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A Sequential-Arrivals Model of Territory Acquisition II

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Birds arrive sequentially at their breeding ground where the nest sites vary in value (measured by reproductive success). Each bird may choose a vacant site or challenge an occupier for its site. In the latter case, the occupier is presumed to be the more-likely winner; the loser incurs a cost and must go to a vacant site. In a previous paper (Broom *et al*., 1997, *J. theor. Biol.* **189,** 257–272), we considered the optimal strategy. However, that optimal strategy was complex and perhaps could not be realized in real bird populations, making possibly costly demands both perceptually and at the coding level. With this in mind we introduce certain restricted classes of strategy, and consider how populations might evolve. Computer simulations of various populations have been performed to model the competition amongst several strategies in the presence of recurrent mutations. Certain combinations of strategies persisted and corresponded approximately to the ESSs found in Broom *et al*. (1997).

1. Introduction

1.1. GAME THEORY

Game theory has featured strongly in modelling the natural world, particularly in the area of animal conflicts. It has provided explanations for apparently paradoxical situations, for example, the practice of heavily armed animals engaging only in ritualistic contests (Maynard Smith, 1982) and the tendency of (especially male) animals to develop extremely costly signals to acquire mates (Grafen, 1990a, b). The concept of an evolutionarily stable strategy (ESS), introduced in Maynard Smith & Price (1973), has been especially useful, and has been central to a large body of literature; some important examples include Bishop & Cannings (1976), Cressman (1992), Haigh (1975), Hofbauer & Sigmund (1988, 1998) and Maynard Smith (1982). Most of this work has concentrated on games between only two players. This is understandable for two reasons.

(i) Many natural conflicts involve only two players and thus the theory of pairwise games is widely applicable.

(ii) The mathematics involved in pairwise games is simpler than that for multi-player games, and thus it is easier to obtain results both in theory and in practical application.

Game theory has its roots in economics originating with Von Neumann & Morgenstern (1994)

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[see also Axelrod & Hamilton (1981) and Binmore (1992)] and multi-player games have always been central to its theory. See Luce & Raiffa (1957) for a general discussion (including a description of its application to voting schemes). However, there has so far been little work in the area of multi-player game theory applied to biological situations [examples include Broom *et al.* (1997b), Cannings & Whittaker (1994) and Haigh & Cannings (1989)]. But there are many biological situations which cannot be modelled by pairwise games. This is either because more than two individuals compete simultaneously or alternatively pairwise games occur within a structure which effectively makes them multi-player, e.g. dominance hierarchies in social animals (Barnard & Burk, 1979) or, as in the current paper, birds nesting at a colonial breeding site (Broom *et al.*, 1996, 1997a). Even in classical examples such as the competition of males for mates, the pairwise contests involved are likely to be dependent. Thus, it is important to consider multi-player models (both theoretically and practically) to extend the already impressive contribution of game theory to the study of biology.

1.2. A SEQUENTIAL-ARRIVALS MODEL OF TERRITORY ACQUISITION

In many species birds nest together in very large areas with many hundreds or even thousands of sites. An example is kittiwakes along the ledges of a cliff. At the beginning of the nesting season, birds (or more properly breeding pairs of birds) have to find a nest site. The potential sites will be of varying value (as measured by the expected number of surviving offspring), depending upon various factors such as access by predators, amount of shelter, etc. In the model of Broom *et al.* (1997a) the birds are supposed to arrive at their breeding ground one at a time, their position in the sequence of arrivals is randomly determined and they cannot influence this position, e.g. by postponing their actions at the breeding ground. For a consideration of this problem where birds can affect their arrival time, see Kokko (1999). On arrival, a bird may either occupy a vacant site or challenge for one which is already occupied. A loser in a fight resulting from such a challenge must move to an unoccupied site and at the same time incurs a cost. From the species point of view, the best strategy is just to fill up the sites in an orderly fashion without any conflict, since this maximizes the total payoff to the group. However, selection operates at the individual level, and thus behaviour which is beneficial to the individual (even at the expense of its group-mates) will become prevalent in the population. Thus, the behaviour which evolves should be approximately the same as that which would occur if the birds were thinking rationally and selfishly about their options.

In Broom *et al.* (1997a), we considered what was the "optimal behaviour" for a population of birds in the sense that each individual adopted what was optimal for them given the situation they faced, and assuming that all subsequent arrivals would also behave optimally. It was assumed in that paper that the occupier of a site was the more likely winner of a contest. A recursive argument was employed to derive both general results regarding this optimal behaviour and also to solve certain particular cases (i.e. values of the costs, rewards, and probability) to illustrate some of the features of those solutions. It was shown that for a reasonable set of nest sites (e.g. linear payoffs) the birds which arrive first tend to do better than those which arrive later. Initially, the birds do well to occupy empty sites until the quality of these become too poor, after which they risk contesting the better sites. An interesting and important result is the existence of a threshold value. Birds which arrive before a certain time do not challenge and birds which arrive after it do. The very last birds contest the top sites, previous ones challenge on sites further from the best. There can be a "second wave" or "third wave", etc. of challenges when birds further from the end will start to contest the top sites. The model describes an interesting pattern of behaviour of the population as a whole.

We assume that the information used to choose a nesting strategy is coded for genetically. There is evidence that this is true for related behaviour in the type of migratory birds that we are considering, especially the direction of migration (e.g. Berthold *et al.*, 1992). Thus, we do not envisage a bird making complex decisions, but simply responding to pre-programmed cues telling it how to behave. Successful strategies, however, will resemble those which would be chosen by a rational individual. The solution found in Broom *et al.* (1997a) was a unique optimal strategy for every bird in every situation but it required a precise knowledge of the values of all the sites. The solution is extremely complex, requiring a very large look-up table exactly specifying what to do in each possible situation for each possible set of site values. Thus, the genetic system may not be capable of coding for this. Also the site values will vary from year to year (as will the number of sites), so that the "best" strategy for one year may not be the best one in subsequent years. In any case, this may be an expensive process; simpler information storage requires less brain capacity, and so the cost of simpler storage systems to the bird is likely to be less than more complex ones.

We see that there are several reasons to think that birds will be programmed with a strategy which resembles how a rational player would behave, but without the level of complexity of Broom *et al.* (1997a). It should be noted, however, some species are capable of making complex decisions, rather than simply being genetically preprogrammed, see Clayton & Dickinson (1999) for an example. Thus, they may be able to evaluate a good strategy conditional upon their environment, which, if not up to the complexity level of Broom *et al.* (1997a), may be more complex than the type of strategy that we envisage in this paper.

We consider here certain restricted classes of strategies which might be reasonable for a population of birds, and find the best strategies within each class. The type of strategies chosen are those that resemble the optimal strategy in certain key features, whilst keeping the amount of information stored to a minimum. There are a number of sites of decreasing value, and a bird may either challenge upon an occupied site or occupy a vacant site. If there are good sites still available it does not make sense to challenge for a slightly better site and risk receiving an injury, so a bird should just occupy one of the free sites. However, if the remaining sites are poor compared to some occupied ones then it will be worth the risk to fight and try to obtain a good site.

We consider three types of strategy: Type 1, Type 2 and Type 3. In Type 1, the birds pick the best free site until a critical number have been occupied, after which they challenge for one of the top sites, each with equal probability. Thus, the "threshold" result is maintained. Recall that this result depends upon the assumption that the occupier of a site is more likely to win a contest than the challenger. This assumption will apply throughout this paper without further comment. We show that there is no pure ESS within this class. Type 2 is an extension of this idea; the probability that a bird challenges for a given site is now not constant over the top sites. There is also no pure ESS within this second class. However, there is a pure strategy, *the pivotal strategy*, which resists opponents with a single mutation (in a sense to be defined later). Each strategy of Type 2 is equivalent to a combination of strategies of Type 1. It is observed that for the pivotal strategy, the early occupiers of the top sites do worse than the occupiers of some lower sites, thus a further refinement is introduced (Type 3 strategies) where early birds do not occupy the top sites. The properties of this third type of strategy are investigated. An advantage of this type of strategy to that of Broom *et al.* (1997a) is that it is robust to environmental changes. Thus, in a fluctuating environment where optimality decisions are difficult, a relatively simple strategy such as this might be best. For a general treatment of optimality decisions in fluctuating environments, see McNamara *et al.* (1995).

Section 2 describes the sequential-arrivals model and the simple strategies that we consider. In Section 3, the existence of the pivotal strategy in the limiting case when the number of sites is infinite is proved, and the form of the pivotal strategy is found for the case where the intrinsic values of the sites are linearly dependent upon the site number. In Section 4, we describe computer simulations of populations playing strategies restricted to the chosen types and examine how the populations behave. Section 5 is a discussion of our results.

2. A Sequential-Arrivals Model

2.1. THE MODEL

Suppose that a set of n birds $B_1, \dots, B_n$ arrive sequentially at n nest sites $S_1, \dots, S_n$. The value of the site S_i is V_i ($\geqslant 0$) for the bird occupying that site at the end of the process, i.e. when all birds are settled on a site, where $V_i \geqslant V_j$ if $i < j$. If there are more sites than birds we can ignore the worst sites, if there are more birds than sites we can create phantom sites with zero value.

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

> The challenger wins with probability $p \leqslant 0.5$, otherwise the occupier wins. The winner becomes the occupier of the contested site, the loser pays a cost C, (receives a payoff of $-C < 0$) and must retreat to an unoccupied site of its choice.

Thus, a bird may not make any challenge after its initial one, and must remain at the site it has occupied (although it may be removed by the challenges of other birds). If the bird was allowed to challenge again then it would be in the same position as the previous new arrival had been, and would thus make the same decision, resulting in an infinite number of challenges (and costs) for each bird, so that it would not be sensible for any bird to challenge. When a bird loses a contest in this model it receives an injury, which may prevent it from making any more challenges. It is possible to make this model more complicated (e.g. variable values of p and C depending upon which site the contest takes place, more than one challenge per bird); however, the present model seems to have the most important feature (choose a free site or fight) and is amenable to analysis.

The contest finishes after the arrival of the final bird. The payoff 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.

In this paper, a variety of parameters are used in a number of contexts. Table 1 gives a list of all the parameters used, together with their meaning.

2.2. SIMPLE STRATEGIES

In Broom *et al.* (1997a), the birds played rationally conditional upon the positions of all the birds which had arrived before them and upon the assumption that all subsequent birds would also behave rationally. As indicated in the Introduction, the strategies which result are

TABLE 1
Model parameters and definitions

Parameter	Definition
n	The total number of birds arriving at the breeding ground
B_j	The j-th bird to arrive at the breeding ground
S_i	The i-th most valuable nest site at the breeding ground
V_i	The value of site S_i
p	The probability that the challenging bird wins a contest
C	The cost incurred by the loser of a contest
I	The lowest value site considered "good" by a simple strategy player
J	The lowest value site considered "medium" by a simple strategy player
p_i	The probability of a Type 2 bird challenging on S_i if the available free sites are not sufficiently good
X	The lowest value site considered "good" in the asymptotic case
Y	The lowest value site considered "medium" in the asymptotic case
B_t	The bird to arrive at time t in the asymptotic case
S_x	The nest site with proportion x less valuable in the asymptotic case
U_x	The value of site S_x
$f(x)$	The density of challenges by Type 2 birds on S_x in the asymptotic case if the available free sites are not sufficiently good
X^*	A different value of "X" chosen by a mutant bird
Y^*	A different value of "Y" chosen by a mutant bird
$W_{x,t}$	The expected payoff to the occupier of S_x at time t
$\phi(z)$	The expected payoff to B_{1-z}
$h(x)$	$pY f(x)$
$g(x)$	A different value of "$h(x)$" chosen by a mutant bird
$P_t(x)$	The probability that the occupier of S_x at t still holds it at time 1

very complicated and here we consider three, relatively simple, types of strategy.

Type 1 divides sites into three categories; good sites $(1, \ldots, I)$, medium sites $(I+1, \ldots, J)$ and poor sites $(J+1, \ldots, n)$. A bird will occupy the best free site if a good or medium site is available. However, if only poor sites are free it will challenge for a good site chosen at random with each site having an equal probability of being chosen (if it just chose the best site then it would probably be challenged several times by other birds also playing this strategy, and so may well lose the site). If the bird loses a contest, whether as challenger or challenged, it occupies the best free site. Thus, a strategy is described by an integer pair (I, J).

Type 2 is a refinement upon Type 1. In Type 1 all the players challenge the top sites with an equal probability. However, it may be more sensible to allocate a higher probability to the best of these sites (or vice versa!), so we introduce a probability vector $\mathbf{p}$ so that p_i is the probability that a bird will challenge upon site i $(1 \leqslant i \leqslant I)$. A strategy is defined by a vector and a pair of integers $(\mathbf{p}; I; J)$. Note that given the values of the (p_i), I is determined; it is simply the largest i for which $p_i > 0$.

Type 3 is a different refinement of Type 1. For late birds, the only free sites are the poor ones and so they challenge for the top sites. Thus, the early occupiers of these very good sites face the prospect of being evicted from these sites, having to go to a poor site and receiving an injury in the process. A Type 3 strategy attempts to take this effect into account by allowing the early birds to ignore the best I sites. Later birds occupy or challenge a site from the top I.

More formally the three types of strategy are defined as follows:

Type 1: If S_i is free for some $i \leqslant J$ then go to the best free site, otherwise challenge upon S_k $(1 \leqslant k \leqslant I)$ with probability $1/I$. If a contest is lost, go to the best free site. A strategy is defined by the pair (I, J).

Type 2: If S_i is free for some $i \leqslant J$ then go to the best free site, otherwise challenge upon S_k $(1 \leqslant k \leqslant I)$ with probability p_k. If a contest is lost, go to the best free site. Setting $\mathbf{p} = (p_i)$ $(i = 1, \ldots, I)$ a strategy is defined by $(\mathbf{p}; I, J)$.

Type 3: If S_i is free, for some $i \in [I+1, J]$, go to the best free site within $[I+1, J]$, otherwise go to S_k $(1 \leqslant k \leqslant I)$ with probability $1/I$. If S_k is occupied then of course a challenge occurs. If a contest is lost, go to the best free site. Strategies of this type are defined by the pair (I, J).

3. Asymptotic Results

As has been remarked in the Introduction, many species of birds nest together in very large groups of hundreds or even thousands of sites and so it is of interest to consider the behaviour of populations where n is large. We investigate the properties of strategy types (1) and (2) as n tends to infinity. Let $X = (n-I)/n$, $Y = (n-J)/n$ and in general $x = (n-i)/n$, so that in the limit of large n the sites have indices which are continuous over (0, 1]. Define U_x as the reward for occupying site S_x at the end of the contest. We shall assume that U_x is a continuous and monotone increasing function on (0, 1] (x is decreasing with site number and so increasing with site value).

Define $f(x)$ $(X \leqslant x < 1)$ by the requirement that $f(x)\,\mathrm{d}x$ is the probability that a (challenging) bird challenges on a site in the interval x to $x + \mathrm{d}x$. Strategies are thus of the form $(f; X; Y)$. As well as modelling large populations, the asymptotic results given below give an indication of how populations with smaller numbers of birds and sites may behave (see Section 4.2 for a comparison when the number of sites is ten).

3.1. ASYMPTOTIC RESULTS FOR GENERAL PAYOFFS

It is clear that no pure strategy can form an ESS within the class defined by Type 1 (or that formed by Type 3), except in the situation where the cost of losing a contest is high so that it is best for nobody to challenge and $X = 1$, $Y = 0$ is an ESS. Suppose there were such as ESS $(X; Y)$ $X < 1$, $Y > 0$ for Type 1. If almost all players play this strategy, then each arrival after $(Y, 1]$ are filled is equally likely to challenge upon any site S_x; $x \in (X, 1]$, and since $U_x > U_y$ when $x > y$, there is a greater expected payoff associated with challenging upon S_x than S_y for any particular bird. This means that a bird which chooses a strategy $(X^*; Y)$ where $X^* > X$, will have a greater payoff than the original strategy (at least when the number of players of strategy (X^*, Y) is small), and so can invade. The argument is the same for Type 3. Note that mixed ESSs (comprising players of different strategies) are not excluded by this argument.

This argument does not hold for the finite site case in one special case: namely when there is only a single site which should be challenged upon, so that the rational strategy defined in Broom *et al.* (1997a) can be expressed as a Type 1 strategy and so is an ESS of that class.

For example, when $n=6$, $V_1=60$, $V_2=4$, $V_3=3$, $V_4=2$, $V_5=1$, $V_6=0$, $C=0$, $p=0.4$. In this case, the first bird should go to S_1, and every other bird should challenge on S_1, the loser going to the best free site. Thus, $I=J=1$ is an ESS (there are no "medium" sites).

We now consider strategies of Type 2, and proceed to find a strategy which is resistant to invasion, although it is not an ESS. In the process we show that there is no pure ESS of Type 2. To do this we need some definitions.

We suppose that, as in the finite case, birds arrive in a strict order so that B_r arrives before B_s if and only if $r<s$. Thus, when B_r arrives, the set of previous arrivals is $\{B_s : s<r\}$. We shall define *time t* as the time of the arrival of B_t. Note that our temporal scale need not be a linear function of real time, but is a strictly increasing function of it. Times $t=0$ and 1 will correspond to the arrival of the first and last birds, respectively.

We define $W_{x,t}$ to be the expected payoff to an occupier of site x at time t, i.e. birds have arrived up to and including B_t, and the occupied sites are S_w; $w \in [1-t, 1]$.

Further we define the *expected future payoff* $\phi(z)$ to a bird arriving at time $1-z$ as the mean payoff received by such a bird. For a bird which arrives at time t, the best free site is S_{1-t}. If a bird does not challenge, its expected future payoff is the expected payoff to a bird occupying that site, i.e. $\phi(z)=W_{z,1-z}$. If it challenges on the site with value U_r, then the expected future payoff is $\phi(z)=pW_{r,1-z}+(1-p)(W_{z,1-z}-C)$.

If all of the population play (f; X; Y) then

$$W_{x,t}=U_x(x<X, \text{for all } t) \text{ and } W_{x,1}=U_x \text{ for all } x.$$

Theorem 1. *There is a unique strategy (f; X; Y) which cannot be invaded by any strategy which is a single mutation away* (i.e. *it differs in Y or f/X only*). *This strategy is not an ESS and will be called the* pivotal strategy.

Theorem 1 is proved in Appendix A.

Since the pivotal strategy is the only pure strategy which can resist invasion by a strategy a single mutation away, it is the only candidate ESS. Since it is in fact not an ESS, we conclude there is no pure strategy ESS for Type 2.

Following the argument in the proof of Theorem 1, the pivotal strategy can be invaded by a small group of a sufficiently similar strategy. The advantage of this new strategy is lost if too many players adopt it. This leads us to conjecture that there is a stable collection of strategies centred around the pivotal strategy which form a mixed ESS. Evidence in support of this claim is found in the simulations of the next section.

Note that a strategy of Type 2 is a combination of strategies of Type 1. If we have an infinite combination of strategies all with the same Y but with varying X we can construct any decreasing density function (a pivotal strategy clearly has a decreasing $f(x)$ due to condition (A.3) in the proof of Theorem 1).

3.2. ASYMPTOTIC RESULTS FOR LINEAR PAYOFFS

We will now consider a special case where there is a linear relationship between the number of the site and its value. This seems a plausible scenario, for instance, if sites are along a cliff edge where the worst sites are those inland closest to terrestrial predators. This case was also considered in Broom *et al.* (1997a). We find an expression for the pivotal function.

We define the function $h(x)$ by

$$h(x)=pYf(x).$$

Theorem 2. *When $p>C/(C+1)$ and $U_x=x$, the strategy defined by Theorem 1 satisfies the following equations*:

$$x+C+\frac{Y}{h(x)}=\frac{h(x)}{1-\mathrm{e}^{-h(x)}}\left(X-\frac{Y}{2}+C+\frac{Y}{h(x)}\right), \tag{1}$$

$$\int_X^1\left[\left(\frac{x+C}{Y}\right)h(x)\mathrm{e}^{-h(x)}-1+\mathrm{e}^{-h(x)}\right]\mathrm{d}x=C, \tag{2}$$

$$\int_X^1 h(x)\,\mathrm{d}x=pY. \tag{3}$$

TABLE 2

The values of X and Y for the pivotal strategy (for the asymptotic case with linear payoffs $U_x = x$) for various values of C and p

C	$p = 0.1$	$p = 0.2$	$p = 0.3$	$p = 0.4$	$p = 0.5$
0.1	0.944, 0.030	0.783, 0.284	0.720, 0.345	0.673, 0.379	0.636, 0.398
0.2	1, 0	0.913, 0.034	0.767, 0.190	0.699, 0.260	0.652, 0.296
0.3	1, 0	1, 0	0.854, 0.061	0.747, 0.153	0.678, 0.214
0.4	1, 0	1, 0	0.950, 0.006	0.797, 0.085	0.713, 0.147
0.5	1, 0	1, 0	1, 0	0.863, 0.034	0.747, 0.101

Theorem 2 is proved in Appendix B. If $p \leqslant C/(C+1)$ then $X = 1$ and $Y = 0$, i.e. no challenges take place.

For given C and p, we can arbitrarily choose the values of X and Y and thus solve eqn (1) for $h(x)$. Equations (2) and (3) now provide two conditions from which X and Y may be found. In general, there is only one initial pair (X, Y); $0 < Y \leqslant X \leqslant 1$ which generates identical values; these are the true values of X and Y. A curious feature of the numerical solutions is that $h(x)$ is always well-approximated by a linear function (Table 2).

4. Simple Strategy Simulations

In this section, we consider populations of strategies either from Type 1 or Type 3. In each case, $V_i = n - i + 1$. There were two different types of simulations:

(a) a single large area with many (1000) sites,

(b) many small areas, each with a few sites (1000 areas of 10 sites each).

4.1. A DISCUSSION OF SIMULATION (a)

C was chosen to be either 100 or 150, p to be 0.3 and each bird starts with a base capital (reserves) of 100. Initially, the population is made up of 100 players of each of ten different strategies (chosen randomly). These players are then ordered randomly and arrive at the area in that order, playing their strategy, until all players have arrived. The payoffs for the sites occupied and the costs accrued (making a negative contribution) are then added together for all the birds playing a given strategy, to give a total payoff for each strategy. The number of birds playing a strategy in the next round is proportional to that strategy's total payoff from the previous round (to the nearest whole number, and so that the total stays close to 1000). The process is repeated for successive rounds. If the mean payoff of birds playing a particular strategy is greater than the mean payoff of the population as a whole then the numbers playing that strategy will increase. If any of these payoffs becomes negative (or less than 0.5) then that strategy is eliminated and a new strategy is introduced at random with ten players; the overall number is adjusted to make the total 1000.

(i) To choose a random strategy of Type 1 or Type 3, we need to obtain a pair of integers I and J between 1 and 1000 inclusive, with $I < J$. To do this, two uniform random variables were chosen from (0, 1), multiplied by 1000, the integer part taken and increased by 1, then the larger of these was J and the smaller I. The possible number of strategies in this case is very large, of the order of 10^6. A new strategy appeared roughly once in every two generations, so that many generations are required to be reasonably certain that a particular strategy has entered the population at some point in time. It is, of course, not guaranteed that it will remain in the population even if it has occurred, because the level of introduction is low and its representatives may be assigned unfavourable positions in the queue. Hence, the population is unlikely to settle down quickly and indeed it was found that the mixture in the population continually changed.

(ii) To reduce the number of strategies, I and J were restricted so that they could only take values which were multiples of 100. This is perhaps more realistic than the previous example. Real birds would not count exactly how many other birds had arrived or know the exact quality of each site, but might be able to distinguish large differences. In some cases, this led to more obviously stable behaviour than in (i), with some strategies persisting for long periods of time.

Figure 1(a) shows the evolution of a population with $p = 0.3$, $C = 100$ and strategies of Type 1. The proportions of the population playing the most dominant strategies is shown; the plotted points being "running means of 1000" (i.e. the mean proportion from the last 1000 generations). A total of 100 000 generations are considered. There are four strategies which together make up most of the population. Generally, two or three of them are present in the population in large numbers at any particular time. At any time the most common strategy is usually (200, 600), but sometimes (200, 700), and one or both of (100, 700) and (300, 600) is also present. For clarity, the figure only shows three of these strategies [(200, 700) is excluded].

Figure 1(b) shows the same plot as Fig. 1(a), except that $C = 150$. There are again four common strategies with (200, 700) easily the most common, often making up 70% of the population. Generally, there is one other strategy which co-exists with this, namely one of (100, 700), (100, 800) or (300, 700). The strategy (100, 800) is omitted from the plot, again for clarity.

In both cases, although the actual mixture in the population changes the basic features remain the same. There is a mixture of values of I 100, 200 and 300, which resembles the pivotal strategy from the previous section. The value of J is less variable, sometimes almost all players have $J = 700$ in Fig. 1(b), but sometimes there is another value of J also present. The only type of strategy that can invade the pivotal strategy is one where J is larger and I smaller, or vice versa. This is precisely the type of strategies which occur in Fig 1(a) and (b) (larger I tend to be associated with smaller J). Thus, these figures provide evidence to support the hypothesis of a co-existing band of strategies close to the pivotal strategy.

Figure 1(c) shows the same plot as Fig. 1(a), except that the strategies are of Type 3 instead of Type 1. Now there is one common strategy (300, 500) which occurs with a wide range of other strategies. The mixture is very variable, with (300, 500) making up just under half the population, but no other strategies making a large contribution. The most significant other strategies are (200, 500) and (200, 600). When C is increased to 150 there is no persistent dominating

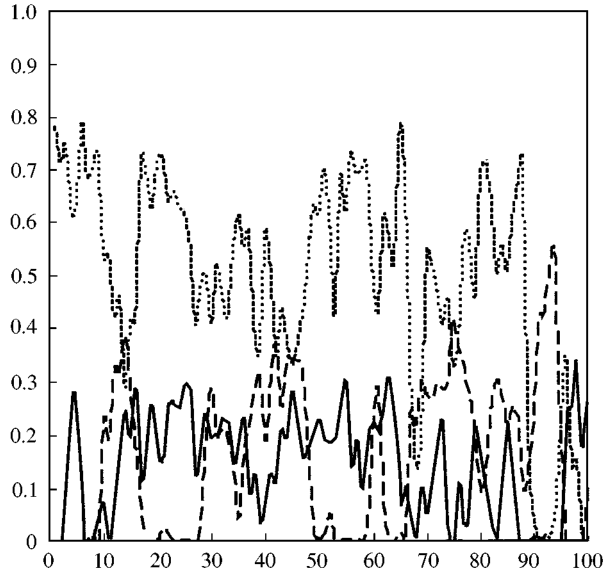

FIG. 1(a). Proportion of players of given strategies of Type 1, when $p = 0.3$, $C = 100$ plotted as running means of 1000 generations for a single large area of 1000 nest sites. —— (100, 700); – – – – (300, 600); · · · · · (200, 600).

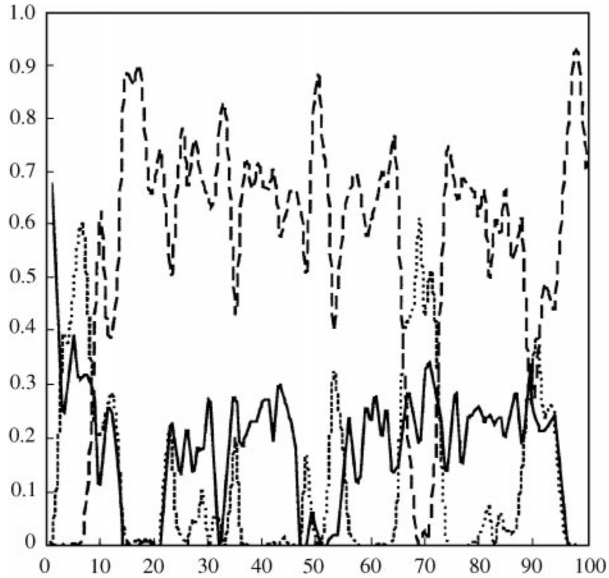

FIG. 1(b). Proportion of players of given strategies of Type 1, when $p = 0.3$, $C = 150$ plotted as running means of 1000 generations for a single large area of 1000 nest sites. —— (100, 700); – – – – (200, 700); · · · · · (300, 700).

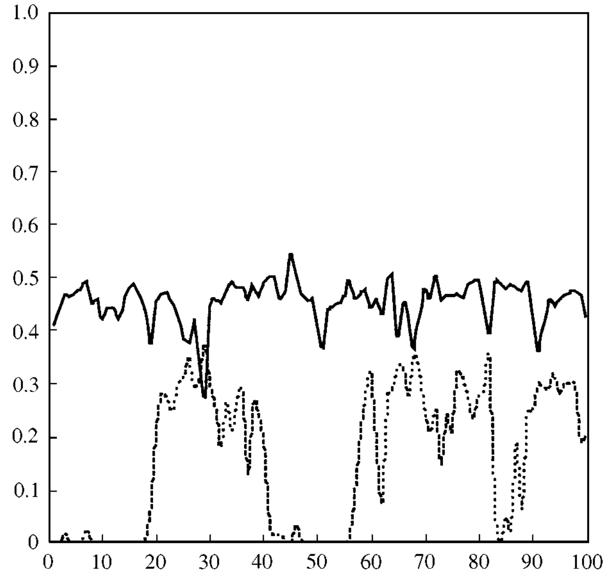

FIG. 1(c). Proportion of players of given strategies of Type 3, when $p = 0.3$, $C = 100$ plotted as running means of 1000 generations for a single large area of 1000 nest sites. —— (300, 500); · · · · · (200, 500); and (200, 600).

strategy or mixture of strategies. The most common overall strategy is (200, 500), which can dominate the population for a while, but then it is eliminated only to return and dominate the population again.

The existence of relatively stable strategy mixtures in Fig. 1(a) and (b) for Type 1 strategies is in contrast to Type 3 strategies [Fig. 1c]. Individuals start filling up the sites from I, so avoiding challenges with players of the same strategy. Thus, there is conflict between strategies with different values of I and there are no longer stable mixtures. In each case, there appears to be a clearly best strategy; however, if its numbers are reduced due to chance (since the population is small) it loses its advantage and can be removed from the population completely; this is especially true in the case when $C = 150$. Thus, in this case the dominant strategies do not resemble the pivotal strategy.

4.2. A DISCUSSION OF SIMULATION (b)

C was chosen to be either 1 or 1.5, p was again 0.3 and each bird had a base capital of 1. Note that if the values of the sites V_i, the cost C and the base pay-off are all multiplied by a constant the simulation results are identical. Multiplying by 100 gives site values 1000, 900, …, 100 over a similar range to simulation (a). The cost becomes 100 or 150 and the base pay-off becomes 100 exactly as in simulation (a). Thus, values of the parameters have been chosen to make the results from the two simulations comparable.

Strategies were chosen in a similar way to (a). One thousand different areas of ten birds were simulated and the total payoffs won by each strategy were collected together from all of the sites. The proportion of the total payoff won by each strategy again becomes the proportion of players of that strategy for the next generation. If any total payoff for a strategy is negative, then a new strategy is chosen randomly and introduced with 100 birds (a proportion 0.01 of the population) the numbers for the other strategies being adjusted to make 10 000 birds in total).

Figure 2(a) shows the evolution of a population with $p = 0.3$, $C = 1$ and strategies of Type 1. The proportion of the population playing the most dominant strategies is shown; the plotted points again being "running means of 1000" (i.e. the mean proportion from the last 1000 generations). A total of 100 000 generations are considered. Generally, there are three co-existing strategies: (2, 6) (the most common), (1, 7) and (3, 6). However, the population may lose either (1, 7) or (3, 6) temporarily.

In Fig. 2(b), C is now 1.5. For almost all of the time, there is a mixture of two strategies: (2, 7) (easily the most common) and one of (1, 7) and (1, 8). As for Fig 1(a) and (b), Fig 2(a) and (b) show a stable strategy mixture which resembles the pivotal strategy. The mixture is less variable, probably due to the increased population size (10 000 rather than 1000).

Figure 2(c) shows the same plot as Fig. 2(b), except that the strategies are of Type 3 not Type 1. The strategies (2, 5) and (2, 6) dominate the population. The frequencies are virtually equal, with no other strategy featuring to any significant extent. If C is increased to 1.5, the strategy (2, 5) completely dominates the population, always accounting for over 90% of the population.

The stable mixtures of Fig. 2(a) and (b) with differing values of I are replaced by single dominant I values, as in Fig. 1 but with two notable differences. Firstly, the dominant strategies are very stable; for Type 3 strategies, when $C = 1.5$

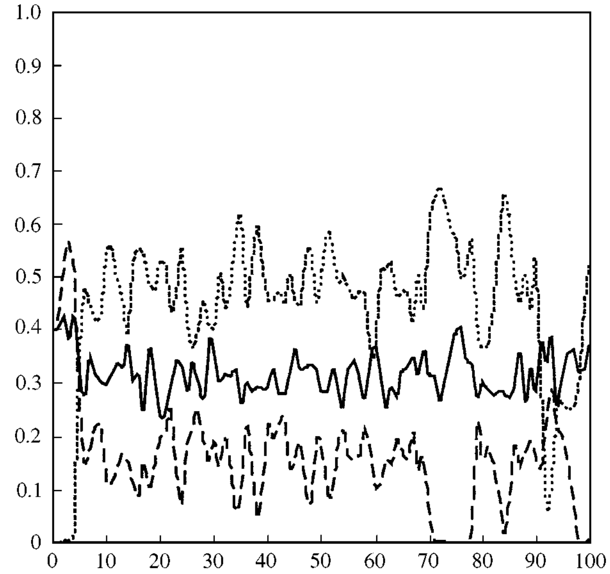

FIG. 2(a). Proportion of players of given strategies of Type 1, when $p = 0.3$, $C = 1$ plotted as running means of 1000 generations for a 1000 areas of ten nest sites. —— (1, 7); - - - - (3, 6); · · · · · (2, 6).

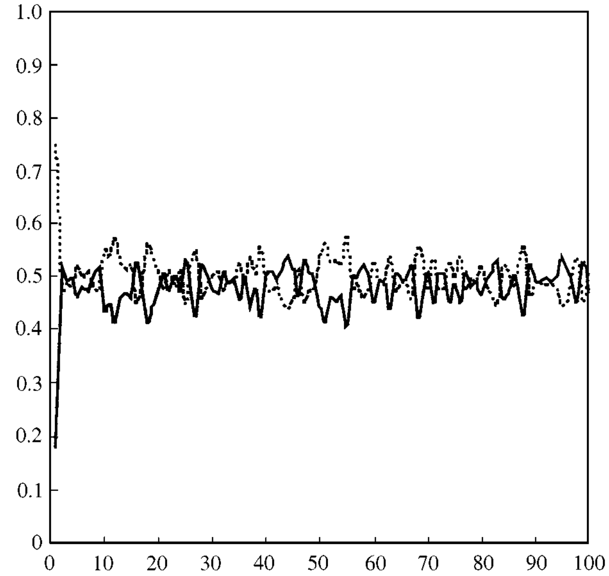

FIG. 2(c). Proportion of players of given strategies of Type 3, when $p = 0.3$, $C = 1.5$ plotted as running means of 1000 generations for a 1000 areas of ten nest sites. —— (2, 5); · · · · · (2, 6).

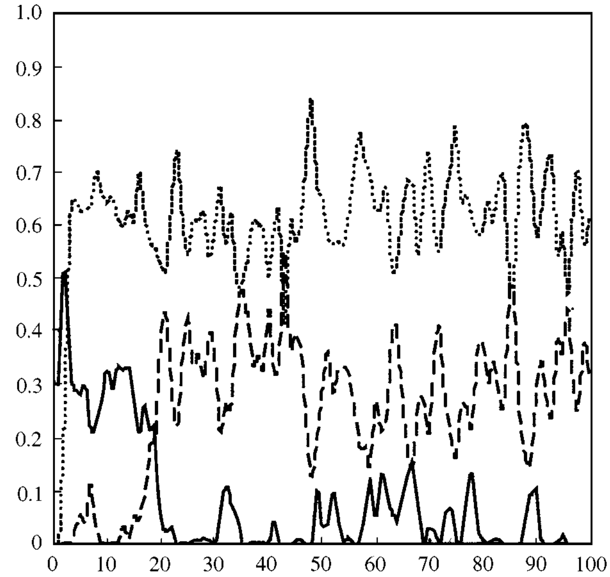

FIG. 2(b). Proportion of players of given strategies of Type 1, when $p = 0.3$, $C = 1.5$ plotted as running means of 1000 generations for a 1000 areas of ten nest sites. —— (1, 7); - - - - (1, 8); · · · · · (2, 7).

a single strategy completely dominates the population. Secondly, in Fig. 2(c) there is a mixture of two strategies with the same I but different J. This mixture is again stable, and it is presumed that the true "best" value of J lies between 5 and 6, thus allowing the strategies from either side to dominate the population.

4.3. A COMPARISON WITH OPTIMAL PLAY

In this paper, we have considered simple strategies which had some features in common with the optimal play from Broom *et al.* (1997a). However, do the best strategies from this restricted class resemble the optimal strategy numerically?

When the number of sites is 1000, $C = 100$, and $p = 0.3$, as in Fig. 1(a), the optimal value of J lies between 600 and 700. Thus, the mean overall payoff is 500.5 − 100 multiplied by the proportion of challenges, so is approximately $500.5 - 100 \times 350/1000 \approx 465$. The maximum value of I occurring regularly (and so the lowest site commonly challenged upon) was 300. Finding the optimal strategy with these parameters, the first bird to challenge is B_{588}, so that the number of challenges is 413, and so the mean expected payoff is 459.2. The lowest site challenged upon is S_{364}. Thus, there is a rough correspondence between our simplified case and the optimal one. The main difference appears to be that individuals are not challenging enough in the simplified case, and could thus be exploited by more aggressive players with more complex strategies.

Figure 2(a) shows that when the number of sites is ten, $C = 1$ and $p = 0.3$ then the most common value of J is 6. Thus, the mean overall payoff is $5.5 - 0.4 = 5.1$. The maximum value of I which commonly occurs is 3. For the optimal strategy, the first bird to challenge is B_7, thus there are four challenges and the mean payoff is 5.1. The lowest site to be challenged upon is S_3. Thus, there is a strong resemblance between the two strategies.

5. Discussion

Severinghaus (1996) studied the behaviour of Brown Shrike *Lanius cristatus* arriving at a breeding ground. The locations of the territories of early arrivals tended to be scattered throughout the study area, and later birds filled the gaps between them. The sizes of territories varied greatly amongst birds; although early occupied territories were not generally larger, they may have been in preferred locations. Initially, there was little aggression between birds, but as the breeding ground filled up this aggression increased and some territory owners had to defend their territories several times. This agrees with our general predictions of the first birds occupying good sites, and later birds challenging for a site when only poor sites remain free, and in particular closely approximates the threshold phenomenon found in Broom *et al.* (1997a). It was also noticed that prior residence granted the defender an advantage in any contest, again as in our model. Note that the behaviour of birds in this case was complicated by a large number of "transient" birds who stopped at the site only briefly, before continuing on to other sites. This introduced "wait and see" strategies, where a bird would choose an inferior site temporarily, and wait for a transient bird on a superior site to leave, and then occupy the newly vacant site.

In Broom *et al.* (1997a), we found the optimal site-choice strategy for a group of birds arriving sequentially at a nesting area. This turned out to be complicated, but did possess some important features which were simple, for instance the threshold phenomenon. It is unreasonable to assume that real birds will be able to evaluate very complicated (and parameter-sensitive) strategies, and so in this paper we have introduced strategies which possess the important features of Broom *et al.* (1997a) without their complexity.

When birds which do not challenge always occupy the best free site, simulations (Figs 1(a), (b), 2(a), (b)) show a population fluctuating around an equilibrium, which we refer to as the pivotal strategy. By comparing the values of the parameters I and J obtained to the theoretical results from Broom *et al.* (1997a), we notice that the simple strategy is a good approximation to the optimal strategy. If birds are allowed to choose a free site other than the best (particularly the best that birds playing the same strategy would never challenge upon), then the resemblance to the pivotal strategy is no longer in evidence. There is either little structure as for simulations of type (a), or there is a highly stable strategy or mixture of strategies as for simulations of type (b).

The results of our previous work (Broom *et al.* 1997a) were rather daunting in that it concluded that the best strategy was extremely complicated. It is quite unreasonable to believe that any organism (including human) could calculate it. But here we see that quite simple rules can produce behaviour which effectively mimics the best strategy. We suggest that this might be a common feature of evolution: life is complex and situations can change without warning; do not try to solve the full problem, but find simple robust rules which work well most of the time.

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Appendix A

Proof of Theorem 1

Suppose that almost all players in the population play $(f; X; Y)$. Consider a bird playing this strategy which arrives at time $1 - z$, so that the best free site is site z. The expected payoff to it is $\phi_1(z)$ where

$$\phi_1(z) = \begin{cases} W_{z,1-z} = W_{z,1-Y} & (X < z < 1), \\ W_{z,1-z} = U_z & (Y < z < X), \\ (1-p)(U_z - C) + p\displaystyle\int_X^1 f(x) W_{x,1-z}\,\mathrm{d}x & (0 < z < Y). \end{cases}$$

Note that when $X < z < 1$, the site a bird occupies will be subject to challenges later. However, these only occur when an incoming bird finds the best free site to be of low value, that is when $z < Y$. Thus, no challenges occur before time $1 - Y$ and the expected payoff to the occupier is not affected until this time, i.e. $W_{z,1-z} = W_{z,1-Y}$.

Thus, the expected payoff to a bird playing $(f; X; Y)$ is

$$\phi_1 = \int_X^1 W_{z,1-Y}\,\mathrm{d}z + \int_Y^X U_z\,\mathrm{d}z + (1-p)\int_0^Y (U_z - C)\,\mathrm{d}z + p\int_0^Y\int_X^1 f(x) W_{x,1-z}\,\mathrm{d}x\,\mathrm{d}z.$$

Now, consider a bird playing $(g; X^*; Y^*)$ in a population playing $(f; X; Y)$. If $(g; X^*; Y^*)$ is only a single mutation away from $(f; X; Y)$ then either $X^* = X$ or $Y^* = Y$ and so $Y^* < X$. The expected payoff to it is thus $\phi_2(z)$ where

$$\phi_2(z) = \begin{cases} W_{z,1-z} = W_{z,1-Y} & (X < z < 1), \\ W_{z,1-z} = U_z & (Y^* < z < X), \\ (1-p)(U_z - C) + p\displaystyle\int_{X^*}^1 g(x) W_{x,1-z}\,\mathrm{d}x & (0 < z < Y^*). \end{cases}$$

Thus, the expected payoff to a bird playing $(g$: X^*; $Y^*)$ is

$$\phi_2 = \int_X^1 W_{z,1-Y}\,\mathrm{d}z + \int_{Y^*}^X U_z\,\mathrm{d}z + (1-p)\int_0^{Y^*} (U_z - C)\,\mathrm{d}z + p\int_0^{Y^*}\int_{X^*}^1 g(x) W_{x,1-z}\,\mathrm{d}x\,\mathrm{d}z.$$

The difference between the payoffs is therefore

$$\phi_1 - \phi_2 = \int_Y^{Y^*} U_z\,\mathrm{d}z + (1-p)\int_{Y^*}^Y (U_z - C)\,\mathrm{d}z + p\int_0^Y\int_X^1 f(x)\,W_{x,1-z}\,\mathrm{d}x\,\mathrm{d}z - p\int_0^{Y^*}\int_{X^*}^1 g(x)\,W_{x,1-z}\,\mathrm{d}x\,\mathrm{d}z. \qquad (\text{A.1})$$

To prevent the new strategy from invading the population, the above expression must be positive.

Firstly, we suppose that $f(x) = g(x)$ for all x, and thus $X = X^*$. Here eqn (A.1) reduces to

$$\phi_1 - \phi_2 = \int_Y^{Y^*} \left(U_z - (1-p)(U_z - C) - p \int_X^1 f(x)\, W_{x,1-z}\, \mathrm{d}x \right) \mathrm{d}z.$$

This needs to be positive for values of Y^* slightly greater than Y, and also for values of Y^* slightly less than Y. Both $f(x)$ and $W_{x,t}$ are continuous, and so the bracketed term is continuous and thus must be equal to zero when $z = Y$. Thus, to prevent strategies of the type $(f;\, X;\, Y^*)$ invading we require

$$U_Y + \frac{1-p}{p} C = \int_X^1 f(x)\, W_{x,1-Y}\, \mathrm{d}x. \quad \text{(A.2)}$$

To prove that this is sufficient, all we need to show is that

$$pU_z + (1-p)C - p \int_X^1 f(x) W_{x,1-z}\, \mathrm{d}x$$

is an increasing function of z. This is clearly true, since U_z is an increasing function of z, and $W_{x,1-z}$ is the expected future payoff to a bird at the site with value x after time $1 - z$, and all expected future payoffs are non-decreasing with time (there are less birds to challenge on the site) and thus non-increasing with z.

Now, suppose that $Y^* = Y$. Letting $X_m = \min(X, X^*)$, eqn (A.1) reduces to

$$\begin{aligned}\phi_1 - \phi_2 &= p \int_0^{Y^*} \int_{X_m}^1 (f(x) - g(x)) W_{x,1-z}\, \mathrm{d}x\, \mathrm{d}z \\ &= p \int_{X_m}^1 (f(x) - g(x)) \left(\int_0^Y W_{x,1-z}\, \mathrm{d}z \right) \mathrm{d}x.\end{aligned}$$

This must be nonnegative for arbitrary values of $f(x) - g(x)$, the only restrictions being that the function has an integral of zero and is non-positive for $x < X$. Thus, we require

$$\int_0^Y W_{x,1-z}\, \mathrm{d}z$$

to be constant for $X < x < 1$ and to take a value less than or equal to that constant for all other values of x. It is clear from considering the value of this function when $x = X$ [see condition (A.4)] that

$$\int_0^Y W_{x,1-z}\, \mathrm{d}z = YU_X. \quad \text{(A.3)}$$

Here we have only shown that no invading strategy can have a larger payoff than a strategy that fulfils this condition. To prevent invasion, we need to show that an invader does worse when it is played by a non-zero but small proportion of the population.

If a small proportion now play $(g;\, X^*;\, Y)$, then the number of challenges upon values of x for which $g(x) > f(x)$ increases and so its expected future payoff decreases. But since $g(x) > f(x)$, the occupier of these devalued sites is more likely to be an invader than the proportion of the population that are invaders implies. Similarly, the number of challenges upon values of x for which $g(x) < f(x)$ decreases and so its expected future payoff increases. Since $g(x) > f(x)$, the occupier of these sites is more likely to be a $(f;\, X;\, Y)$ player than would be expected through choosing a random player. Thus, the payoff to the $(g;\, X^*;\, Y)$ players is less than that of the $(f;\, X;\, Y)$ players, and so they cannot invade the population.

Under the assumption of continuity of $f(x)$, we know that

$$f(X) = 0 \quad \text{(A.4)}$$

[in fact, if the assumption of continuity of $f(x)$ was made only for $x \in (X, 1]$, it is fairly straightforward to prove that this is true]. Thus, any strategy which satisfies eqns (A.2–A.4) cannot be invaded by another strategy which is a single mutation away.

That for every game defined by C, p, U_x there is exactly one such strategy can be seen from the following argument.

It is clear that for any $x > X$ if $f(x) = 0$ then $W_{x,1-Y} \geqslant U_X$ and for sufficiently large $f(x)$, $W_{x,1-Y} < U_X$. Thus, by allowing $f(x)$ to vary, and not imposing the restriction that $f(x)$ integrates to unity, for given values of Y and X there is a unique function $f(x)$ which solves eqns (A.3) and (A.4).

For a given Y, there will be exactly one value of X which generates an $f(x)$ with an integral of unity. Clearly, when $Y \to 0$ (nobody challenges) the value of X for which eqn (A.3) is satisfied approaches one. Further notice that if Y increases and the value of X does not decrease, then since the value of $W_{x,1-y}$ decreases with y, the value of $f(x)$ must decrease. But this is true for all x, so that $f(x)$ would no longer integrate to unity. Thus, if Y increases, X must decrease.

Note that this argument breaks down for Y sufficiently close to 1, when the corresponding X would be less than Y. However, since we know that

$$U_Y + \frac{1-p}{p} C = \int_X^1 f(x) W_{x,1-Y}\,\mathrm{d}x < U_X,$$

i.e. the value of Y which solves eqn (A.2) must be less than X, such cases are of no interest. In fact, it can be seen that since the solution to eqns (A.3) and (A.4) has the value of X decreasing with Y, and that there is a solution $X = 1$, $Y = 0$, there will be a unique solution which also solves eqn (A.2), and thus a unique pivotal strategy.

The pivotal strategy, however, is not an ESS. Equation (A.2) implies that every player playing a strategy $(g; X^*; Y)$ performs identically within a population of $(f; X; Y)$ players. Suppose, however, that a new strategy plays $Y^* = Y + \varepsilon$, for small positive ε. Then, on average, it does not matter what g is chosen for the birds arriving after time $1 - Y$. However, those arriving between times $1 - Y^*$ and $1 - Y$ will face a situation in which it is better to challenge on a site near X rather than 1 (the value to an occupier of all these sites is on average equal and the sites near 1 get better relative to those near X as we get nearer to the last arrival). Thus, a g which is larger than f for x near X in conjunction with $Y^* > Y$ can invade. Similarly, if ε is negative a g can be chosen which is larger than f when x is near unity, such that $(g; X; Y^*)$ can invade. □

Appendix B

Proof of Theorem 2

The intrinsic value of S_x is $U_x = x$ and the density function of challenges is $f(x)$. To satisfy condition (A.2) it is required that the payoff to B_{1-Y} is the same whether the bird challenges or not. If there is no challenge the payoff is just $U_Y = Y$. If there is a challenge then the expected payoff is

$$p \int_X^1 f(x) W_{x,1-Y}\,\mathrm{d}x + (1-p)(Y - C),$$

which implies that

$$\int_X^1 f(x) W_{x,1-Y}\,\mathrm{d}x = \frac{1-p}{p} C + Y.$$

The value on the left-hand side of this equation cannot exceed unity. Thus, the values of p and C must satisfy

$$\frac{(1-p)}{p} C < 1 \quad \text{or} \quad p > \frac{C}{1+C}.$$

If this inequality is not satisfied then the cost of injury is so large that no challenges take place.

Let $P_t(x)$ be the probability that a bird occupies S_x at time t given that it occupies it at time $1 - Y$. Thus, $P_{1-Y}(x) = 1$ and

$$\frac{\partial}{\partial y} P_t(x) = -f(x) p P_t(x)$$

$$\Rightarrow P_t(x) = \mathrm{e}^{-f(x)p(Y-1+t)} \Rightarrow P_1(x) = \mathrm{e}^{-f(x)pY}.$$

It follows that

$$W_{x,1-Y} = x\mathrm{e}^{-pf(x)Y} + \int_{1-Y}^1 (1 - t - C)\mathrm{e}^{-f(x)p(Y-1+t)} f(x) p\,\mathrm{d}t$$

and setting $y = 1 - t$ gives

$$W_{x,1-Y} = x\mathrm{e}^{-pf(x)Y} + \int_0^Y (y - C)\mathrm{e}^{-f(x)p(Y-y)} f(x)\, p\,\mathrm{d}y.$$

The first term is the payoff for holding S_x multiplied by the probability of doing so, the second term combines all the possible sites which the bird could be displaced to, integrating the product of the payoff at S_y minus the cost, the probability of still holding S_x at time y and the probability density of being successfully challenged at y. Thus,

$$W_{x,1-Y} = x\mathrm{e}^{-h(x)} - C(1-\mathrm{e}^{-h(x)}) + Y\left(1-\frac{1-\mathrm{e}^{-h(x)}}{h(x)}\right)$$

$$\Rightarrow \int_X^1 f(x)\left(x\mathrm{e}^{-h(x)} - C(1-\mathrm{e}^{-h(x)}) + Y\left(1-\frac{1-\mathrm{e}^{-h(x)}}{h(x)}\right)\right)\mathrm{d}x = Y + C\frac{1-p}{p}.$$

Multiplying both sides by pY and rearranging gives the following:

$$\int_X^1 (h(x)x\mathrm{e}^{-h(x)} + Ch(x)\mathrm{e}^{-h(x)} - Y[1-\mathrm{e}^{-h(x)}])\,\mathrm{d}x = YC$$

$$\Rightarrow \int_X^1 \left(\frac{x+C}{Y}h(x)\mathrm{e}^{-h(x)} - 1 + \mathrm{e}^{-h(x)}\right)\mathrm{d}x = C.$$

This is eqn (2).

The expected payoff to a challenger on S_x at time $1 - y > 1 - Y$ is

$$p\left(x\mathrm{e}^{-pf(x)y} + \int_0^y (z-C)\mathrm{e}^{-f(x)p(y-z)}f(x)p\,\mathrm{d}z\right) + (1-p)(y-C)$$

using similar reasoning as above. Thus, the expected payoff to a random player arriving from time $1 - Y$ to 1 conditional on that player challenging upon x [let this be $E(x)$] is just the integral of this w.r.t. y over Y to 1, divided by Y. This gives us

$$E(x) = (1-p)\left(\frac{Y}{2}-C\right) - \frac{px}{Y}\left[\frac{\mathrm{e}^{-f(x)py}}{f(x)p}\right]_0^Y + \frac{p}{Y}\int_0^Y\left(\left[(z-C)\mathrm{e}^{-f(x)p(y-z)}\right]_0^y - \int_0^y \mathrm{e}^{-f(x)p(y-z)}\,\mathrm{d}z\right)\mathrm{d}y$$

$$= (1-p)\left(\frac{Y}{2}-C\right) + px\frac{1-\mathrm{e}^{-h(x)}}{h(x)} - Cp\left(1-\frac{1-\mathrm{e}^{-h(x)}}{h(x)}\right) + p\frac{Y}{2} - p\frac{Y}{h(x)} + Yp\frac{1 \div e^{-h(x)}}{[h(x)]^2}.$$

As $x \to X$, $h(x) \to 0$, so that for condition (A.3) to hold we require the above expression to be equal to $(1-p)(Y/2 - C) + pX$, the mean payoff for a challenger at X (there is probability 0 of being displaced by another bird), thus

$$\frac{1-\mathrm{e}^{-h(x)}}{h(x)}\left(x + C + \frac{Y}{h(x)}\right) = \frac{Y}{h(x)} - \frac{Y}{2} + X + C$$

which rearranges to give eqn (1).

In addition to the above we require that

$$\int_X^1 f(x)\,\mathrm{d}x = 1 \Rightarrow \frac{1}{pY}\int_X^1 h(x)\,\mathrm{d}x = 1$$

which gives eqn (3) and so Theorem 2 is proved. □