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A Sequential-Arrivals Model of Territory Acquisition

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Birds arrive sequentially at their breeding ground where the nest sites vary in value (measured by reproductive success). Each bird must either choose a vacant site or challenge an occupier for its site. In the latter case we assume the occupier to be the more likely winner. The loser of the contest incurs a cost and must go to a vacant site. The rational strategy for such a contest is found. There is a threshold phenomenon; early arrivals occupy vacant sites, late arrivals fight. This result is intuitively reasonable, but the sequence of sites chosen is complex. A recursive method for specifying the solution is described and applied explicitly to some illustrative cases.

1. Introduction

Game theory has proved to be a valuable tool for analysing and understanding conflicts in nature, providing a mechanism for understanding the behaviours observed in intra-species conflicts. Most models of such conflicts have considered only pair-wise conflicts. Here we deal with an *n*-player game, appropriate as a model for the arrival of a population of birds at a nesting area, or of males at a lek. The birds arrive sequentially and must either occupy a vacant site or challenge for one which is already occupied. The aim is to predict how birds should behave and in particular to determine when it is best to challenge and, if it is, then to determine which site should be contested. This is an initial attempt to model such situations which we believe gives some insights and raises some issues of interest.

It is not uncommon among birds for large numbers to nest close together. For example there may be thousands of kittiwakes nesting on a sea-cliff. At the beginning of a nesting season birds (or more properly breeding pairs) have to establish themselves on a nest site. These sites will not all have the same value (as measured by the expected number of offspring) because of access by predators, the degree of shelter, inherent suitability etc. The birds must decide whether to occupy a free site or contest for an already occupied one. From the species point of view, the best strategy would be for the birds to fill the sites in an orderly fashion without any disputes. However, selection operates at the individual (or gene copy) level and it is to be expected that behaviour which is beneficial for the individual will become prevalent in the population. Thus, the behaviour which evolves should be approximately the same as would occur if the birds could analyse the situation logically and find the strategy which maximises their pay-off on the assumption that all birds arriving later will also do the best for themselves. The resulting strategy will be referred to as the *rational* one.

If a bird challenges for a site then it is supposed that the loser of the contest suffers a cost (which may be an injury or depletion of energy) and has to depart, and to settle a vacant site. We have chosen to set the model up with certain restrictions on the parameters, assuming for example that the probability of an occupier defeating a challenge is constant, rather than

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dependent on the owner's history and the value of the site. Moreover, we shall, in the main, only consider the case where the challenger has a probability less than one-half of winning, a situation we refer to as "occupier-advantage". This case will be substantially different from the case where there is occupier-disadvantage (as we shall see below if there are only two sites then with owner-advantage the first bird to arrive must settle on the better site, but with owner-disadvantage the first bird may settle the poorer site). The loser of a contest is faced with the same situation (in terms of occupied nest sites) as the bird that has just challenged had faced prior to its challenge, but because of its recent defeat we suppose that it must go to a vacant site. Having reached a site it (or the pair) recover and can fight off any subsequent challenge as successfully as any other occupier. In the analysis later it will be assumed that the probability of a challenge being successful is always the same and is dependent upon neither the quality of the site nor the past experiences of the occupiers. However, in the model formulation any functional form for the probability could be incorporated. Likewise the model allows for variation in the cost of injury (perhaps because birds are prepared to risk more for the better sites) but this will not be used in the examples. The constancy of the probability of winning may be partly justified by the consideration that both challenger and occupier may contest more vigorously for a better site so that the question of who wins is not seriously affected by site value. The most important factor in deciding the outcome of a challenge is which birds are the occupiers. We are in the process of applying similar modelling considerations to the establishment of hierarchies and there it is certainly necessary to take the history of the contestants into account but here the effect is less important. Our aim is to analyse as simple a model as possible which retains the essential features of the situation. It will be seen that even for this (perhaps naive) model the solution is surprisingly complex and it is quite plausible that the rational strategy might not actually evolve in its complex form. We shall return to this point in a later paper where simpler strategies will be considered.

There has been much work on ESSs and two-player conflicts, starting with the classic paper by Maynard Smith & Price (1973). The idea has been extended and applied to a wide variety of situations (e.g. Bishop & Cannings, 1976; Haigh, 1975; Vickers & Cannings, 1988), and there are excellent treatments in Maynard Smith (1982); Hofbauer & Sigmond (1988) and Cressman (1992). However, little work has been done in the field of multi-player games in the evolutionary context. Haigh & Cannings (1989) consider the n-player war of attrition, Cannings & Whittaker (1994) consider a finite horizon war of attrition with sequential conflicts, and Sjerps & Haccou (1994) apply the War of Attrition to patch-leaving decision making. In general it is easy to extend the concepts used in two player games to n players although the mathematics involved in comparing and evaluating strategies is more difficult.

In Section 2 we shall describe the model in detail and in Section 3 demonstrate the existence of a unique rational strategy, show how this may be calculated (in Section 4), and how the actual plays required in a population of such players can be derived in a simple fashion. It will be shown that, when there is occupier-advantage, there always exists a k such that if a bird is among the first k birds to arrive then it occupies a free site and if it arrives later it challenges for an occupied site. This is a very natural threshold result but the complexity of the solution lies in the specification of which site should be taken or contested, and, if there is a contest, specifying the destination of the loser. We include in Section 5 some examples of the rational strategy for different sets of parameters of the model. These are simple cases with a small number of sites designed to show some interesting features of the solution. Section 6 derives expressions for the number of possible alternate strategies. In an attempt to consider cases where there are a large number of sites we examine (Section 7) the case where the number of sites tends to infinity and additionally (in Section 8) where the values of the sites decrease in a linear fashion. In particular we determine conditions under which the maximum number of challenges occuring upon any single site, takes various small values.

2. The Model

Suppose that a set of n birds (or breeding pairs) $B_1, \ldots, B_n$ arrive sequentially at a nesting area which has n nest sites $S_1, \ldots, S_n$. The value of the site S_i is $V_i(\geq 0)$ for the bird occupying that site at the end of the process, i.e. when all birds are settled on a site, where the sites have been ordered so that $V_i \geq V_j$ if $i < j$. (If there are more sites than birds we can ignore the worst sites and if there are more birds than sites we can create phantom sites with values zero).

When a bird arrives it may choose to go to any vacant site or to challenge the resident of any occupied site. A challenge is a contest of the following form:

the challenger wins with probability $p \leq 0.5$,

> otherwise the occupier wins. The winner becomes the occupier of the contested site, the loser pays a cost C, C positive, (receives a pay-off of $-C$) and must retreat to an unoccupied site of its choice.

The values p and C are taken to be constant for all sites for the sake of simplicity (although they might depend in reality upon many factors; the method of deriving the rational strategy below would not be affected). However, this model retains the most important feature *choose a free site or fight* and is amenable to analysis.

Note that we assume that the choice made by a loser does not depend on whether it had just arrived and challenged unsuccessfully or just been displaced. Indeed we suppose that decisions are only ever based on which sites are currently occupied, and not on any aspect of the specific history of any of the birds, e.g. how many times they have previously been displaced.

Only when a bird arrives may it make a challenge. Birds must remain at a site unless challenged and defeated by a later arrival. It is possible to extend the model to one where the loser of a challenge is permitted to challenge at another site, although we do not consider this case here. In the class of models considered here, where an arriving bird's strategy depends only on the set of sites occupied (and of course the site values and the probability of a challenge being successful) and not on the history of the process, the number of allowable challenges by each bird would have to be finite, or probabalistic. If this were not the case then the displaced bird would find itself in an identical position to the most recent arrival and there would follow an infinite sequence of challenges upon the same site (each of the birds receiving infinite cost) and so it would never be sensible to challenge. Since the loser of a contest incurs a cost, perhaps in the form of an injury or loss of energy, it is not unreasonable to assume, as here, that it would avoid another immediate contest.

The contest finishes after the final bird has arrived, made its choice of action and any subsequent contest is resolved. The pay-off to a bird is the value of the site it occupies at the end of the contest minus any penalties it has received for losing challenges.

3. The Rational and the Best Strategy

We seek to investigate the strategy birds might employ. A *strategy* must specify precisely the behaviour of an individual in every possible situation. When a bird arrives the situation faced is defined exactly (assuming costs and site values are known) by the specification of $\mathbf{X}$, the set of sites which are occupied (and not by the history of the process). A strategy is thus a specification of the behaviour to be used for each $\mathbf{X}$. In our model it is clear that there is no need to consider probablistic strategies, since each decision is made by a single bird, and all decisions are open and unambiguous.

We suppose that the reproductive success of a bird is the value of the site that the bird finally occupies minus any costs which are incurred when the bird loses contests. The reproductive success of a strategy is then taken to be the expected success of a bird which adopts that strategy, expectation being taken with respect both to all the possible outcomes of the fights (should they occur) and to the possible position of the bird in the order of arrival. Actions should be based on the *expected future pay-off*, and a bird should choose to behave so as to maximize its own expected future pay-off. There is, of course, a major biological problem here. How much information can a bird have about the behaviour of subsequent arrivals, and how much can it process? In fact we do not envision the problem in quite this way. Birds are programmed to adopt certain strategies depending on some set of cues, but strategies which are evolutionarily successful must mimic the one(s) which match that (those) which would be rationally deduced if all relevant information were available, assuming that the genetic system is capable of coding for this (and that the costs involved in such coding does not alter the pay-off structure too much). Thus, in deducing rational and best strategies, we are not implying that the birds can carry out an approximation to the calculations of this paper, but that evolution will programme them to behave in that manner. Of course the accuracy of the birds' perception, of the quality of sites and of the number of birds likely to arrive at that area, will affect the nature of the final strategy produced by natural selection. Here we assume that the birds know with complete accuracy the parameters of the problem, and the sites occupied when they arrive.

The issue of what strategies might be available to the birds and how a population of such birds might evolve is discussed further in Broom *et al.* (1996a, b).

We now derive what we shall call the *rational strategy*, a unique strategy which is a Nash equilibrium (i.e. any bird which unilaterally deviates in a population playing the "rational" strategy will receive a pay-off which is no larger than it would have received had it not deviated). One needs to be careful in interpreting what is meant by a Nash equilibrium in this context. We shall consider a population of birds with a large (effectively infinite) set of available breeding areas. On each breeding area there are n sites and so the conflict which occurs on each area constitutes an n-player game. A Nash equilibrium, Θ, then corresponds to the first condition required for an evolutionarily stable strategy, i.e. that no alternative strategy does better when playing against $(n-1)$ Θ-players than Θ does against $(n-1)$ Θ-players (Haigh & Cannings, 1989).

In order to derive this strategy, we introduce the notion of a rational individual (hinted at above). An individual is said to be rational, and to adopt a rational strategy if, given that sites $\mathbf{X}$ are occupied when it arrives, it chooses the behaviour (from the permitted repertoire) which maximises its expected future pay-off under the assumption that all subsequent arrivals will also act rationally. Note that such a strategy is well defined since the final bird has no subsequent arrivals to consider, and so can easily determine its rational behaviour, and once this choice is known for all possible $\mathbf{X}$ with one free site, the penultimate bird can determine its choice, and so on. Note also that the term rational is rather restrictive, since it presupposes subsequent birds act rationally, although not preceeding ones. We assert, however, that our definition of rational is appropriate in the evolutionary context precisely because this kind of rationality will be imposed by natural selection. We should note that we will formally derive the rational behaviour for every $\mathbf{X}$ even though we show that if all the birds adopt the rational strategy then there is a unique $\mathbf{X}$ appropriate at every stage, and a unique decision for each of these $\mathbf{X}$, except in certain non-generic cases where two possible strategies have the same expected future pay-off, as might happen if two sites had equal value.

Having established that there is a unique rational strategy we need to be careful how we interpret this is the context of some population dynamic. As pointed out above, when all the members of the population adopt the rational strategy there is a specific sequence of $\mathbf{X}$ and of decisions by arrivals. This sequence is the behaviour which would be observed for such a population and we term this the *best behaviour*. Note that the best behaviour is not a strategy. In fact there is a set of strategies which match the best behaviour, one of which must be the rational strategy. If all the birds in a population use the best behaviour then that population is indistinguishable from any other such population. There would be no necessary tendency for the rational strategy to increase in frequency, indeed it might be entirely absent. On the other hand, we might expect that a population would be subject to frequent, albeit small, perturbations and that there would therefore be some pressure to select for the rational strategy, and against other strategies with best behaviour.

3.1. THE MATHEMATICAL DESCRIPTION

Suppose $\mathbf{S}$ is the set of sites $S_1, S_2, \ldots, S_n$ ordered in decreasing intrinsic value.

We define a triplet of functions $\phi(\mathbf{X},u)$, $\Phi(\mathbf{X},(u,v))$ and $\Psi(\mathbf{X},v))$ where $\mathbf{X}\subset\mathbf{S}$ in each case is, as above, the set of occupied sites, $u\in\mathbf{X}$ and $v\in\mathbf{S}\backslash\mathbf{X}$.

Let $\phi(\mathbf{X},u) =$ expected future pay-off to the individual occupying site $u\in\mathbf{X}$ when all subsequent behaviour is the rational.

$\Phi(\mathbf{X},(u,v)) =$ expected future pay-off to an individual who on arrival finds $\mathbf{X}$, challenges on $u\in\mathbf{X}$, the loser going to $v\in\mathbf{S}\backslash\mathbf{X}$, when all subsequent behaviour is rational.

$\Psi(\mathbf{X},v) =$ expected future pay-off to an individual who on arrival finds $\mathbf{X}$ and occupies site $v\in\mathbf{S}\backslash\mathbf{X}$, when all subsequent behaviour is rational.

Note the requirement that in each case subsequent behaviour is required to be rational, though earlier behaviour need not have been so. This requirement applies not only to the behaviour of each subsequent arrival, but also to any bird they might displace, even if that bird had arrived before the requirement of rationality was imposed (i.e. had arrived to find a set of occupied sites which was a subset of $\mathbf{X}$.

We now derive recurrence relations between the above functions which will allow us to compute $\phi(\mathbf{X},u)$, $\Phi(\mathbf{X},(u,v))$ and $\Psi(\mathbf{X},v)$ for all $\mathbf{X}u\in\mathbf{X},v\in\mathbf{S}\backslash\mathbf{X}$, and so enable the rational strategy to be found. Suppose we have evaluated $\phi(\mathbf{Z},u)$ for all $u\in\mathbf{Z},\mathbf{Z}\subset\mathbf{S}$ and $|\mathbf{Z}|\geq k$ then for all $\mathbf{X}$ where $|\mathbf{X}| = k-1)$ we have

$$\Phi(\mathbf{X},(u,v)) = p\phi(\mathbf{X}\cup\{v\},u) + (1-p)[\phi](\mathbf{X}\cup\{v\},v) - C]$$

where p is the probability that a challenger wins a contest, $u\in\mathbf{X},v\in\mathbf{S}\backslash\mathbf{X}$. We confine our analysis to the case where p is a constant. This equation follows by considering the fate of an individual who arrives to find $\mathbf{X}$ and challenges on u; if it wins, which occurs with probability p, then it occupies u, if it loses it occupies v, thus giving r.h.s. of the equation. Note that p could be made a function of X, u and v, both here and below.

Now suppose that $r_X\in\mathbf{X},s_X\in\mathbf{S}\backslash\mathbf{X}$ and

$$\Phi(\mathbf{X},(r_X,s_X)) \geq \mathit{\Phi}(\mathbf{X},(u,v))$$

for all $u\in\mathbf{X}$, $v\in\mathbf{S}\backslash\mathbf{X}$ and equality only if $(u,v) = (r_X,s_X)$, i.e. if the bird is to challenge then it maximises its pay-off by challenging on r_X, and the loser goes to s_X. Note that if a challenge takes place then it must occur on the site which has maximal expected pay-off after the challenge. We note that exceptionally either, or both, of r_X and s_X may not be unique, in which case we would choose some arbitrary rule to resolve the ambiguity. For convenience we suppose that if a bird is indifferent, on the basis of future expected pay-off, between a challenge or settling a vacant site then it does the latter. If at any stage it is indifferent between challenging (settling) on two distinct sites then it challenges (settles) on the one with higher intrinsic value.

Further

$$\Psi(\mathbf{X},v) = \phi(\mathbf{X}\cup\{v\},v)$$

where $v\in\mathbf{S}\backslash\mathbf{X}$ since the l.h.s. corresponds to a bird going to an unoccupied site. Suppose $t_X\in\mathbf{X}$ is such that

$$\Psi(\mathbf{X},t_X) \geq \Psi(\mathbf{X},v)$$

for all $v\in\mathbf{S}\backslash\mathbf{X}$ with equality if, and only if, $v = t_X$, i.e. if the bird is to choose an unoccupied site then it should choose t_X (again ambiguities can be resolved by an arbitrary rule).

Now consider the effect of the arrival of the $|\mathbf{X}| + 1$'th bird on the pay-off of a bird occupying $u\in\mathbf{X}$.

$$\phi(\mathbf{X},u) = \begin{cases} = p[\phi(\mathbf{X}\cup\{s_X\},\mathrm{s_X}) - C] + (1-p)\phi(\mathbf{X}\cup\{s_X\},u) \\ \text{if } u = r_X \text{ and } \Phi(\mathbf{X},(r_X,s_X)) > \Psi(\mathbf{X},t_X); \\ = \phi(\mathbf{X}\cup\{s_X\},u) \\ \text{if } u \neq r_X \text{ and } \Phi(\mathbf{X},\ (r_X,s_X)) > \Psi(\mathbf{X},t_X); \\ = \phi(\mathbf{X}\cup\{t_X\},u) \\ \text{if } \Phi\ (\mathbf{X},(r_X,s_X)) \leq \Psi(\mathbf{X},t_X): \end{cases}$$

Now we assumed $\phi(\mathbf{Z},u)$ was defined for all $u\in\mathbf{Z}$, and $|\mathbf{Z}| \geq k$, so that $\Phi(\mathbf{X},(u,v))$ and $\Psi(\mathbf{X},v)$ are defined for $|\mathbf{X}| = k-1$, and thus $\phi(\mathbf{X},u)$ is also defined for $|\mathbf{X}| = k-1$. Defining $\phi(\mathbf{S},u) = \mathbf{V}_u$, that is the expected future pay-off of u when all sites are occupied is just the value of the site u, we have that ϕ, Φ, Ψ are specified for all values of their arguments.

Note that for each $\mathbf{X}$ the rational behaviour of a new arrival is defined, and so the rational strategy is fully specified.

4. Finding the Rational Strategy

In the previous section we demonstrated how one could find the rational strategy in any particular case. Our aim in subsequent sections is to demonstrate that one does not need to calculate every part of the rational strategy, but can find the best behaviour more economically. First we give an example of the calculation of the rational strategy.

Example 1

Suppose that $n = 4$, $V_1 = 20$, $V_2 = 19$, $V_3 = 18$ and $V_4 = 0$, $p = 0.4$ and $C = 0$. We have $\phi(\{1,2,3,4\},i) = V_i$ and first consider the rational behaviour of a bird arriving to find sites 1, 2 and 3 occupied. Then,

$$\Psi(\{1,2,3\},4) = \phi(\{1,2,3,4\},4) = 0$$

i.e. reward is zero if the bird settles on the unoccupied site S_4. We examine the three values $\Phi(\{1,2,3\},(i,4))$ for $i = 1,2,3$. For example

$$\begin{aligned} &\Phi(\{1,2,3\},(1,4)) \\ &\quad = p\phi(\{1,2,3,4\},1) + (1-p)(\phi(\{1,2,3,4\},4) - \mathrm{C}) \\ &\quad = 8 \end{aligned}$$

while $\Phi(\{1,2,3\},(2,4)) = 7.6$ and $\Phi(\{1,2,3\},(3,4)) = 7.2$. Thus, for $\mathbf{X} = \{1,2,3\}, s_X = 4$ necessarily, $t_X = 4$ necessarily while $r_X = 1$. Since,

$$\Phi(\{1,2,3\},(1,4)) > \Psi(\{1,2,3\},4)$$

the bird challenges on S_1 and the loser goes to the only vacant site S_4. We can now calculate the three values $\phi(\{1,2,3\},i)$ for $i = 1,2,3$. We have

$$\phi(\{1,2,3\},i) = \phi(\{1,2,3,4\},i) \text{ for } i = 2,3$$

since S_2 and S_3 are not affected by the behaviour of the new arrival. Also

$$\begin{aligned} &\phi(\{1,2,3\},1) \\ &\quad = (1-p)\phi(\{1,2,3,4\},1) + p(\phi(\{1,2,3,4\},4) - C) \\ &\quad = 12. \end{aligned}$$

Note that if the arrival is to challenge i.e. on r_X and the loser go to s_X then since they must share the sites and incur a cost C we have that

$$\phi(\mathbf{X},r_X) = \phi(\mathbf{X}\cup\{s_X\},r_X) + \phi(\mathbf{X}\cup\{s_X\},s_X) - \Phi(\mathbf{X},(r_X,s_X)) - C$$

and all the terms on the right are known.

For completeness we give in Table 1 $\phi(\mathbf{X},u)$ for all values, and the rational behaviour for each $\mathbf{X}$.

Having evaluated all of the necessary functions, one can now specify how a rational bird behaves in any situation which will arise in a population of such birds, i.e. the best behaviour. We have $\phi(\{u\},u)$ evalulated for all u and so B_1 can pick u to maximize $\phi(\{u\},u)$, and then if the value of u chosen is u_1 say then B_2 picks u to maximize $\phi(\{u_1,u\},u)$, and so on. In this example choosing $u = 3$ maximizes $\phi(\{u\},u)$, and so the first bird settles on S_3. The next bird to arrive has $\mathbf{X} = \{3\}$ and so challenges on S_3 the loser going to S_2. The third bird has $\mathbf{X} = \{2,3\}$ and so

TABLE 1
The rational behaviour for the case $C = 0$, $p = 0.4$, $V_1 = 20$, $V_2 = 19$, $V_3 = 18$, $V_0 = 0$

X	u	ϕ	Behaviour	**X**	u	ϕ	Behaviour
{1, 2, 3, 4}	1	20.0		{1, 2}	1	12.0	CH S_2
{1, 2, 3, 4}	2	19.0		{1, 2}	2	18.6	Oc S_3
{1, 2, 3, 4}	3	18.0		{1, 3}	1	12.0	
{1, 2, 3, 4}	4	0.0		{1, 3}	3	18.0	Oc S_2
{1, 2, 3}	1	12.0		{1, 4}	1	19.12	Ch S_1
{1, 2, 3}	2	19.0	Ch S_1	{1, 4}	4	0.0	Lo S_2
{1, 2, 3}	3	18.0	Lo S_4	{2, 3}	2	16.2	Ch S_2
{1, 2, 4}	1	19.2		{2, 3}	3	18.0	Lo S_1
{1, 2, 4}	2	19.0	Ch S_1	{2, 4}	2	19.0	Oc S_1
{1, 2, 4}	4	0.0	Lo S_3	{2, 4}	4	0.0	
{1, 3, 4}	1	19.6		{3, 4}	3	18.0	Oc S_1
{1, 2, 4}	3	18.0	Ch S_1	{3, 4}	4	0.0	
{1, 3, 4}	4	0.0	Lo S_2	{1}	1	12.0	Oc S_2
{2, 3, 4}	2	19.0		{2}	2	16.2	Oc S_3
{2, 3, 4}	3	18.0	Oc S_1	{3}	3	17.28	Ch S_3
{2, 3, 4}	4	0.0					Lo S_2
				{4}	4	0.0	Oc S_1

Key: Ch = challenge; Oc = Occupy; Lo = Loser.

challenges on S_3 the loser going to S_2. The third bird has $\mathbf{X} = \{2,3\}$ so challenges on S_2 with the loser going to S_1. The final bird has $\mathbf{X} = \{1,2,3\}$ so challenges on S_1 with the loser necessarily going to S_4.

More generally we find the best behaviour as follows. Define $\mathbf{Z}_i \subset \mathbf{S}$, for $= 1, \ldots, n$ recursively; $\mathbf{Z}_0 = \phi$ (ϕ is the empty set) and $\mathbf{Z}_k = \mathbf{Z}_{k-1} \cup \{u\}$ where u is such that $\phi(\mathbf{Z}_{k-1} \cup \{v\}, v)$ is maximized over $v \in \mathbf{S} \backslash \mathbf{Z}_{k-1}$ by $v = u$.

5. Finding the Best Behaviour

The previous section demonstrated how one can find the rational strategy. However, when $p \leq 0.5$, it is possible to shortcut some of the work if one only wishes to find the best behaviour. In particular Theorem 1 demonstrates that, when $p \leq 0.5$, given the complete set of $\phi(\mathbf{X},u)$'s for given $\mathbf{Z}_k$, the set of sites occupied after k birds have arrived if birds are adopting best behaviour, one can infer which was the last site to be occupied. Indeed it is the site with the least expected future pay-off. Thus, if $\mathbf{Z}_{k-1}$ is defined, one can then calculate the $\phi(\mathbf{Z}_{k-1},u)$'s for this new set, infer $\mathbf{Z}_{k-2}$, and so on. This enables one to find the best behaviour while only evaluating the pay-offs for those sets of sites which are actually occupied at each stage, rather than, as in the example above, for all possible sets of sites.

In the case where $p > 0.5$, the above scheme fails. For example, if $p = 0.6$, $V_1 = 1$, $V_2 = 0$, and $C = 1$ then B_1 settles on S_2, and B_2 settles on S_1. Thus, after both have settled the most recent arrival is on the site with the higher expected future pay-off (just V_1 here).

We denote $\phi(\mathbf{Z}_k, S_i)$ by V_i^k for all $S_i \in \mathbf{Z}_k$, and by $V(^k_{(j)})$ the jth largest of these, and the corresponding site by $S^k_{(j)}$. The notation $S^k_{(j)}$ will in fact be used both to denote a site and the index of that site.

Our proof, which is inductive, proceeds in two parts. We prove in Lemma 1, that if the theorem were not true, so that the last site occupied were not the one with the lowest expected future pay-off, then that site would have been the last occupied one step earlier. We can then, in the main proof, use this to demonstrate a specific contradiction to the hypothesis of the theorem. If the last site occupied at some time is not that hypothesised in the theorem then that site was occupied one step earlier, and we can demonstrate that a superior behaviour would be to reverse the order of occupation.

5.1. LEMMA 1

For $p \leq 0.5$, if the most recently occupied site after j arrivals is not $S^j_{(j)}$ then $S^{j-1}_{(j-1)} = S^j_{(j)}$.

5.1.1. *Proof*

When a new bird arrives, say the jth, and challenges, the expected future pay-offs of those birds not challenged remains unaltered. Thus, $V_i^{j-1} = V_i^j$ for unchallenged sites, while the bird challenged, the one on $S^j_{(1)}$ (see Section 3.1), has

$$V^{j-1}_{S^j_{(1)}} = (1-p)V^j_{(1)} + p(V^j_m - C)$$

(note the use of $S^k_{(j)}$ as an index in the equation above) where S_m is the site to be occupied by the loser. Since a challenge is only made when $V^j_m < pV^j_{(1)} + (1-p)(V^j_m - C)$ we have that

$$V^j_m < pV^j_{(1)} + (1-p)(V^j_m - C) \leq (1-p)V^j_{(1)} + p(V^j_m - C) = V^{j-1}_{S^j_{(1)}}$$

(recall $p < 0.5$). Thus, a site which is challenged for by the jth bird has a higher expected pay-off before the challenge than the new site to be occupied i.e. $V^{j-1}_{S^j_{(1)}} > V^j_m$. When the jth bird challenges and the new site to be occupied is not the one with the smallest expected future pay-off in $\mathbf{Z}_j$, then $V^{j-1}_{S^j_{(1)}} > V^j_m > V^j_{(j)} = V^{j-1}_{S^j_{(j)}}$. Since for $i \notin \{1,m\} V^{j-1}_{S^j_i} = V^j_{S^j_i} \geq V^j_{S^j_{(j)}}$ and $V^{j-1}_{S^j_{(1)}} > V^{j-1}_{S^j_{(j)}}$, the minimal value for V^{j-1}_u occurs for $u = S^j_{(j)}$. On the other hand if there is no challenge by the jth bird we have $V^{j-1}_i = V^j_i$ for all $i \in \mathbf{Z}_{j-1}$ so a similar result holds.

5.2. THEOREM 1

When the population follows the rational strategy and $p \leq 0.5$, the most recently occupied site after k

arrivals, i.e. site $\mathbf{Z}_k \backslash \mathbf{Z}_{k-1}$, has the lowest expected future pay-offs amongst the sites of $\mathbf{Z}_k$.

5.2.1. *Proof*

The proof is by induction. Suppose all birds are playing the rational strategy. The hypothesis of the theorem is clearly true when $k = 1$, there being only one occupied site. Suppose it is true for all $k \leq l$.

Suppose that $l + 1$ birds have settled and the set of sites occupied is $\mathbf{Z}_{l+1}$, and thus the expected future pay-offs are $V_{(i)}^{l+1}$ for $i = 1, \ldots, l + 1$. Suppose that the most recently settled site is $S_{(r)}^{l+1}$. If $r = l + 1$ then there is no more to prove. Suppose that $r \neq l + 1$ then $\mathbf{Z}_l = \mathbf{Z}_{l+1} \backslash \{r\}$ and, by assumption, $\mathbf{Z}_l \backslash \mathbf{Z}_{l-1}$, i.e. the site settled last of the l, is $S_{(l)}^{l}$. We proved in Lemma 1 that $S_{(l)}^{l} = S_{(l+1)}^{l+1}$.

Thus we have that, in the case where $r \neq l + 1$, $S_{(l)}^{l} = S_{(l+1)}^{l+1}$ and under the assumption that the statement of the theorem holds for $k \leq l$ we can infer that $S_{(l+1)}^{l+1} = \mathbf{Z}_l / \mathbf{Z}_{l-1}$. We now compare the given $\mathbf{Z}_l$ and $\mathbf{Z}_{l+1}$ and the corresponding pay-offs with those which would accrue if the order of the last two new sites was reversed, i.e. if $\mathbf{Z}_{l-1}$ was unchanged, $S_{(r)}^{l+1}$ was chosen by the lth bird and $S_{(l+1)}^{l+1}$ by the $l + 1$th. In this case if the $l + 1$th bird goes to $S_{(l+1)}^{l+1}$ without a challenge, or there is a challenge to $S_{(1)}^{l+1}$ but $r \neq 1$, then the expected future pay-off on $S_{(r)}^{l+1}$ when the lth bird arrives will be $V_{(r)}^{l+1}$ which exceeds $V_{S_{(l+1)}^{l+1}}^{l} = V_{(l+1)}^{l+1}$. Thus the lth bird to arrive should choose to occupy $S_{(r)}^{l+1}$ rather than $S_{(l+1)}^{l+1}$, with or without a challenge. On the otherhand if $r = 1$ then the $l + 1$th bird might challenge on r but, as established above, a site on which a challenge takes place has a higher expected pay-off before the challenge than the site settled subsequently. Thus, we have established that the lth bird will do better by settling $S_{(r)}^{l+1}$ than $S_{(l+1)}^{l+1}$. Thus, the assumption that $r \neq l + 1$ is not possible given that the rational strategy has the specified $\mathbf{Z}_j$'s, and so under the rational strategy the newly occupied site after $l + 1$ birds have arrived is precisely $S_{(l+1)}^{l+1}$. The theorem follows by induction on l.

We can now easily compute the best behaviour for any given set of V_i's, $p \leq 0.5$ and C. First we have that when B_n arrives the vacant site must be S_n, so $\mathbf{Z}_{n-1} = \{1, 2, \ldots, n - 1\}$ and we can evaluate $\phi(\mathbf{Z}_{n-1}, u)$, infer which is the newly occupied site, and so on.

5.3. EXAMPLE 1 (AGAIN)

For the example given earlier we begin with $\mathbf{Z}_4 = \{1, 2, 3, 4\}$ for which the expected future pay-offs are the original V_i^4's 20, 19, 18 and 0. Thus, the last site occupied is S_4 so $\mathbf{Z}_3 = \{1, 2, 3\}$. As calculated earlier the fourth bird will challenge on S_1 so $V_1^3 = 12$, the V_i^3's are 12, 19, and 18 for sites S_1, S_2 and S_3 respectively, so S_1 is the newly occupied one. Thus, we infer that the third bird will challenge on S_2, and a similar process allows us to infer that the second bird would challenge on S_3, so the first bird settled on S_3.

5.4. A THRESHOLD RESULT

Theorem 1 allows a fairly straightforward calculation to determine the best strategy. It does still require, however, that one decides at every stage whether a challenge should occur or not. The following theorem allows a simplification of this process since it is demonstrated that if at some stage, in the backward recursion, it is found that a bird should settle an unoccupied site rather than challenge, then all earlier birds should settle rather than challenge. Thus, at this stage no further calculations are required, and we infer that if we know B_j settles rather than challenges and we have $V_{(i)}^{j}$ then B_i settles $S_{(i)}^{i}$ for all $i \leq j$.

5.5. THEOREM 2

For the best behaviour when $p \leq 0.5$, there exists a threshold k s.t. the first k birds do not challenge and afterwards all birds challenge.

5.5.1. *Proof*

It follows from Theorem 1 that if $V_{(1)}^{i} - V_{(i)}^{i} < C(1 - p)/p$, then B_i does not challenge and so it goes to the best (future) free site $S_{(i)}^{i}$. Otherwise it challenges $S_{(1)}^{i}$ and the loser of the challenge goes to $S_{(i)}^{i}$.

The bird B_i challenges if $V_{(1)}^{i} - V_{(i)}^{i} > C(1 - p)/p$. It is clear that

(i) $V_{(1)}^{i}$ is a non-decreasing function of i, since as each bird arrives the only change in the situation is that there will be one less challenge in the future at one of the sites, so that the future payoff cannot decrease,

and

(ii) $V_{(i)}^{i}$ is a non-increasing function of i. We proved in Lemma 1 that a site which is challenged for by the jth bird has a higher pay-off before the challenge than the new site, S_m to be occupied, i.e. $V_{S_{(1)}^{j}}^{j-1} > V_{Sm}^{j}$, thus $V_{S_{(1)}^{j}}^{j-1} > V_{(j)}^{j}$. For any other occupied site $V_{S_{(i)}^{j}}^{j-1} = V_{S_{(i)}^{j}}^{j} \geq V_{(j)}^{j}$. We have therefore that $V_{(j)}^{j} \leq V_{j-1}^{j-1}$.

It follows that $V_{(1)}^{i} - V_{(i)}^{i}$ is non-decreasing with i, so that once it becomes larger than $C(1 - p)/p$ it remains larger than it, i.e. the first such term is when $i = k + 1$ and the theorem is proved.

Note that when $C = 0$ every bird after the first should challenge. Our example above is of this type.

Define $E[B_i]$ as the expected pay-off to the ith bird to arrive. Then, if B_i does not challenge

$$E[B_i] = V^i_{(i)}$$

and if B_i does challenge

$$E[B_i] = pV^i_{(1)} + (1 - p)(V^i_{(i)} - C)$$

5.6. COROLLARY

(a) Up to the threshold the pay-offs to the B_i are non-increasing.

(b) If a challenged bird is involved in its first contest, then its expected pay-off is greater than or equal to the challenger's.

(c) (a) and (b) together imply that $E[B_1] \geq E[B_2]$.

5.6.1. *Proof*

(a) follows directly from (ii) in Theorem 2.

(b) If a bird has not been involved in a contest then its expected future pay-off is the same as the expected future pay-off of its site before B_i challenges (this has remained constant since the bird occupied that site) and this value is

$$V^i_{(1)}(1 - p) + p(V^i_{(i)} - C) \geq E[B_i], \text{ since } p \leq 1/2$$

For B_i to challenge we need $V^i_{(1)} - V^i_{(i)} > C(1 - p)/p$. The challenge will be on $S^i_{(1)}$, the loser going to $S^i_{(i)}$ (this is also the site B_i will go to if there is no challenge). See the explanatory paragraph after the proof of theorem 1.

To find the (future) values of all the sites after the arrival of B_i, we must know the behaviour of $B_{i+1}, \ldots, B_n$. Thus we must start with the last bird, in this case B_4, and work backwards.

If B_i challenges on site S_j and the loser goes to site S_l we write $B_iChS_j(S_l)$ and if it simply occupies S_l we write $B_i \to S_l$.

5.7. EXAMPLES

Example 1 (*again*)

$n = 4$, $V_1 = 20$, $V_2 = 19$, $V_3 = 18$, $V_4 = 0$, $C = 0$, $p = 0.4$.

Since the cost $C = 0$, as demonstrated above, B_i will challenge unless the V^i_j are constant, which does not occur here. Clearly B_4 will challenge on S_1, i.e.

$B_4ChS_1(S_4)$ and $E[B_4] = 0.4 \times 20 = 8$
$V^3_1 = 0.6 \times 20 = 12, \quad V^3_2 = 19, \; V^3_3 = 18$
$B_3ChS_2(S_1)$, $E[B_3] = 0.4 \times 19 + 0.6 \times 12 = 14.8$
$V^2_2 = 0.6 \times 19 + 0.4 \times 12 = 16.2, \; V^2_3 = 18$
$B_2ChS_3(S_2)$, $E[B_2] = 0.4 \times 18 + 0.6 \times 16.2 = 16.92$
$V^1_3 = 0.6 \times 18 + 0.4 \times 16.2 = 17.28 \Rightarrow E[B_1] = 17.28$

These results are summarised in the following table:

Bird	B_1	B_2	B_3	B_4
Site	S_3	$ChS_3(S_2)$	$ChS_2(S_1)$	$ChS_1(S_4)$
Pay-off	17.28	16.92	14.8	8

The first three sites have similar values, the fourth is much worse, so the birds are playing the policy which minimises their chances of ending up with the bottom site, the last bird has a very low expected pay-off which is maximised by challenging the top site, consequently the top site is the second worst to be in occupation of before the last bird arrives. Filling up from the lowest of the "good" sites is the best thing to do in such a situation.

Example 2

$n = 5$, $V_1 = 5$, $V_2 = 4$, $V_3 = 3$, $V_4 = 2$, $V_5 = 1$, $C = 0.4$, $p = 0.4$

$V_1 - V_5 = 4 > 0.4 \times 0.6/0.4 = 0.6 \Rightarrow B_5ChS_1$ (B_5 challenges on S_1), $E[B_5] = 0.4 \times 5 + 0.6 \times (1 - 0.4) = 2.36$.

$V^4_1 = 0.6 \times 5 + 0.4 \times (1 - 0.4) = 3.24$. $V^4_2 = 4$, $V^4_3 = 3$, $V^4_4 = 2 \Rightarrow S^4_{(1)} = S_2$, $S^4_{(4)} = S_4$.

$V^4_2 - V^4_4 = 4 - 2 = 2 > 0.6 \Rightarrow B_4ChS_2$, $E[B_4] = 0.4 \times 4 + 0.6 \times (1 - 0.4) = 2.56$

$V^3_1 = 3.24$, $V^3_2 = 0.6 \times 4 + 0.4 \times (2 - 0.4) = 3.04$, $V^3_3 = 3 \Rightarrow S^3_{(1)} = S_1$, $S^3_{(3)} = S_3$.

$V^3_1 - V^3_3 = 3.24 - 3 \leq 0.6$ so there are no more challenges and $B_1 \to S_1$ $E[B_1] = 3.24$, $B_2 \to S_2$ $E[B_2] = 3.04$, $B_3 \to S_3$ $E[B_3] = 3$.

These results are summarised in the following table:

Bird	B_1	B_2	B_3	B_4	B_5
Site	S_1	S_2	S_3	$ChS_2(S_4)$	$ChS_1(S_5)$
Pay-off	3.24	3.04	3	2.56	2.36

The top two lines of the above table, listing each bird and which site it occupies/challenges for (as well as which site the loser of a challenge occupies) will be referred to as an *arrival profile*.

Example 2 shows the type of profile associated with a set of V_i's which decrease steadily and p not too large, C not too small, a fairly frequent situation (perhaps) in the field. The first birds tend to do better than the last, they fill up the first few sites, the last birds challenge the top sites.

Example 3

$n = 6$, $V_1 = 60$, $V_2 = 4$, $V_3 = 3$, $V_4 = 2$, $V_5 = 1$, $V_6 = 0$, $C = 0$, $p = 0.4$

As above all birds will challenge because $C = 0$.

$B_6ChS_1(\to S_6)$, $E[B_6] = 0.4 \times 60 = 24$. $V^5_1 = 0.6 \times 60 = 36$

$B_5ChS_1(\to S_5)$, $E[B_5] = 0.4 \times 36 + 0.6 \times 1 = 15$. $V^4_1 = 0.6 \times 36 + 0.4 \times 1 = 22$

$B_4ChS_1(\to S_4)$, $E[B_4] = 0.4 \times 22 + 0.6 \times 2 = 10$. $V^3_1 = 0.6 \times 22 + 0.4 \times 2 = 14$

$B_3ChS_1(\to S_3)$, $E[B_3] = 0.4 \times 14 + 0.6 \times 3 = 7.4$. $V^2_1 = 0.6 \times 14 + 0.4 \times 3 = 9.6$

$B_2ChS_1(\to S_2)$, $E[B_2] = 0.4 \times 9.6 + 0.6 \times 4 = 6.24$. $V^1_1 = 0.6 \times 9.6 + 0.4 \times 4 = 7.36$

$B_1 \to S_1$, $E[B_1] = 7.36$

The above results are summarised in the following table:

Bird	B_1	B_2	B_3	B_4	B_5	B_5
Site	S_1	$ChS_1(S_2)$	$ChS_1(S_3)$	$ChS_1(S_4)$	$ChS_1(S_5)$	$ChS_1(S_6)$
Pay-off	7.36	6.24	7.4	10	15	24

Here it is all important to occupy S_1 and it does not matter that much which other site a bird occupies if it does not occupy S_1. The last birds do better because there is only one good site, the earlier a bird arrives the less chance it has of keeping S_1 if it has it (note that B_1 does better than B_2 as it must always do from 3.4).

Example 4

$n = 10$, $V_i = 11 - i$; $i = 1, \ldots, 10$; $p = 0.4$, $C = 0.11$

The working is longer than for the other examples and is omitted. The results are given in the following table:

Bird	B_1	B_2	B_3	B_4	B_5	B_6	B_7	B_8	B_9	B_{10}
Site	S_3	S_2	S_5	$ChS_5(S_1)$	$ChS_2(S_4)$	$ChS_1(S_6)$	$ChS_4(S_7)$	$ChS_3(S_8)$	$ChS_2(S_9)$	$ChS_1(S_{10})$
Pay-off	5.956	5.952	5.864	5.796	5.850	5.476	5.134	4.934	4.734	4.534

This example shows that even for linearly spaced rewards the pay-offs do not necessarily decrease with arrival position (B_5 receives a larger pay-off than B_4).

6. The Number of Different Arrival Profiles

Suppose that C, p and the V_i's are variables (s.t. the V_i's are ordered), then what is the number of possible arrival profiles for (a) any strategy and (b) the best behaviour?

We find that the ratio of the number of possible best behaviour profiles to the total number of profiles is of order $1/n!$, so that for a population if we know the ordering of the sites in terms of their intrinsic values (though not the actual values) then the set of different profiles that could occur if the birds were playing the best behaviour strategy is relatively small compared to the total number of profiles.

(a) There are n possible sites for the first bird to choose, the second then has $n - 1$ free sites to choose from or it can challenge on the occupied site and then go to any of the free sites. In general after i birds have arrived the next can go to any of $n - i$ free sites or can challenge on any of the i occupied sites and then go to any of the free sites. This gives $(n - i) + i(n - i) = (n - i)(i + 1)$ different possibilities for the $i + 1$th bird. The total number of profiles is thus

$$\prod_{i=0}^{i=n-1} \{(n - i)(i + 1)\} = (n!)^2.$$

On the other hand if we take into account the threshold result, so that the first i sites are settled without challenge, and the last $n - i$ involve challenges the number of ways is

$$n! + n!(n - 1)! \sum_{i=1}^{i=n-1} 1/\{i!\}.$$

(b) Suppose we have k birds, C and p fixed, and corresponding expected future values $V^k_{(i)}$. Now we know that the kth bird either settled on $S^k_{(k)}$ so $V^k_{(i)} = V^{k-1}_{(i)}$ for $i = 1, k - 1$, or challenged on $S^k_{(1)}$ the loser going to $S^k_{(k)}$. In this latter case we have, for some $j, 1 \le j \le k - 1$,

$$\mathrm{V}^{\mathrm{k}}_{(\mathrm{i}+1)} = \mathrm{V}^{\mathrm{k}-1}_{(\mathrm{i})}, 1 \le \mathrm{i} \le \mathrm{j} - 1,$$

$$\mathrm{V}^{\mathrm{k}}_{(\mathrm{i})} = \mathrm{V}^{\mathrm{k}-1}_{(\mathrm{i})}, \mathrm{j} + 1 \le \mathrm{i} \le \mathrm{k} - 1,$$

$$(1 - \mathrm{p})\mathrm{V}^{\mathrm{k}}_{(1)} + \mathrm{p}(\mathrm{V}^{\mathrm{k}}_{(\mathrm{k})} - \mathrm{c}) = \mathrm{V}^{\mathrm{k}-1}_{(\mathrm{j})}$$

$$\mathrm{V}^{\mathrm{k}}_{(\mathrm{k})} < \mathrm{V}^{\mathrm{k}}_{(\mathrm{k}-1)}.$$

If the kth bird settled then there is no choice for the earlier birds but to settle without challenge, by the threshold result, and the order is determined by the $V^{k-1}_{(i)}$, the lth bird settling on $S^{k-1}_{(l)}$ for $l \le k - 1$. If there is a challenge then there are $k - 1$ possible values of j, i.e. orders of the $V^k_{(i)}$ relative to the $V^{k-1}_{(i)}$. Thus if we define the number of possible arrival profiles under optimal play for k sites as A_k, then

$$A_k \le 1 + (k - 1)A_{k-1}.$$

In fact we can show that $A_k = 1 + (k - 1)A_{k-1}$. To achieve this we observe that given the $V^{k-1}_{(i)}$ corresponding to some specific profile for the first $k - 1$ we can easily construct a set of $V^k_{(i)}$ which satisfy the above equations for each possible value of j. $V^k_{(i)}$ is defined for $2 \le i \le k - 1$. We only need to define appropriate values for $i = 1$ and $i = k$. This can be readily achieved by picking a sufficiently small value for $V^k_{(k)}$ and a sufficiently large value for $V^k_{(1)}$, with

$$(1 - p)V^k_{(1)} + p(V^k_{(k)} - c) = V^{k-1}_{(j)}.$$

Thus,

$$A_n = 1 + (n - 1)A_{nk-1} \Rightarrow A_n$$

$$= (n - 1)! \sum_{j=0}^{n-1} 1/j! \approx e(n - 1)!$$

We illustrate the above by considering the case where $n = 4$, all the possible profiles are given in Table 2.

The entry in the first column represents the only profile with no challenges, 1234. If there is at least one challenge then this must be on S_1 with the loser going to S_4, which yields three possible orders for the sites before B_4 arrives. If there are no more challenges, then each of these represents an arrival profile (column two). If there is another challenge it is upon the highest of these sites, with the loser going to the lowest site, which then yields two possible profiles each and so on. The top entry in the final column, represents the profile S_1, $ChS_1(S_2)$, $ChS_1(S_3)$, $ChS_1(S_4)$.

Figure 1 represents the different arrival profiles for four birds when the values of the sites are $V_1 = 4$, $V_2 = 3$, $V_3 = 2$, $V_4 = 1$ and C and p vary over all possible values; only 10 strategies are possible for these values of the V_i's. On the other hand if the values of the sites are $V_1 = 5$, $V_2 = 4.5$, $V_3 = 4$, $V_4 = 1$, then all 16 of the profiles are possible.

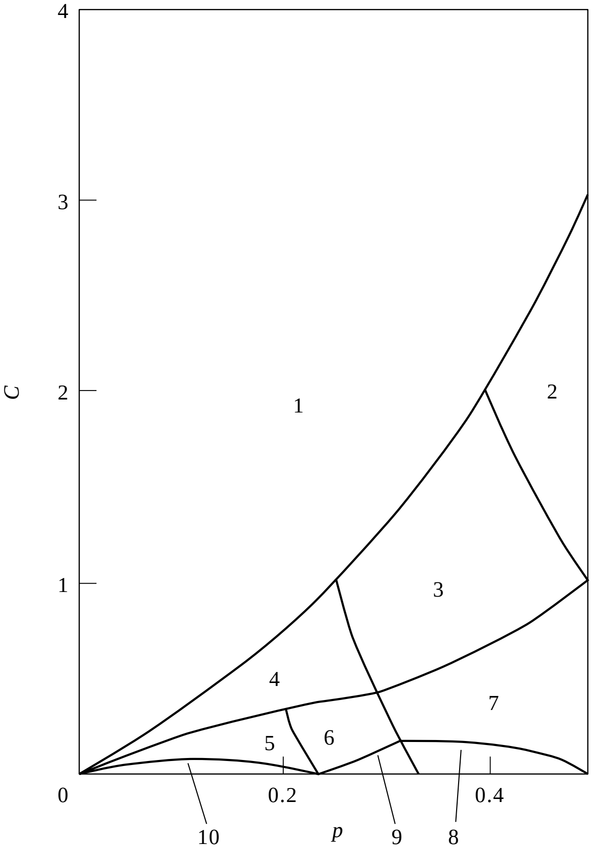

FIG. 1. Profile regions for $n = 4$. Correspondence of regions to optimal strategies for $V_1 = 4$, $V_2 = 3$, $V_3 = 2$ and $V_4 = 1$. Correspondence of regions to optimal strategies [$i(j)$ means challenge upon S_i and the loser goes to S_j.

Region	B_1	B_2	B_3	B_4
1	1	2	3	4
2	1	2	3	1(4)
3	2	1	3	1(4)
4	2	3	1	1(4)
5	1	2	1(3)	1(4)
6	2	1	1(3)	1(4)
7	1	2	2(3)	1(4)
8	1	1(2)	1(3)	1(4)
9	2	2(1)	1(3)	1(4)
10	1	1(2)	2(3)	1(4)

7. The Asymptotic Case

We now turn our attention to the case where a nesting area has a large number of nest sites. We allow $n \to \infty$ and suppose that the intrinsic value of the sites has a density function $f(x)$ defined on [0,1]. Suppose we linearly transform the site values to lie between 0 and 1, and similarly transform the cost C. Birds are supposed to arrive at a fixed rate of unity, so that all the birds arrive in total time 1. The methods developed earlier for the finite case generalise straightforwardly, in particular Theorems 1 and 2. These generalisations will be used (proofs are similar to the finite versions) and we investigate M_{ch}, the maximum number of challenges which occurs on any one site, as a function of C and p. This is of interest as a measure of how many challenges are taking place generally and how much they are concentrated on particular sites (note that the top site does not necessarily receive the most challenges).

TABLE 2
Arrival profiles for four birds when site values are $V_1 = 5$, $V_2 = 4{,}5$, $V_3 = 1$ *and* $V_1 = 1$

No challenges	One challenge	Two challenges	Three challenges
{1, 2, 3, 4}	{1, 2, 3, 1(4)}	{1, 2, 1(3), 1(4)}	{1, 1(2), 1(3), 1(4)}
		{2, 1, 1(3), 1(4)}	{2, 2(1), 1(3), 1(4)}
	{2, 1, 3, 1(4)}	{1, 2, 2(3), 1(4)}	{1, 1(2), 2(3), 1(4)}
		{2, 1, 2(3), 1(4)}	{2, 2(1), 2(3), 1(4)}
	{2, 3, 1, 1(4)}	{2, 3, 2(1), 1(4)}	{2, 2(3), 2(1), 1(4)}
		{3, 2, 2(1), 1(4)}	{3, 3(2), 2(1), 1(4)}

Suppose the birds play rationally. We introduce two sets and two functions to describe the situation at time t, i.e. after a proportion t of the birds have arrived and settled. Let $\mathbf{Z}_t$ be the set of sites (indexed by their intrinsic values) settled at time t (note $|\mathbf{Z}_t| = t$), $V(x,t)$ = expected future pay-off at time t of the site whose intrinsic value is x (so $V(x,t)$ is only defined for $x \in \mathbf{Z}_t$), $\mathbf{W}_t$ is the set of future expected values at time t [i.e. the range of $V(x,t)$] and $g(x,t)$ is the density of future pay-offs at time t $(g,(x,t)$ is defined for $x \in \mathbf{W}_t$). Also we define $B(t) = \max_{x \in \mathbf{Z}_t} V(x,t)$, $W(t) = \min_{x \in \mathbf{Z}_t} V(x,t)$, $D(t) = B(t) - W(t)$, and $T(t,[u,v)) = \int_u^u g(x,t)\mathrm{d}x$. Note that the total density at time t, $T(t,[W(t),B(t))) = t$.

Now, as in the finite case, we work backwards in time. At $t = 1$ all the birds have settled so $\mathbf{Z}_1 = \mathbf{W}_1 = [0,1]$, $V(x,1) = x$ and $g(x,1) = f(x)$. Consider the situation at time t and the change that has taken place in $(t - \delta t,t)$ during which time δt birds have arrived. Analogously to the behaviour demonstrated in Theorem 1, if $D(t) > C(1 - p)/p$ the new arrivals in $(t - \delta t,t)$ will have challenged with losers going to the sites which had the lowest values among $V(x,t)$ or if $D(t) \le C(1 - p)/p$ will simply have settled those latter sites. This implies that $\mathbf{W}_t$ is a closed interval which justifies the use of maximum and minimum in the definitions of $B(t)$ and $W(t)$ above. More precisely, suppose we have $\mathbf{Z}_t$, $V(x,t)$, $\mathbf{W}_t$ and $g(x,t)$.

If $D(t) \le C(1 - p)/p$, then the arriving birds settle sites without challenging, so $\mathbf{W}_{t-\delta t} = \mathbf{W}_t \backslash (W(t), W(t) + \epsilon)$ where

$$T(t,[W(t),W(t) + \epsilon)) = \delta t$$
$$g(x,t - \delta t) = g(x,t) \text{ for } x \in \mathbf{W}_{t-\delta t}$$
$$V(x,t - \delta t) = V(x,t) \text{ for } x \in \mathbf{W}_{t-\delta t}$$

ϵ being the range of values of sites settled by the δt birds.

If $D(t) > C(1 - p)/p$ so that arriving birds challenge, then, provided δt is small enough, $\mathbf{W}_{t-\delta t} = \mathbf{W}_t \backslash (W(t), W(t) + \epsilon)$ and we have

$$\begin{aligned} T(t,[W(t),W(t) + \epsilon)) &= T(t,[B(t) - \epsilon^*,B(t))) \\ &= \delta t \\ &= g(t,W(t))\epsilon \\ &= g(t,B(t))\epsilon^* \end{aligned}$$

where ϵ^* is the range of values of sites challenged by the δt birds.

Thus,

$$V(x,t - \delta t) = \begin{cases} V(x,t) \\ \text{for } x \in [W(t) + \epsilon, B(t) - \epsilon^*) \\ V(x,t)(1 - p) + (V(x^*,t) - C)p \\ \text{for } x \in [B(t) - \epsilon^*, B(t)] \end{cases}$$

where x^* is such that

$$\begin{aligned} T(t,[W(t),x^*)) &= T(t,[x,B(t))) \\ &= g(t,W(t))(x^* - W(t)) \\ &= g(t,B(t))(B(t) - x). \end{aligned}$$

Therefore,

$$\frac{x - W(t)}{B(t) - \epsilon} = \frac{\epsilon}{\epsilon^*}$$

and so

$$\begin{aligned} x^* &= \frac{\epsilon(B(t) - x)}{\epsilon^*} + W(t) \\ &= \frac{g(t,B(t))}{g(t,W(t))}(B(t) - x) + W(t). \end{aligned}$$

We can thus derive the length over which density δt is added from the above expressions as

$$|(\epsilon p - \epsilon^*(1 - p)|$$

so we have

$$g(x,t - \delta t) = \begin{cases} g(x,t) + \dfrac{\delta t}{|\epsilon^*(1 - p) - \epsilon p|} \\ \text{for } x \in [B(t) - \epsilon^*, B(t)] \\ g(x,t) \\ \text{for } x \in [W(t) + \epsilon, B(t) - \epsilon^*). \end{cases}$$

One could determine the complete behaviour by this backward recursion, as for the discrete case to any required degree of approximation and for any $f(x)$. However, the consideration of a specific "linear" case is more illuminating, and this is addressed in the next section.

8. The Asymptotic Linear Case

A particular case which is reasonably amenable to analysis and generates some interesting examples is that where $f(x) = 1$ i.e. the density of intrinsic values is uniform so site value drops off linearly. This case is made easier by virtue of the fact that at every stage the density function $g(x,t)$ is piecewise uniform, that is $\mathbf{W}_t$ *can be divided into* $l(t)$ sub-intervals $[x_i(t),x_{i+1}(t))$, $i = 1$, $l(t)$ where $g(x,t) = c_i$ if $x \in [x_i(t),x_{i+1}(t))$. It is then possible to, in theory, specify the values of t at which changes occur in the sub-intervals, other than via changes in $x_1(t)$ which occurs at all t as, in reverse time, sites are removed.

Specifically, suppose we take a collection of nest sites with values $a - b(i - 1)$ $i = 1, \ldots, n$, i.e. the pay-off of a site is a linear function of the number of that site. Under the rational, or the best, strategy the decision to challenge or not depends on the sign of $(V^i_{(1)} - V^i_i) - (1 - p)C/p$. Thus the rational strategy is independent of a. We fix a to be one and b to be $1/(n - 1)$, so that the values of the sites vary from one to zero. The situation with large n can thus be approximated by taking a continuous set of sites with a uniform density for the values (0,1], as in the

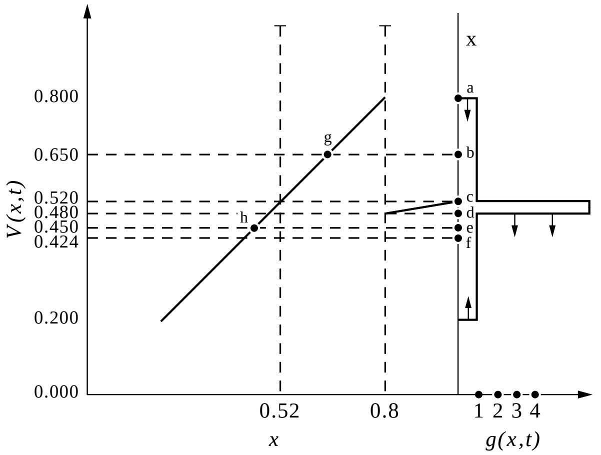

FIG. 2. Situation before final set of challenges. The values of $V(x,t)$ and $g(x,t)$ at time 0.8 for the case where $p = 0.4$ and $C = 0.2$. After 0.8 the situation is that the occupied sites are those with intrinsic values from 0.2 to 1.0. Challenges will occur during the remains of the contest on sites value 0.8 up to 1.0 the loser settling on the sites from 0.2 to 00.

examples shown in Figs 2 to 5 which are discussed in detail below.

We begin with an example for the discrete, linear case with a relatively large number of sites.

Example 5

Suppose we have 100 sites which have intrinsic values 1 to 100, when $C = 0$ and $p = 0.4$. We have proved earlier that in this case every arrival results in a challenge. Tables 3 and 4 give the details of the sites settled, challenged for, and the number of challenges per site. Table 5 gives the number of challenges on the top sites for various values of p near 0.4 with $C = 0$.

As can be seen from Table 4 a single site (here that with intrinsic value 82) may have up to eight challenges and the pattern is fairly complex.

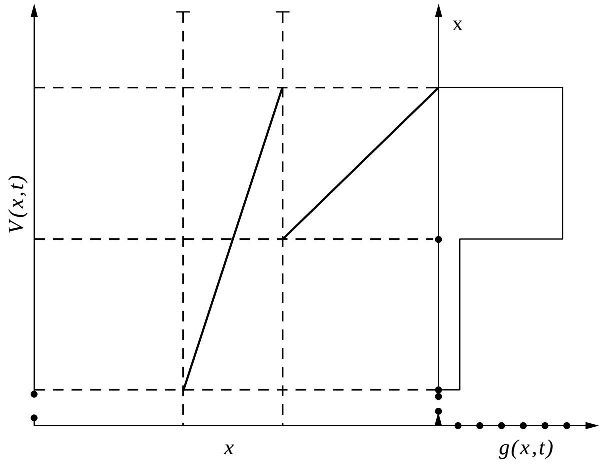

FIG. 3. Critical point at start of final set of challenges. The form of $V(x,t)$ and $g(x,t)$ at the value $t = 1 - p - pC$ when challenges can occur prior to this, and for all subsequent t.

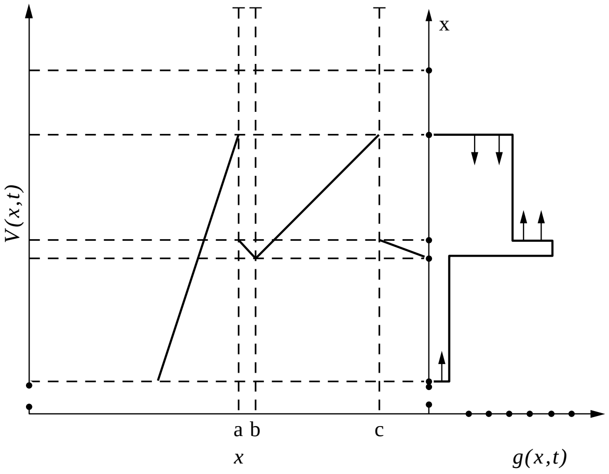

FIG. 4. Penultimate set of challenges. The form of $V(x,t)$ and $g(x,t)$ *during the period when second challenges are occurring* (*in reverse time*) *when* $p \leq 0.25$.

The import of Table 5 is that it emphasizes the critical effect of discreteness and that one needs to be careful in approximating the asymptotic result from even fairly large values of the number of sites.

THE MAXIMUM NUMBER OF CHALLENGES, M_{CH}

We investigate the value of the maximum number of challenges which occurs on any one site M_{ch} as a function of C and p.

The values of C and p which yield $M_{ch} = 0$, 1, 2 have been found analytically.

In addition to the analytical approach above, a numerical approach was used to find the regions where M_{ch} held values between 3 and 8, using linear site values and varying C and p for 1000 birds. These are shown in Figs 6(a) and (b).

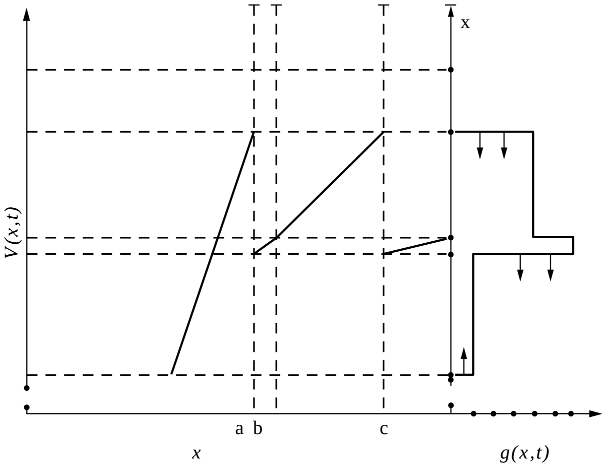

FIG. 5. Penultimate set of challanges. The form of $V(x,t)$ and $g(x,t)$ during the period when second challenges are occurring (in reverse time) when $p \geq 0.25$.

TABLE 3

The sequence of sites challenged and settled for $C = 0$ *and* $p = 0.4$ *for the* 100-*site linear case*, *site i has value* $V_i = 101 - i$

82	82(76)	82(86)	82(84)	82(83)	83(87)	84(81)	84(77)
83(57)	86(88)	83(92)	84(85)	76(91)	77(75)	81(59)	57(80)
92(58)	82(90)	83(79)	76(56)	84(78)	57(90)	92(74)	85(93)
86(73)	77(55)	87(72)	88(94)	91(71)	58(95)	89(70)	56(69)
78(96)	90(68)	79(54)	80(97)	81(67)	82(66)	57(60)	83(65)
84(98)	85(64)	86(63)	87(53)	58(99)	88(62)	89(100)	90(61)
91(52)	92(51)	59(50)	93(49)	91(18)	95(17)	96(16)	97(15)
60(44)	98(43)	99(42)	100(41)	61(40)	62(39)	63(38)	64(37)
65(36)	66(35)	67(34)	68(33)	69(32)	70(31)	71(30)	72(29)
73(28)	74(27)	75(26)	76(25)	77(24)	78(23)	79(22)	80(21)
81(20)	82(19)	83(18)	84(17)	85(16)	86(15)	87(14)	88(13)
89(12)	90(11)	91(10)	92(9)	93(8)	94(7)	95(6)	96(5)
97(4)	98(3)	99(2)	100(1)				

Even for small values of n the pictures are approximately the same as the above figures, as can be seen from the following diagrams. These represent the values of M_{ch} for 10 birds [Fig. 7(a)] and for 30 birds [Fig. 7(b)].

Note that the boundary lines in Figs 6 and 7 correspond to non-generic cases, i.e. $V^j_k = V^j_l$ *for some* j and $k \neq l$.

We now derive conditions on C in terms of p under which M_{ch} takes the values 0, 1 and 2.

$M_{ch} = 0$

If we have $D(t) \leq C(1-p)/p$ at any stage then there are no challenges before t. In particular, since for $t = 1$ we have $D(t) = 1$ there are no challenges, so $M_{ch} = 0$, if and only if, $1 \leq C(1-p)/p$ i.e. $C \geq p/(1-p)$.

$M_{ch} = 1$

Suppose that $C < p/(1-p)$ so that the later birds must challenge, then $M_{ch} \geq 1$. Thus, $\mathbf{W}_t = [1-t, t]$ and $V(t,t) = (1-p)t + p((1-t) - C)$ for t sufficiently close to 1. The function $V(x,t)$ and the density $g(x,t)$ are shown for such a t in Fig. 2 where the parameter values are $p = 0.4$ and $C = 0.2$. As t decreases the set $\mathbf{W}_t$ reduces being of "length" $D(t) = (2t-1)$ at time t. This phase of the process continues either until $D(t) = C(1-p)/p$, when no earlier challenges would occur, or until $t = (1-p)1 + p(-C) = 1 - p(1+C)$, the value of the site with the highest intrinsic value just before the challenge at time $t = 1$, when the best sites are that with index 1 and that with index $(1-p) - pC$, so that a second challenge on the former would occur. Thus, if only one challenge is to occur we require that $D(t) = C(1-p)/p$ occurs for a t no smaller than $1 - p(1+C)$ i.e. that $D(1-p(1+C)) = (2(1-p(1+C)) - 1) = 1 - 2p - 2pC \leq C(1-p)/p$ so $M_{ch} \leq 1$ if $C \geq p(1-2p)/(1-p+2p^2)$.

TABLE 4

Number of challenges by site for $C = 0$ *and* $p = 0.4$ *for the* 100-*site linear case*, *site i has value* $V_i = 101 - i$

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	2	2	2
3	8	6	6	3	4	3	3	3	3	3	4	2	2	2	2	2	2	2	2

TABLE 5

Each row specifies the number of challenges on sites 81 *through* 100 *for the appropriate values of p*

$p = 0.3999$	3	4	7	6	3	7	3	3	3	3	3	4	2	2	2	2	2	2	2	2
$p = 0.4$	3	8	6	6	3	4	3	3	3	3	3	4	2	2	2	2	2	2	2	2
$p = 0.4001$	3	3	4	6	3	8	3	3	3	3	3	4	2	2	2	2	2	2	2	2

Note that the number of challenges on other sites is as per Table 4 with the exception of site 57 which has six challenges when $p = 0.4001$.

In the example shown in Fig. 3 $p = 0.4$, $C = 0.2$ and $t = 0.8$. We have that

$$V(x,t) = \begin{cases} (1-p)x + p(1-p-C) & \text{if } x > t \\ x & \text{if } (1-t) \leq x \leq t. \end{cases}$$

As t is decreased the density is changed as indicated by the arrows. For $t = 0.8$, as in diagram, a challenge is about to occur (in $[t, t-\delta t]$), on the site with intrinsic value 0.8, so that the value of $V(0.8,t)$ will switch from 0.8 to 0.48, while the site with intrinsic value 0.2 will no longer be occupied. Thus, $g(x,t)$ has a range which reduces at a and i, and is built up below d, as shown by the arrows in the figure. If this process could continue until a "reached" c then d would have reached f, where $x = 0.424$. However, when a "reaches" b (where $x = 0.65$), and d has 'reached' e the range of site values is equal to 0.3 ($= (1-p)C/p$) so no challenge can occur prior to the corresponding value of t, ($= 0.65$). Best behaviour is therefore specified as follows for this case:-

for $t \in [0.0, 0.13)$ settle site with intrinsic value $(0.65 - t)$,

for $t \in [0.13, 0.55)$ settle sites $(0.52 - \delta t)$ and $(1.00 - 5\delta t)$ where $\delta t = (t - 0.13)/6$,

for $t \in [0.55, 0.65)$ settle site $(1-t)$,

for $t \in [0.65\ 1.00]$ challenge on site t, the loser going to $(1-t)$.

Figure 3 illustrates the situation which occurs when t is such that $t = (1-p) - pC$ so that for the first time (in reverse) there are two sites which have $V(x,t) = \max_x[V(x,t)]$ (e.g. in the example considered here this would correspond to $t = 0.52$ and then for $x = 1.00$ and $x = 0.52$ one would have $V(x,t) = 0.52$;

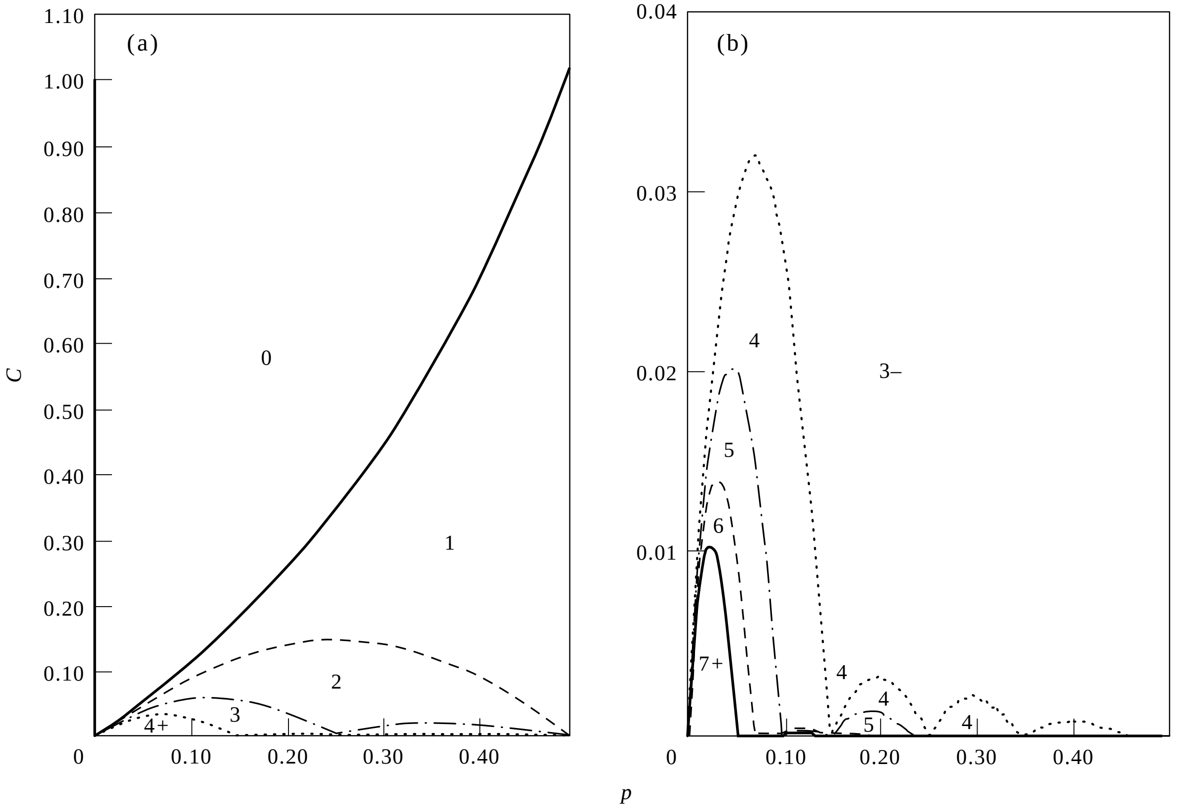

FIG. 6. Maximum number of challenges for large *n*. Maximum number of challenges by any bird for large $n(=1000)$ for various p and C showing (a) regions for 0, 1, 2, 3, ≥ 4 and (b) regions for ≤3, 4, 5, 6, ≥ 7 as maximum.

though as pointed out above this situation is not reached in this case).

$M_{ch} = 2$

Suppose $C < p(1-2p)/(1-p+2p^2)$ so that there will be at least two challenges. When $t = (1-p(1+C))$ we reach the situation shown in Fig. 3 where

$$fx,t = \begin{cases} 1 \\ \text{for} \quad x \in [p(1+C), 1-2p(1-p)(1+C)] \\ 2(1-p)/(1-2p) \\ \text{for } x \in [1-2p(1-p)(1+C(,1-p(1+C)) \end{cases}$$

This is easily derived since, taking the range of site values as $[y_2,y_1]$, we have $y_1 = 1-p(1+C)$ and $y_2 = p(1+C)$, and the total density from $[y_1,1]$, i.e. $p(1+C)$ has been reallocated to the range $[y_1(1-p)+(y_2-C)p,y_1]$.

Now at this point there are two possible types of behaviour. We know that if at any stage there is to be a challenge when the value of the currently best site before that challenge was $(1-p)B(t)+p(W(t)-C) = P(t)$ say. Then, $\mathrm{d}P(t)/\mathrm{d}t = (1-p)\mathrm{d}B(t)/\mathrm{d}t + p\mathrm{d}W(t)/\mathrm{d}t$ and since the densities functions are piecewise uniform we have $\mathrm{d}B(t)/\mathrm{d}W(t) = -f(W(t),t)/f(B(t),t)$ so $\mathrm{d}P(t)/\mathrm{d}t = [(1-p) - pf(B(t),t)/f(W(t),t)]\mathrm{d}B(t)/\mathrm{d}t$ so since $\mathrm{d}B(t)/\mathrm{d}t$ is necessarily negative we have that $\mathrm{d}P(t)/\mathrm{d}t > 0$ if, and only if, $[(1-p) - pf(B(t),t)/f(W(t),t)] < 0$, or equivalently $f(B(t),t)/f(W(t),t) > (1-p)/p$.

Thus at the current stage we have $f(W(t),t) = 1$ and $f(B(t),t) = 2(1-p)/(1-2p)$ so $\mathrm{d}P(t)/\mathrm{d}t > 0$ if, and only if $2(1-p)/(1-2p) > (1-p)/p$ i.e. if, and only if, $p > 0.25$.

Case 1. $p < 0.25$. In this case we have a similar situation to that of the analysis for $M_{ch} = 1$. We require that $y_2 - x_2 \le C(1-p)/p$. Now x_2 is determined by requiring that the density in $[x_1,x_2)$ equals that in $[y_2,y_1)$ which is $1-y_2$. Thus we have $x_2 = x_1 + 1 - y_2 = 1 - 1 + 2p(1-p)(1+C) = p(3-2p)(1+C)$ and so $y_2 - x_2 = 1-2p(1-p)(1+C) - p(3-2p)(1+C) = 1-p(5-4p)(1+C)$ so that there will be two challenges provided $1-p(5-4p)(1+C) \le C(1-p)/p \Rightarrow C \ge p(1-4p)(1-p)/(1-p(1-4p)(1-p))$. This is illustrated in Fig. 4.

Having reached the situation shown in Fig. 3, challenges continue (in reverse time) on sites with intrinsic values 1.00 and $1-p-pC$, and Figure 4

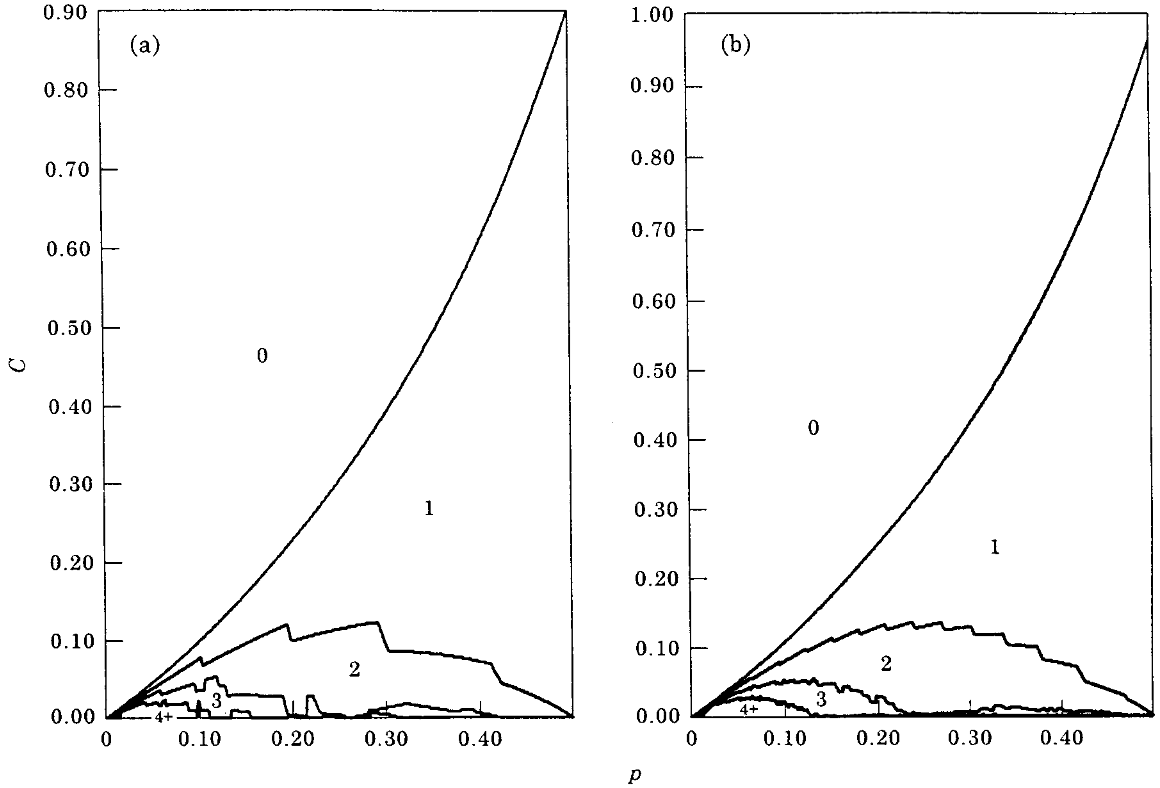

FIG. 7. Maximum number of challenges by birds. Maximum number of challenges by any bird for (a) $n = 10$ and (b) $n = 30$ for various p and C showing regions for 0, 1, 2, $3 \geq 4$ as maximum.

shows the position reached where challenges has just occurred on sites with intrinsic values a and b, and current value a.

Case 2. p > 0.25. This case is considerably more difficult and we omit the details. The situation is illustrated in Fig. 5, details are similar to those of Fig. 4. The condition under which there are two challenges when $p > 0.25$ is

$p > 0.25$:

$$\frac{32p^6 - 104p^5 + 128p^4 - 74p^3 + 20p^2 2p}{-32p^6 + 104p^5 - 112p^4 + 38p^3 + 10p^2 - 11p + 3} \leq C < \frac{p(1-2p)}{2p^2 - p + 1}$$

9. Discussion

In nature many, perhaps most, conflicts will involve more than two players, yet almost all of the theory of evolutionary conflicts is for pairwise conflicts. Exceptions to this are the "play the field" models where an individual's strategy is tested against the whole of the population at each stage (Maynard Smith, 1982), and variants of the War of Attrition (Haigh & Cannings, 1989; Sjerps & Haccou, 1994; Cannings & Whittaker, 1994). There are various ways in which one can approach multi-player games. One is simply to specify in complete generality the pay-off an individual playing i receives against each possible set of opponents. Unsurprisingly such models are intractable. A second approach is to consider a specific class of pay-offs. It is this approach that Broom *et al.* (1997) have adopted, introducing certain symmetries. A third possibility is to construct a multi-player conflict in such a way that it is composed of a system of pairwise trials. One can for example have knockout or round-robbin tournaments, as is common in humans (e.g. chess, tennis) in which players rewards are determined by how far, or how well, they progress. Alternatively, as here, one can assume a sequential structure, which leads naturally to a dynamic programming problem.

The particular problem discussed here was that of birds arriving at a nesting area and competing over nest sites. This is clearly a problem that birds face regularly and appropriate behaviour must have evolved. However, we are unaware of any attempt to model the process; hence the current attempt. We should make clear that we are not claiming that our model will realistically represent the behaviour of any specific species. We would argue that to criticise modelling, such as carried out here, on grounds of lack of realism is misplaced; missing the point of the exercise. The purpose of the model presented is not to model any specific situation in any specific species (or group of species) but to focus attention on some of the issues, assumptions and difficulties in attempting to model such a complex behaviour, and also hopefully to suggest possible questions which might be examined in the labortory or field.

Our model makes various assumptions. Firstly, we assume that the birds have a complete knowledge of their situation, knowing how many birds have arrived before them and how many will arrive after, knowing which sites are currently occupied and the values of all sites, and the probability of displacing an occupier and the cost of losing. In practice they will, presumably, have a rough estimate of each of these values, though not in a numerical form, or may spend time exploring the area to assess these values (perhaps an additional sequential process). Secondly, there are assumptions about the behaviour which is preprogrammed into the birds. We assume that the birds arrive in a random order and challenge an occupier or settle immediately (i.e. before another bird arrives), while losers settle rather than challenge again. Thus the behaviour which controls arrival time is not subject here to evolution. It is clear in some of our results that it would be advantageous for individuals on occasion to hide when they arrive and thus alter their position in the order. We do not allow this. On the other hand our model predicts that this type of behaviour might be advantageous under certain circumstances, and allow one to check when this would be the case.

The other main assumption is that the probability p that a challenger will displace an occupier is independent of the value of the site, and of the history of the occupier (who may have fought several contest already). This assumption is not vital for the method of deriving the rational strategy, that carries through as per the theory and example given, but is crucial (together with the assumption that $p \leq 0.5$) for the theorems which then allow simpler derivation of the best behaviour. The examples thus considered are easier to interpret and still provide good evidence of the types of behaviours and the complexity of those behaviours.

We have argued in the text that evolution might be expected to programme bird to behave in a manner which approximated to the rational, at least in aggregate if not at the individual level. One way this might happen is if birds individually adopted strategies based on a limited number of cues rather than on complete knowledge. For example if they classified sites as good, moderate or poor then they could develop simpler decision rules. We have addressing this possibility via the development of a simulation model, and have reported some preliminary results in Broom & Cannings (in preparation). Further results will be reported elsewhere.

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