$

says that arbitrarily large display times incur arbitrarily large penalties. What should $p(x)$ be for such a penalty function q ?

The simplest way to analyse this situation is to shift our point of view and imagine the animal choosing an acceptable penalty rather than an acceptable display time. In this case, an identical argument to that of Maynard-Smith shows that the probability density function should be

$$p(q) = \frac{1}{v} \exp(-q/v). \tag{2}$$

What then is p as a function of x ? Well, $p(q) dq$ is the probability of choosing a penalty between q and $q+dq$. Hence $p(x) dx$, the probability of choosing a time between x and $x+dx$ must be $p[q(x)]q'(x) dx$ since the dq which corresponds to dx is $q'(x) dx$. Hence

$$p(x) = \frac{1}{v} q'(x) \exp[-q(x)/v]. \tag{3}$$

This then gives the stable equilibrium strategy for a general penalty function. The mathematical details behind this formula are set out in a preprint available from the authors.

We can invert equation (3) to obtain

$$q(m) = -v \ln \left[1 - \int_0^m p(x) dx \right]. \tag{4}$$

Equations (3) and (4) give us a one-to-one correspondence between continuous probability density functions p and penalty functions q which are positive, differentiable and non-decreasing, with

$$q(0) = 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} q(x) = \infty.$$

[If

$$\int_0^m p(x) dx = 1$$

for some finite m , then $q(x)$ will actually be infinite for $x > m$.]

Finally, it is worth noting that $p(0) = q'(0)/v$: the initial value of p is determined by the initial slope of q , and the payoff for winning.

The graphs in Fig. 1 are designed to provide some insight into the qualitative relationship between the slope of q and the shape of p . One useful way to look at the differences between various penalty functions is to interpret

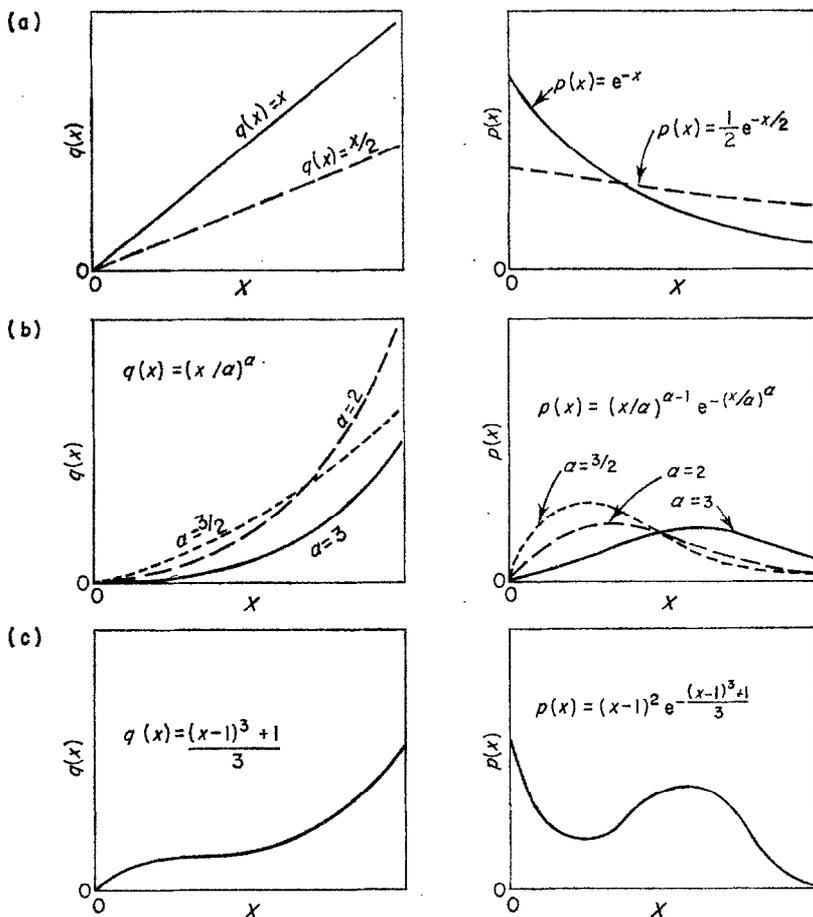


FIG. 1. Evolutionary stable strategies of persistence time $p(x)$ for various penalty functions $q(x)$, with v standardized to 1.

the derivative $q'(x)$ as the marginal penalty: that is $q'(x)$ is the extra penalty incurred by an animal who displays for an additional small unit of time, if he has already displayed for time x . For linear q , $q(x) = kx$, and the marginal penalty is constant. If q is concave up like Fig. 1(b), the marginal penalty increases with display time, perhaps corresponding to a game for which there is some significant advantage in interacting for a short period of time versus not interacting at all, thus shifting the mode of p away from zero. Figure 1(c) is an example where marginal penalty decreases at first, and then increases. The penalty is like Fig. 1(a) for short contests, but long

contests are much more taxing. The corresponding ESS has two maxima. In this population one expects contests either to be settled quickly, or to go on for a reasonable length of time, those of intermediate duration being rare. Are there such populations in nature?

Thus we conclude that p and q are interdependent and from a biological perspective it would seem that the penalty function determines the nature of the ESS. The penalty function in turn should be determined by the nature of the game being played.

3. Discussion

Let us then ask what kinds of games would have linear or non-linear penalty functions. The answer is not clear. However, in an intraspecific context the concept of varying penalty functions corresponds closely to Parker's (1974a,b) theory of resource holding power (RHP), fitness budgets and assessment strategies in animal conflicts. Parker defined a fitness budget as the difference in fitness change due to withdrawal by the resource holder and the fitness change due to attacker withdrawal, with and without escalation. This relation determines the number of fitness units available for expenditure in contests, which in connection with the penalty functions should determine patterns of persistence time and the nature of an ESS.

Little information is available on persistence time in wild populations. Parker (1974b) found a roughly negative exponential distribution of persistence times spent searching for females around droppings by males of the dung fly, *Scatophaga stercoraria*. Though this is strictly an "n-player" rather than a "two-player" game it appears to corroborate the predictions of Maynard-Smith (1973). An example of another type of persistence strategy is illustrated in Fig. 2. The patterns of contest persistence times are for four wild, individually marked, male brown-headed cowbirds (*Molothrus ater*) observed during the 1974 breeding season at Delta, Manitoba, Canada. Three of the males were dominant mated birds and displayed according to a normal type distribution of contest length; the fourth male, a young unmated subordinate, that did not hold a territory, showed a negative exponential type distribution of contest length. Interpretation of patterns of contest length is complicated because a given contest only indicates the loser's persistence time. In the case of the winner we only know that his persistence time, for that contest, was relatively greater than the loser's. In Fig. 2 note that the distribution of contest length on a male's territory is the distribution of the losing contestants' persistence times since the graphs are only for the contest wins of the indicated bird. Thus the off territory distributions for lost contests give the best indication of a bird's persistence

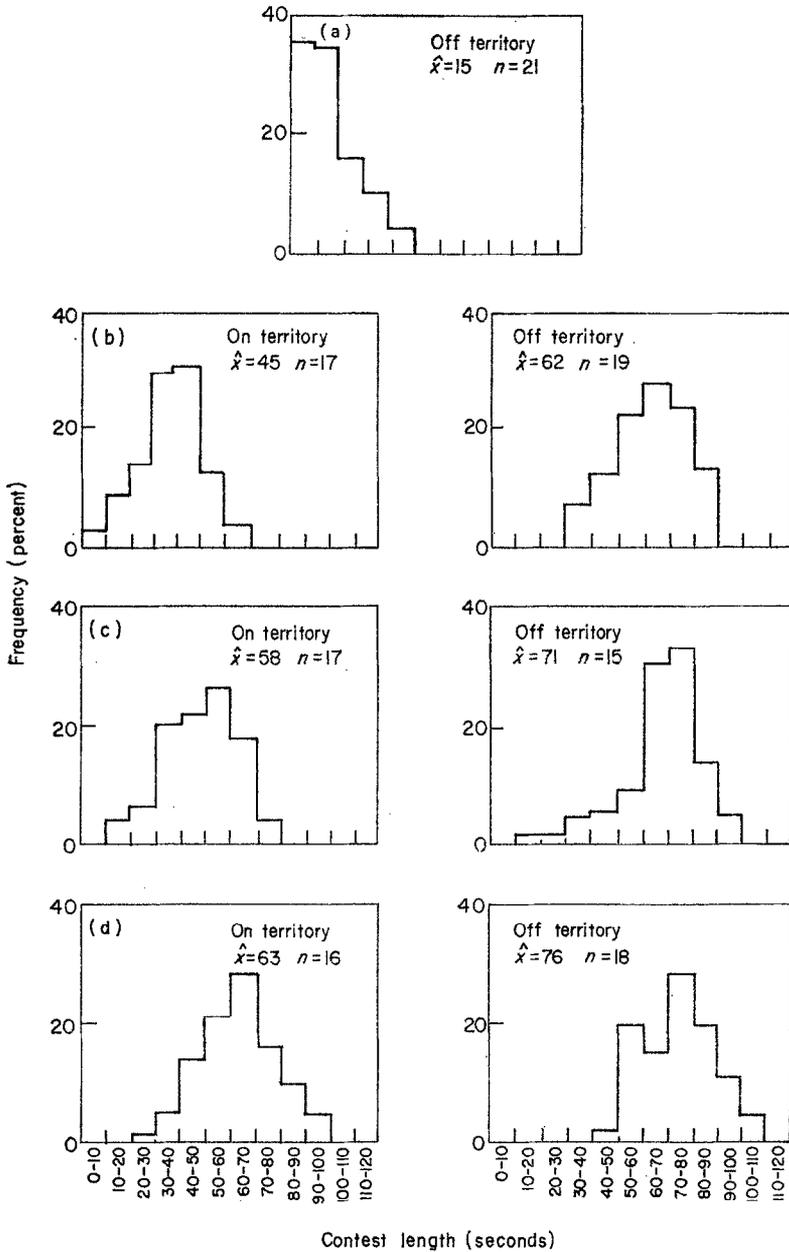


FIG. 2. Distributions of display persistence time of four male Brown-headed Cowbirds for two-bird displays both on and off territory: (a) unmated male LWBW, (b), (c) and (d) mated males LWW, TWRW and LWWTW respectively. On territory distributions are only for won contests, and off territory distributions are only for lost contests of the specified male.

time distribution. Mated males may not use the same strategy of persistence times while displaying on and off their territories.

The agonistic behavior of cowbirds during the breeding season corresponds closely to the game theory models of agonistic contests and assessment strategies that were advanced by Maynard-Smith (1974) and Parker (1974*a,b*). During an interaction, male cowbirds perform an alternating sequence of aggressive threat postures and appeasement displays. That is, opponents simultaneously display an aggressive posture in an alternating sequence. Contention during displays is usually for females, and males guard their mates. The displays are usually given with constant intensity, and a one-to-one correspondence between postures until near the end of the contest, when intensity varies. Before withdrawal the winner displays with increasing intensity and frequency of aggressive postures, and the loser almost exclusively adopts appeasive postures in response to aggressive threats. Males seem to be assessing each other throughout the interaction and escalation rarely occurs. The differences in patterns of persistence time between male *Molothrus* probably reflect different fitness budgets for mated and unmated individuals.

The basis of the different distributions of persistence time for *Scatophaga* and *Molothrus* is not clear. If these mixed strategies of persistence time are evolutionary stable then the above data indicate that *Scatophaga* and *Molothrus* may be playing games with different penalty functions. The different distributions of $p(x)$ for *Scatophaga* and *Molothrus* may also be influenced by effects of contest asymmetries and departures from a "two-person" game in the case of *Scatophaga*. Differences of such magnitude could be due entirely to such effects.

An understanding of the possible interrelations between various penalty functions, the corresponding ESS, and the kinds of games being played by different species may require a consideration of their respective reproductive strategies. For *Scatophaga* and *Molothrus* a strict games comparison is not valid because for *Scatophaga*, persistence time is not how long males display to an opponent, but rather how long he searches at dung for females (Parker, 1974*b*). In species playing more comparable games it may be possible to relate the nature of penalty functions to the average number of contests an average player participates in, and the number of breeding seasons in its lifetime. A payoff function can be thought of as being comprised of several parts; a component of metabolic cost of displaying for a given length of time, a component of injury risk should escalation occur, and a component of fitness that varies inversely with the average number of contests an average contestant plays (Maynard-Smith, 1974). In biological games an average player has an average total potential reproductive value \bar{V} [in the sense of

Fisher (1930)], and the fitness payoff component of a game can be thought of as the average proportion \bar{v} , of \bar{V} (where

$$\bar{V} = \sum_{i=1}^{\bar{n}} \bar{v}_i,$$

and \bar{n} is the average number of contests an average contestant plays in its life) which is at stake in a given contest. For an iteroparous species in which a player engages in many contests in its life, the relative reproductive value at stake in a given contest, \bar{v}/\bar{V} , would be less than for a semelparous species in which players display less often, and this may be correlated with lower and higher penalties and payoffs, respectively. For a semelparous species these reproductive characteristics might place a premium on quick assessment of an opponent's resource holding power (RHP) and a relatively high probability of early withdrawal if the opponent's RHP is greater.

Although the data presented here are few they do lend some empirical support for the general derivation of the model and strongly suggest that in this sort of modelling, we are dealing with a complicated system of penalty functions, fitness budgets, fitness payoffs and ESSs that in some mutual way define the type of game being played.

We gratefully acknowledge the support of the National Research Council of Canada and the Delta Waterfowl Research Station, Delta, Manitoba. We wish to thank two anonymous reviewers whose suggestions helped to improve this article. We would like to acknowledge the help of Mrs Samantha Poole in the preparation of this manuscript.

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