

Optimal Floating and Queuing Strategies: The Logic of Territory Choice

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ABSTRACT: This is a response to a recent article by Hanna Kokko and William J. Sutherland (*American Naturalist* 152:354–366), who consider evolutionarily stable territory acceptance rules for animals that face the decision between settling on a poor territory now (which is then retained for life) or waiting for better habitat to become available later (taking a chance of dying before reproducing). In contrast to these authors, we argue that the evolutionarily stable threshold quality above which territories are acceptable does depend on whether individuals compete for a single territory (queuing) or for multiple territories (floating) and also on whether access to territories is determined by a hierarchy among waiting individuals. More specifically, we show the following: First, if the choice is between floating and settling, the evolutionarily stable acceptance threshold is such that threshold territories yield an expected lifetime reproductive success (LRS) of $1 - \mu_F$, the survival probability of a floater. Second, if the choice is between queuing and settling, the evolutionarily stable threshold may correspond to any LRS between $1 - \mu_F$ and unity. Third, the number of nonbreeding individuals in the population is maximized at a threshold of unity. In other words, the evolutionarily stable threshold does not maximize the nonbreeding fraction of the population. We argue that models of territory choice should carefully specify the mechanism of choice because some choice processes (e.g., indiscriminate habitat use above the threshold) do not admit an evolutionarily stable acceptance rule.

Keywords: territory acquisition, floating, queuing, small habitat selection, seasonality, evolutionarily stable strategy.

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Kokko and Sutherland (1998) recently presented a theory of strategic territory choice by animals. The theory concerns animals that face the dilemma whether to occupy a poor territory now, which is then retained for life, or to keep waiting for better habitat to become available later, taking a chance of dying in the meantime (Ens et al. 1992, 1995; Zack and Stutchbury 1992). The basic question is, What is the minimal acceptable territory quality or acceptance threshold favored by natural selection? More specifically, Kokko and Sutherland investigated how the evolutionarily stable or optimal acceptance threshold depends on two factors. The first factor concerns the number of territories a waiting individual can simultaneously compete for. “Floaters” compete for many territories simultaneously, while “queuers” (Ens et al. 1995) focus on just one or a few territories. The second factor is the dominance hierarchy among waiting individuals, the correlation between the order of joining the floaters or a queue and priority in gaining access to a territory.

Under the assumption that the population in question is stationary, Kokko and Sutherland report the following results. First, if the individuals have to decide between settling and floating, they should accept territories yielding an expected lifetime reproductive success (LRS) above unity and reject territories yielding an LRS below unity. Second, the same evolutionarily stable strategy (ESS) is obtained when the individuals have to choose between settling and queuing. Third, the common ESS threshold value of unity has the property that, for this value, the number of nonbreeding individuals in the population is maximized.

In other words, the ESS is robust, and it maximizes the “buffer of surplus individuals.” From this, Kokko and Sutherland draw some general conclusions regarding density dependence and the consequences of habitat loss.

Although we regard Kokko and Sutherland’s article as an important step toward a general theory of optimal territory choice, we are not convinced by their modeling approach and by the derivation of their main results. In particular, Kokko and Sutherland’s modeling approach allows only the simplest of choice processes to be imple-

mented, namely indiscriminate habitat use above the acceptance threshold. As Kokko and Sutherland themselves point out, such behavior can be considered unstable if individuals can seek the best available territory (ideal habitat selection). Yet in Kokko and Sutherland's model, there is no room for ideal habitat selection; hence, there are no grounds for their claim that, for such a choice process, the optimal acceptance threshold equals unity. Kokko and Sutherland's model allows only indiscriminate habitat use because they model population dynamics in continuous time without a seasonal time structure. In essence, only one territory becomes available at a time, floaters can never choose between more than one territory, and, upon acceptance of the territory, owners start reproducing immediately. This is mathematically convenient but biologically not very realistic. In fact, all empirical examples discussed by Kokko and Sutherland concern vertebrates that live in seasonal environments. Furthermore, in the derivation of their main results, Kokko and Sutherland do not account for the variation in LRS caused by the discreteness of a queue.

As a consequence, two of Kokko and Sutherland's results are incorrect or at least misleading. By means of a slightly modified discrete time model, which makes the timing of events and the process of territory choice more transparent, we show the following: First, if individuals have to decide between settling and floating, the optimal acceptance threshold is below unity (it corresponds to an LRS of $1 - \mu_F$, the survival probability of a floater). Second, if individuals have to decide between settling and queuing, in general neither $1 - \mu_F$ nor unity is an ESS (depending on the model parameters, the ESS threshold can be any threshold between $1 - \mu_F$ and unity). Third, the number of nonbreeding individuals is maximized at a threshold of unity.

In other words, the ESS depends on the options of nonbreeders, and it has no obvious relation with the size of the nonbreeding fraction of the population. Accordingly, it would be premature to draw general conclusions for conservation biology.

Assumptions

We now give a list of the main assumptions underlying our analysis, in addition to the standard assumptions of an ESS analysis (e.g., Taylor 1996).

First, there is a large number of territories, differing in quality. Animals can perfectly assess territory quality, which is continuously distributed, according to a probability density that is independent of population size. Production of offspring and mortality of territory owners may vary with territory quality as long as fitness increases with

quality. Kokko and Sutherland's assumption of quality-independent mortality is a special case.

Second, individuals are either floating, queuing, or in possession of a territory. Apart from these state variables and territory quality, there is no other nonrandom source of variation in mortality, competitive ability, or reproductive performance.

Third, switching between territories of different qualities is not allowed. In essence, territories are kept for life.

Fourth, the population is stationary. Expected lifetime reproductive success (LRS) is then a valid fitness measure (Mylius and Diekmann 1995). However, the results below are easily generalized to nonstationary populations by replacing LRS with reproductive value (Fisher 1930; Frank 1998).

Fifth, each individual has an acceptance threshold x such that the individual accepts no territories or joins queues yielding less than $LRS(x)$.

Sixth, in contrast to Kokko and Sutherland, we let breeding occur in periodic discrete time intervals, the period referred to as seasons or years. For our purposes, it is convenient to think of a season as consisting of two parts, a relatively short breeding season in which all reproduction takes place followed by a nonbreeding season in which most of the mortality and competition for territories takes place. The onset of the breeding season will be used as the (arbitrary) time of census; that is, unless stated otherwise, survival means survival from the onset of one breeding season to the onset of the next breeding season. In particular, LRS refers to the expected lifetime production of offspring that survive until the onset of the first breeding season after their birth. The minimum age of first breeding is one season after birth.

Free Floating

In this section we analyze how natural selection affects territory choice in populations with free floaters. Every floater is assumed to compete for all territories simultaneously, and all floaters are equally likely to obtain a given territory that becomes vacant. We first explain verbally why we think floaters should be happy with some territories having an expected LRS smaller than unity. We then verify this by a more rigorous analysis.

Verbal Arguments

Following the standard ESS approach, we consider a population in which all individuals have the same acceptance threshold x^* . To be evolutionarily stable, x^* must be such that the reproductive value of a floater equals the reproductive value of an individual at a threshold quality territory. For if this were not so, either the threshold territory

owner has a higher reproductive value and the floater would benefit from choosing a territory with quality x just below x^* , or the floater has a higher reproductive value and the threshold territory owner would benefit from abandoning its territory and becoming a floater. In a stationary population, surviving offspring have an average LRS of unity. Some surviving offspring become territory owners in their first season; the rest become floaters. Since floaters must have a lower LRS than the offspring that find a suitable territory, the LRS of floaters must be less than unity. But at an ESS, the LRS of threshold territory owners equals that of floaters, hence the LRS of threshold territory owners is also less than unity, in contrast to Kokko and Sutherland's result that $LRS(x^*)$ should be unity.

More precisely, at an ESS, the LRS of floaters and owners of threshold quality territories equals $1 - \mu_F$, where μ_F denotes the yearly mortality of a floater. This can be seen as follows: consider an individual that decides not to breed in the current season. With probability μ_F , such an individual will die and obtain an LRS of 0. With probability $1 - \mu_F$, it will survive and obtain an LRS of unity because, in a stationary population, this is the expected LRS of all individuals entering the population (e.g., surviving offspring). Hence, the expected LRS of an individual that decides to postpone breeding is $\mu_F \times 0 + (1 - \mu_F) \times 1 = 1 - \mu_F$. At the ESS, the LRS of a threshold territory owner must therefore also equal $1 - \mu_F$.

Why do Kokko and Sutherland reach a different conclusion? They make a crucial assumption in their appendix A, in the last paragraph before equation (A1). There it is assumed that mutants with a threshold value $x < x^*$ only breed on territories of quality $x \leq q < x^*$ but never on territories with quality $\geq x^*$. Clearly, if $LRS(x^*) = 1$, one has $LRS(q) < 1$, hence such mutants cannot increase in frequency. Is this a reasonable assumption? In our opinion, there is no general reason to assume that a mutant with threshold $x < x^*$ has no chance to find a territory with quality $\geq x^*$. It is more plausible to assume that such a mutant first competes with the residents for territories with quality $\geq x^*$ and, only if it fails, settles for territories with quality $x \leq q < x^*$. As shown below, such mutants can invade any population with threshold x^* such that $LRS(x^*) > 1 - \mu_F$.

Biologically, Kokko and Sutherland's assumption is equivalent to a choice process of indiscriminate habitat use above the acceptance threshold. Kokko and Sutherland themselves claim that such behavior can be considered unstable if an animal can seek the best territory available (ideal habitat selection). Since Kokko and Sutherland's model does not allow for ideal habitat selection, their claim that under such a choice process the optimal acceptance threshold equals unity is unsubstantiated.

Analytical Results

In appendix A, we present a detailed analysis of an ESS model identical to Kokko and Sutherland's model, with two modifications. First, breeding occurs in discrete time intervals instead of continuously, and second, we allow mortality of territory owners to depend on the quality of their territory. Here we list the main results of the analysis.

Contrary to Kokko and Sutherland, we have the following result:

Result 1. In a stationary population with free floating, the LRS of an individual breeding in a territory with ESS threshold quality x^* equals the LRS of a floater: $LRS(x^*) = LRS_F = 1 - \mu_F$.

In agreement with Kokko and Sutherland, we have the following result:

Result 2. In a stationary population with acceptance threshold x^* , in order for the number of floaters to be maximized, it is required that the LRS of individuals breeding in a territory of threshold quality equals unity; that is, $LRS(x^*) = 1$.

In view of result 1, result 2 shows that, contrary to Kokko and Sutherland's result, floater population size is not maximized in a population at the ESS threshold.

Simulation Results

In order to check the analytical results, we have carried out some individual-based computer simulations. Each individual was represented by a single haploid gene locus coding for an acceptance threshold. In general, offspring inherit the acceptance threshold of their parent, but with a small probability, ν , the threshold mutated to a slightly lower or higher value. A total of 1,000 territories were present, with LRS uniformly distributed in the range [0, 5]. After a round of mortality of breeders and floaters, free territories were selected in a certain order (see below), and for each free territory, floaters were drawn in random order until one was found, if at all, with an acceptance threshold at least as low as the quality of the territory. We used two different methods of selecting free territories, reflecting different interpretations of a one-dimensional acceptance threshold. In scenario 1, which is in line with our interpretation, territories were selected starting with the best and ending with the worst, based on the idea that threshold quality territories are only acceptable at the end of the "choosing season." Scenario 2, selecting free territories in random order, is closer to Kokko and Sutherland's

implicit assumption that floaters accept threshold quality territories at any time of the season.

Figure 1 shows representative examples of simulation runs carried out according to both methods of selecting free territories. The mortality rate of floaters was set at 0.4. At the start of the simulations, all individuals had the same acceptance threshold of unity. In line with our result 1, when free territories are drawn from best to worst, the acceptance threshold evolves to an average value close to 0.6, the survival probability of floaters. On the other hand, when territories are selected at random, there exists no stable acceptance threshold, but instead, a broad range of acceptance thresholds coexists. This shows that the details of the choice process are crucial for selection on a one-dimensional acceptance threshold.

Strict Queuing

In contrast to floaters, who compete for all territories simultaneously, queuers focus on just one or at most a few territories. In this section, we restrict our attention to populations where queues have a strict hierarchy, such that the longest-waiting queuer inherits the territory with certainty. Following Kokko and Sutherland, we say that an individual has a threshold strategy x if it joins queues or accepts empty territories only if these yield an expected

LRS of at least $LRS(x)$. If no such queue or empty territory is available, then the individual stays floating.

Kokko and Sutherland derive two results for stationary populations with strict queuing: first, a threshold of unity is the highest threshold such that no floaters are produced, and second, the ESS threshold equals unity. Therefore, according to Kokko and Sutherland, populations with strict queuing have the same optimal acceptance threshold as populations with free floating.

Verbal Arguments

Before we explain why we disagree, let us summarize the gist of Kokko and Sutherland's argument: in a population with queuing, queue lengths will tend toward an equilibrium where it does not pay to move from one queue to another. Territories differ in quality, but since the queues are longest for the most profitable territories, all offspring have, at the moment of joining a queue, the same expected LRS, namely $LRS(x)$, where x is the acceptance threshold. In a stationary population, $LRS(x)$ has to be larger than or equal to unity. A value above unity cannot be evolutionarily stable since, in this case, floaters would be produced and settling in a territory yielding an LRS of unity is obviously a better option than floating. For $LRS(x) = 1$, an individual joining a queue produces on average just

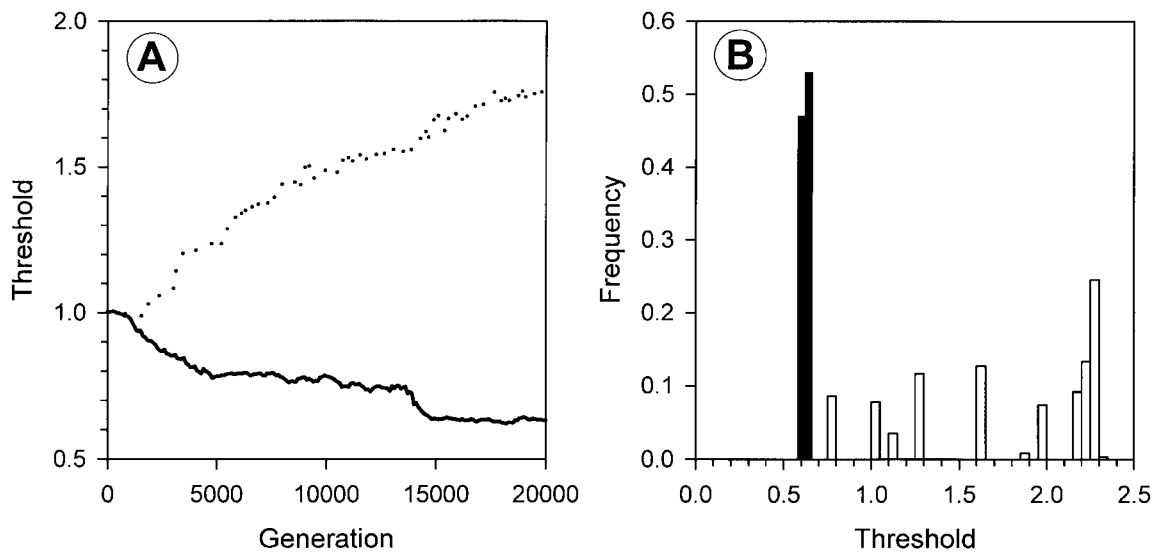


Figure 1: Representative simulation examples of the evolution of acceptance thresholds. *A*, Evolutionary trajectories of the average acceptance threshold. *B*, Acceptance threshold allele distributions after 20,000 generations. Two scenarios are depicted. In scenario 1 (*solid line and dark bars*), individuals compete for the best available territory with quality above their individual threshold. In scenario 2 (*dotted line and light bars*), individuals accept any random territory with quality above their individual threshold. For scenario 1, the population evolves toward a monomorphic state, corresponding to an acceptance threshold close to 0.6, the survival probability of floaters. For scenario 2, the population evolves to a highly polymorphic state where a broad range of acceptance thresholds coexist. Parameter values: mortality rate $\mu_F = 0.4$; mutation rate $\nu = 0.001$ per offspring per generation; mutational changes drawn from $[-0.01, 0.01]$.

enough offspring to replace itself. Hence, no floaters are produced.

Although quite plausible, these arguments are not valid because, even in equilibrium, it is not true that all surviving offspring have the same expected LRS when they join a queue. The problem is that queuing inevitably leads to significant variation in expected, not merely in realized, LRS between offspring. One reason for this variation is the discreteness of queue lengths. Suppose that LRS at the territories is continuously distributed. Then, irrespective of what the ESS is, the acceptable territories can be arranged into nonoverlapping intervals

$$[LRS_0, LRS_1), [LRS_1, LRS_2), \dots, \quad (1)$$

where $[LRS_i, LRS_{i+1})$ correspond to those territories that have a queue length of i . Hence there is a whole spectrum of territory qualities with the same queue length, and it is obvious that an individual joining the queue for a territory with $LRS = LRS_i$ has a lower LRS than an individual joining a queue yielding $LRS = LRS_i + \epsilon < LRS_{i+1}$.

Why is this variation in expected LRS important? Suppose that an acceptance threshold of unity is established in the population. Then unity is the worst possible LRS at the moment of joining a queue. Since individuals joining a queue vary in their expected LRS, the average expected LRS of individuals joining a queue is larger than unity. In other words, queuing individuals produce on average more offspring than necessary to replace themselves, and the supernumerary offspring will have to become floaters. This shows that the first claim of Kokko and Sutherland is not correct: floaters are still produced at a threshold of unity. Moreover, these floaters should accept any empty territory yielding an expected LRS higher than $1 - \mu_F$, the expected LRS of a floater. It is therefore obvious that the second claim of Kokko and Sutherland is also not correct: an acceptance threshold of unity is too strict since a population with a threshold of unity could be invaded by slightly less choosy mutants. Hence, variation in expected LRS among queuers leads us to conclude that the ESS acceptance threshold should be lower than unity and, in fact, somewhere between $1 - \mu_F$ and unity. We will show later that, depending on the model parameters, any value between $1 - \mu_F$ and unity can be realized as an ESS acceptance threshold.

These general arguments show that, in a queuing system, variation in expected LRS among offspring is inevitable and that this variation may have important evolutionary implications. There are three major determinants of variation in expected LRS. First, there is discreteness. As argued above, the discreteness of queue lengths will always induce variation in expected LRS, even in continuous time (the scenario considered by Kokko and Sutherland).

Discreteness of seasons further increases the variation in expected LRS. Because more than one individual per queue may die in a given season, more than one offspring may join the same queue. When queues are strict, one of the offspring ends up lower in the hierarchy. The third determinant of variation in expected LRS is overall habitat quality. More productive habitats with more high-quality territories and/or more protected habitats with lower mortality lead to longer queues. Since longer queues have smaller stochastic fluctuations in the number of queuers that die per season, there will be lower variation in expected LRS.

Analytical Results

In order to derive the optimal acceptance threshold, we must answer the question, What is the lowest expected LRS for an individual that joins a queue or settles in an empty territory? If we assume that individuals always join the best queue available, then, for each queue length, there is exactly one interval of territory qualities where territories have that queue length. Let us denote by LRS_i the LRS at the lowest-quality territory with queue length i . LRS_0 then equals the LRS at the lowest-quality territory that is occupied. Hence, LRS_0 equals the optimal acceptance threshold. If α_i is the probability that an individual at the bottom of the hierarchy in a queue of length i ever obtains the territory (in a strict queue this is the probability for the individual at the end of the line), then the lowest expected LRS in a queue of length i is given by $\alpha_i LRS_i$. Clearly, queue lengths are in equilibrium if and only if

$$\alpha_0 LRS_0 = \alpha_1 LRS_1 = \dots = \alpha_n LRS_n, \quad (2)$$

where $\alpha_0 = 1$ and n is the maximal queue length. The variation in expected LRS of queuing individuals is related to the difference between the α_i . To see this, consider two individuals who were the last ones to queue for territories yielding an LRS just below and just above LRS_i , respectively. The first one can expect an LRS of almost $\alpha_{i-1} LRS_i$ while the second has an expected LRS that does not much exceed $\alpha_i LRS_i$. The difference between $\alpha_{i-1} LRS_i$ and $\alpha_i LRS_i$ can be considerable (fig. 2). For example, $\alpha_0 LRS_1$ is at least twice as large as $\alpha_1 LRS_1$, since $\alpha_0 = 1$ and $\alpha_1 \leq 1/2$. The latter inequality is a special case of

$$\alpha_i \leq \frac{1}{1+i}, \quad (3)$$

which is derived in appendix B.

Our verbal arguments showed that the optimal acceptance threshold x^* in populations with queuing must be

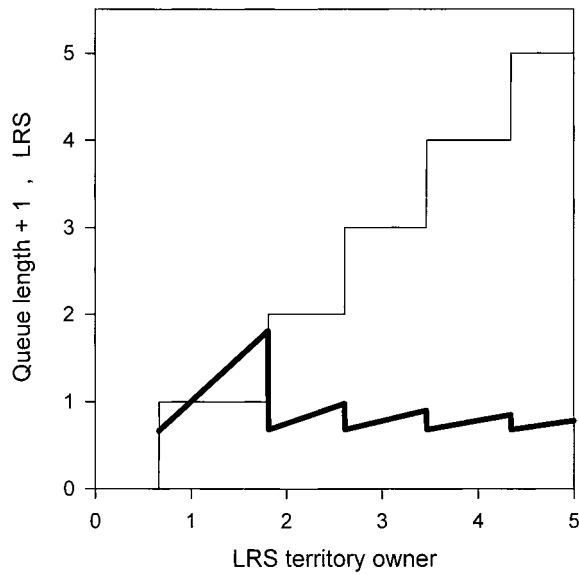


Figure 2: Equilibrium queue lengths including territory owner (*thin line*) and expected LRS for individuals at the end of the queue (*thick line*) as a function of territory quality in a population with strict queuing. Notice the large variation in expected LRS. Mortality rate of queuers and territory owners set at $\mu = 0.4$.

such that $LRS(x^*)$ is between unity and $1 - \mu_F$. In fact, as shown in appendix B and illustrated in figure 3, the optimal acceptance threshold can have any value between $1 - \mu_F$ and unity.

Result 3. For any given value y between $1 - \mu_F$ (the LRS of a floater) and unity, the model parameters can be chosen such that territories at ESS threshold quality x^* yield an LRS of y : $LRS(x^*) = y$.

Simulation Results

Figure 4 depicts an example of an evolutionary trajectory of the average acceptance threshold in a population with strict queuing. The computer simulations were carried out in a similar fashion as in scenario 1 for populations with free floating. After each round of reproduction and mortality of queuers and territory owners, individual floaters and surviving offspring were assigned in random order to the queue or territory with the highest expected LRS, as long as this expectation exceeded or equaled their genetically encoded threshold value. Otherwise they remained floating.

The example shows that the average acceptance threshold evolves downward from unity to a value close to 0.6. After about 5,000 generations, the average acceptance threshold becomes smaller than the LRS at the worst oc-

cupied territory. In appendix B, we explain that this is because acceptance thresholds between the LRS at the worst occupied territory and the survival probability $1 - \mu_F$ of floaters are selectively neutral.

Discussion

On the basis of models for optimal territory choice rather similar to the models studied by Kokko and Sutherland (1998), we arrived at markedly different conclusions. The discrepancies mainly arise because Kokko and Sutherland modeled population dynamics in continuous time. Although mathematically more convenient, this modeling approach has a number of drawbacks. When infinitesimal time steps are the focus, attention is directed away from the mechanism of the choice process. As a result, Kokko and Sutherland are led to the rather implausible assumption that mutants that are less choosy than the rest of the population always end up at territories of a rather bad quality. This assumption restricts the choice process to one of indiscriminate habitat use above the acceptance threshold, even though Kokko and Sutherland claim that their model applies to a much wider range of choice strategies.

We have used a discrete-time approach for a number of reasons: it is more realistic, and one has to be more explicit about the timing of events and the nature of the choice process. This is certainly necessary when one wants

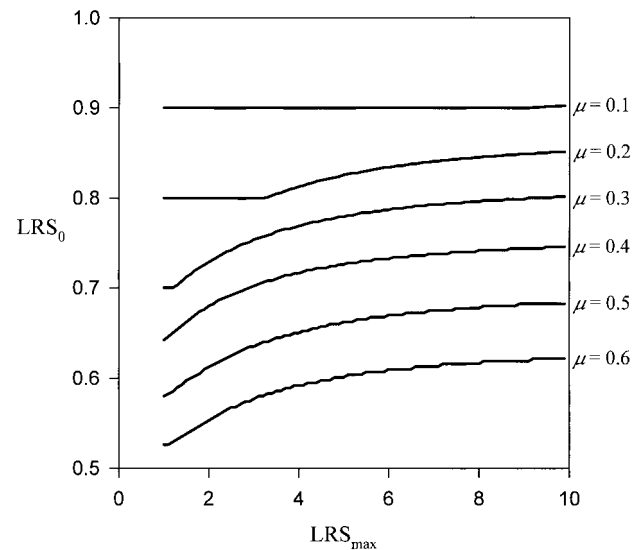


Figure 3: Quality of the worst occupied territory, $LRS_0 = F_0/\mu$, as a function of the quality of the best territory, $LRS_{max} = F_{max}/\mu$, for different mortality rates in populations with strict queuing. The quality of the worst occupied territory increases with overall habitat quality. Territory quality q is exponentially distributed according to the probability density function $\exp(-\lambda q)/\lambda$, where $\lambda = 20$.

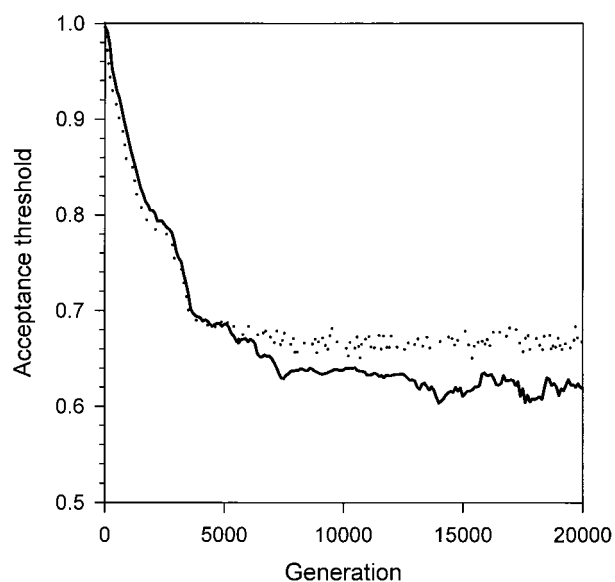


Figure 4: Representative simulated evolutionary trajectory of average acceptance threshold (*solid line*) in population with strict queuing. The dotted line indicates LRS at the worst occupied territory, which stabilizes around 0.67. The average acceptance threshold can evolve below this value because acceptance thresholds below this value are selectively neutral (see app. B). Parameters values as in figure 1.

to do to computer simulations, which is a useful way to check analytical results. We ourselves have detected some inconsistencies in Kokko and Sutherland's exposition after simulations had suggested a very different outcome. Finally, a seasonal time structure suggests that more complex choice strategies should be considered than those that Kokko and Sutherland considered (and we, too, in order to make our results comparable to theirs). It is plausible that animals should get less choosy as the breeding season approaches. In other words, optimal acceptance rules are likely to vary with time in the season, rather than corresponding to a fixed threshold value. The one-dimensional threshold values considered in this article should therefore best be regarded as the minimum value of a time-dependent, or, more generally, a state-dependent strategy (McNamara and Houston 1996; Houston and Lang 1998), because the minimum value determines what one actually observes at the population level in terms of territory oc-

cupancy. Kokko and Sutherland's approach is inconsistent with this interpretation because a mutant that is less choosy than the rest of the population need not always be in a state in which it should be least choosy.

We have not really investigated systematically what the effects are of the two factors considered by Kokko and Sutherland, the number of territories individuals can compete for and the hierarchy among waiting individuals. Just like Kokko and Sutherland, we have only looked at the extremes, free floating and strict queuing. We found different outcomes for the two extremes, which can be due to either factor. What are the likely effects of each factor separately?

It seems very likely that a hierarchy based on age tends to select for higher acceptance thresholds. The reason is that waiting per se automatically leads to a higher expected future success because, for a waiting individual, the future number of competitors will be lower than the present number. The reproductive value of floaters and queuers will therefore be higher than in populations without a hierarchy among waiting individuals. According to our result 1, owners of threshold territories should then also have a higher reproductive value.

It is more difficult to envision what the effect might be of the number of territories an animal can compete for. We saw that the discreteness of queues tends to increase the variation in expected LRS between offspring, compared to populations with floating, where all floaters have the same expected LRS. An increase in variation means there are more "unlucky" individuals with a relatively low expected LRS. These unlucky individuals should therefore accept relatively low-quality territories. Thus, all else being equal, it seems that queuing, when compared to floating, should select for a lower acceptance threshold.

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APPENDIX A

Optimal Acceptance Threshold under Free Floating

Consider an area with a large number of potential territories. Territory quality q is continuously distributed according to a probability density $p(q)$. The area harbors a "normal" (as opposed to "mutant") population composed of n_F

floaters and n_B territory owners or, more compactly, breeders. Normal individuals accept any territory with a quality of at least x^* . The number of occupied territories is therefore given by

$$n_B(x^*) = C \int_{x^*}^{\infty} p(q) dq, \tag{A1}$$

where C is a constant of proportionality. Floaters have yearly mortality μ_F , independently of the threshold quality x^* . The yearly mortality $\mu_B = \mu_B(q)$ of a breeder may depend on the quality q of its territory. The mean mortality of breeders is then

$$\bar{\mu}_B(x^*) = \frac{\int_{x^*}^{\infty} \mu_B(q) p(q) dq}{\int_{x^*}^{\infty} p(q) dq}. \tag{A2}$$

The yearly production of surviving offspring on a territory of quality q is given by $F(q)$. The mean yearly production then equals

$$\bar{F}(x^*) = \frac{\int_{x^*}^{\infty} F(q) p(q) dq}{\int_{x^*}^{\infty} p(q) dq}. \tag{A3}$$

The expected LRS(q) at a territory of quality q is given by $F(q)/\mu_B(q)$, the yearly production of offspring times life expectancy $1/\mu_B(q)$. Clearly, for q to be a useful measure of quality, we want LRS(q) to be an increasing function of q . For there to be any floaters at all, average production of offspring, $\bar{F}(x^*)$, must of course exceed average mortality, $\bar{\mu}_B(x^*)$. The yearly probability that a floater finds an acceptable territory is denoted by $\alpha(x^*)$.

We now have sufficient information to write down the dynamics of the normal population: a population \mathbf{n} , in season t determines the population \mathbf{n}_{t+1} in the next season according to $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$, which is short for

$$\begin{bmatrix} n_F \\ n_B \end{bmatrix}_{t+1} = \begin{bmatrix} (1 - \alpha)(1 - \mu_F) & (1 - \alpha)\bar{F} \\ \alpha(1 - \mu_F) & 1 - \bar{\mu}_B + \alpha\bar{F} \end{bmatrix} \begin{bmatrix} n_F \\ n_B \end{bmatrix}_t. \tag{A4}$$

The population converges at geometric rate to a stable demographic equilibrium with a fixed ratio u_F/u_B of floaters to breeders, given by a dominant right eigenvector $\mathbf{u} = (u_F, u_B)$ of \mathbf{A} . In equilibrium, the population has a yearly growth rate, λ^* , equal to the dominant eigenvalue of \mathbf{A} . Following Kokko and Sutherland, we assume that the population is stationary; that is, we set $\lambda^* = 1$. Mortality is then exactly balanced by natality:

$$u_B(x^*)\bar{\mu}_B(x^*) + u_F(x^*)\bar{\mu}_F(x^*) = u_B(x^*)\bar{F}(x^*). \tag{A5}$$

The stable ratio of floaters to breeders is therefore given by

$$\frac{u_F(x^*)}{u_B(x^*)} = \frac{\bar{F}(x^*) - \bar{\mu}_B(x^*)}{\mu_F}. \tag{A6}$$

Note that this reflects the requirement that \bar{F} must be larger than $\bar{\mu}_B$ for there to be any floaters at all. We can use this equation to determine the threshold value x^* for which floater population size is maximized. Using (A1)–(A3) and omitting the positive constants C and μ_F , we can rewrite (A6) as

$$u_F(x^*) \propto \int_{x^*}^{\infty} F(q) p(q) dq - \int_{x^*}^{\infty} \mu_B(q) p(q) dq. \tag{A7}$$

Applying the fundamental theorem of calculus, we get

$$\begin{aligned} \frac{du_F(x^*)}{dx^*} &= p(x^*)[\mu_B(x^*) - F(x^*)] \\ &= p(x^*)\mu_B(x^*)[1 - \text{LRS}(x^*)], \end{aligned} \tag{A8}$$

since $\text{LRS}(x^*) = F(x^*)/\mu_B(x^*)$. Hence, in order for the floater population size to be maximized, $\text{LRS}(x^*)$ at a threshold quality territory must equal unity. This proves result 2.

The yearly probability $\alpha(x^*)$ for a floater to find an acceptable territory must equal the ratio of the yearly number of territories that become available through the death of their owners and the number of competitors for those territories. The number of territories that become available is given by $\bar{\mu}_B(x^*)u_B(x^*)$, and the number of competitors equals the sum of the number of surviving floaters, $(1 - \mu_F)u_F(x^*)$, and the number of surviving offspring, $\bar{F}(x^*)u_B(x^*)$. Hence,

$$\alpha(x^*) = \frac{\bar{\mu}_B(x^*)u_B(x^*)}{(1 - \mu_F)u_F(x^*) + \bar{F}(x^*)u_B(x^*)}. \tag{A9}$$

Dividing numerator and denominator by $u_B(x^*)$ and substituting (A6) yields

$$\alpha(x^*) = \frac{\bar{\mu}_B(x^*)\mu_F}{\bar{F}(x^*) - \bar{\mu}_B(x^*)(1 - \mu_F)}. \tag{A10}$$

The relative reproductive values of floaters and breeders are determined by a dominant left eigenvector $\mathbf{v} = (v_F, v_B)$ of \mathbf{A} , which is a solution of $\lambda^*\mathbf{v} = \mathbf{v}\mathbf{A}$. The usual interpretation of reproductive values (Fisher 1930; Frank 1998) is that $u_F v_F / (u_F v_F + u_B v_B)$ represents the probability that a gene drawn at random from a population in the far future is present in a floater now. It is easily verified that, for $\lambda^* = 1$, up to a constant multiplier,

$$v_F = 1 - \mu_F, \tag{A11}$$

$$v_B(x^*) = \frac{\bar{F}(x^*)}{\bar{\mu}_B(x^*)}. \tag{A12}$$

The reproductive value of a floater in a stationary population is just its probability of survival, given that the reproductive value of a breeder equals its expected lifetime reproductive success. Note that the expected lifetime reproductive success of a breeder, or rather the expected lifetime reproductive success of floater, given that it will ever find a territory, is not equal to the expected lifetime reproductive success averaged over all territories:

$$\frac{\int_{x^*}^{\infty} \mu_B(q)[F(q)/\mu_B(q)]p(q)dq}{\int_{x^*}^{\infty} \mu_B(q)p(q)dq} = \frac{\bar{F}(x^*)}{\bar{\mu}_B(x^*)} \neq \frac{[F(x^*)]}{[\mu(x^*)]} = \frac{\int_{x^*}^{\infty} [F(q)/\mu_B(q)]p(q)dq}{\int_{x^*}^{\infty} p(q)dq}. \tag{A13}$$

The reason is that not all territories become available at the same rate. In fact, territories with quality q become available at a rate proportional to the mortality rate $\mu_B(q)$.

In order to prove result 1, we investigate the fate of mutants accepting territories of quality $x \neq x^*$. First we consider more choosy mutants that only accept territories with a quality higher than x^* , say of at least $x = x^* + \epsilon$, where ϵ is a small positive number. Later we examine the fate of mutants with a lower than normal standard. The mutants' growth rate is determined by the dominant eigenvalue $\lambda = \lambda(\epsilon)$ of \mathbf{A} , with the normal threshold x^* replaced by the mutant threshold $x = x^* + \epsilon$. Clearly, for $\epsilon = 0$, $\lambda(\epsilon) = \lambda^*$. Now suppose x^* is an ESS. Since the normal population is stationary with yearly growth rate $\lambda^* = 1$, for any $\epsilon > 0$, the mutants must have a yearly growth rate $\lambda(\epsilon) < 1$. This implies that for x^* to be an ESS, we must have

$$\left. \frac{\partial \lambda}{\partial \epsilon} \right|_{\epsilon=0} \leq 0. \tag{A14}$$

According to a standard result (e.g., Taylor 1996), this is equivalent to

$$\mathbf{v} \left. \frac{\partial \mathbf{A}}{\partial \epsilon} \right|_{\epsilon=0} \mathbf{u} \leq 0, \tag{A15}$$

where \mathbf{v} and \mathbf{u} represent reproductive values and equilibrium densities of the normal population (i.e., for $\epsilon = 0$), respectively.

Differentiating \mathbf{A} with respect to ϵ , one obtains

$$\left. \frac{\partial \mathbf{A}}{\partial \epsilon} \right|_{\epsilon=0} = \begin{bmatrix} -\alpha'(x^*)(1 - \mu_F) & -\alpha'(x^*)\bar{F}(x^*) + [1 - \alpha(x^*)]\bar{F}'(x^*) \\ \alpha'(x^*)(1 - \mu_F) & -\bar{\mu}'_B(x^*) + \alpha'(x^*)\bar{F}(x^*) + \alpha(x^*)\bar{F}'(x^*) \end{bmatrix}, \tag{A16}$$

where the primes denote differentiation. In order to calculate these derivatives, we need to know how the mutant's life-history parameters depend on ϵ . This is easy for the average mutant territory owner's mortality $\bar{\mu}_B(x^* + \epsilon)$ and reproduction $\bar{F}(x^* + \epsilon)$, which are given by, respectively,

$$\bar{\mu}_B(x^* + \epsilon) = \frac{\int_{x^*+\epsilon}^{\infty} \mu_B(q)p(q)dq}{\int_{x^*+\epsilon}^{\infty} p(q)dq}, \tag{A17}$$

$$\bar{F}(x^* + \epsilon) = \frac{\int_{x^*+\epsilon}^{\infty} F(q)p(q)dq}{\int_{x^*+\epsilon}^{\infty} p(q)dq}. \tag{A18}$$

To find the yearly probability $\alpha(x^* + \epsilon)$ for a mutant floater to obtain a suitable territory is a bit more tricky because it requires an extra assumption. Following Kokko and Sutherland, we assume that $\alpha(x^* + \epsilon)$ decreases with ϵ because fewer territories become available through the death of their owners, while the number of competitors stays constant. This is reasonable when territory qualities are randomly distributed over space (relaxing the assumption would actually result in a queuing system). It implies that

$$\begin{aligned} \alpha(x^* + \epsilon) &= \frac{\bar{\mu}_B(x^* + \epsilon)u_B(x^* + \epsilon)}{(1 - \mu_F)u_F(x^*) + \bar{F}(x^*)u_B(x^*)} \\ &= \alpha(x^*) \frac{\int_{x^*+\epsilon}^{\infty} \mu_B(q)p(q)dq}{\int_{x^*}^{\infty} \mu_B(q)p(q)dq}. \end{aligned} \tag{A19}$$

The derivatives are now calculated by applying the fundamental theorem of calculus, yielding

$$\bar{\mu}'_B(x^*) = [\bar{\mu}_B(x^*) - \mu_B(x^*)] \frac{p(x^*)}{\int_{x^*}^{\infty} p(q)dq}, \tag{A20}$$

$$\bar{F}'(x^*) = [\bar{F}(x^*) - F(x^*)] \frac{p(x^*)}{\int_{x^*}^{\infty} p(q)dq}, \tag{A21}$$

$$\alpha'(x^*) = -\alpha(x^*) \frac{\mu_B(x^*)p(x^*)}{\bar{\mu}_B(x^*) \int_{x^*}^{\infty} p(q)dq}. \tag{A22}$$

By inserting these derivatives in (A16), we see that every element of the matrix is a multiple of the positive factor $p(x^*)/\int_{x^*}^{\infty} p(q)dq$. We can omit this factor without changing the sign of (A16), which is therefore proportional to

$$\begin{bmatrix} \alpha^*(\mu_B^*/\bar{\mu}_B^*)(1 - \mu_F) & \alpha^*(\mu_B^*/\bar{\mu}_B^*)\bar{F}^* - (1 - \alpha^*)(\bar{F}^* - F^*) \\ -\alpha^*(\mu_B^*/\bar{\mu}_B^*)(1 - \mu_F) & \mu_B^* - \bar{\mu}_B^* - \alpha^*(\mu_B^*/\bar{\mu}_B^*)\bar{F}^* + \alpha^*(\bar{F}^* - F^*) \end{bmatrix}. \tag{A23}$$

Now it is just a matter of inserting (A10) and some tedious algebra to show that the ESS criterion (A15) corresponds to

$$(1 - \mu_F)\mu_B(x^*) - F(x^*) \leq 0, \tag{A24}$$

or equivalently,

$$\frac{F(x^*)}{\mu_B(x^*)} = \text{LRS}(x^*) \geq 1 - \mu_F. \tag{A25}$$

Hence, we have shown that precisely those threshold strategies x^* yielding an LRS greater than or equal to $1 - \mu_F$ at the threshold are stable against invasion by choosier mutants. Let us now investigate the fate of mutants with a lower than normal standard, accepting territories with quality $x = x^* - \epsilon$. We assume that mutants first compete for the same territories as normal individuals. If a mutant fails to obtain such a territory, it will compete for the territories with quality $x \leq q < x^*$. If the mutant fails again, it becomes a floater. A fraction $\alpha^* = \alpha(x^*)$, given by (A10), of the mutants acquires territories with the same quality distribution as the territories occupied by normal individuals. Hence they have the same expected mortality $\bar{\mu}_B^*$ and reproductive output \bar{F}^* , given by (A2) and (A3), respectively. Of the mutants not settling in a territory with quality $\geq x^*$, a proportion β_ϵ settles in a territory of quality $x^* - \epsilon \leq q < x^*$. Obviously, β_ϵ should be an increasing function of ϵ , and β_ϵ should tend to 0 as ϵ goes to 0. Mutants with territory quality $x^* - \epsilon \leq q < x^*$ have average reproductive output $F(\epsilon)$ and yearly mortality $\mu_B(\epsilon)$ which tend to $F(x^*)$ and $\mu_B(x^*)$, respectively, as ϵ tends to 0. The remaining fraction $(1 - \beta_\epsilon)(1 - \alpha^*)$ of the mutants become floaters.

Of the three types of mutants there are m_B mutants with territories of quality $q \geq x^*$, m_L with territory quality $x^* - \epsilon \leq q < x^*$, and m_F floating mutants. These numbers change from one season to the next according to $\mathbf{m}_{t+1} = \mathbf{B}\mathbf{m}_t$, where $\mathbf{m} = (m_F, m_L, m_B)^T$ and

$$\mathbf{B} = \begin{bmatrix} (1 - \beta_\epsilon)(1 - \alpha^*)(1 - \mu_F) & (1 - \beta_\epsilon)(1 - \alpha^*)F(\epsilon) & (1 - \beta_\epsilon)(1 - \alpha^*)\bar{F}^* \\ \beta_\epsilon(1 - \alpha^*)(1 - \mu_F) & 1 - \mu_B(\epsilon) + \beta_\epsilon(1 - \alpha^*)F(\epsilon) & \beta_\epsilon(1 - \alpha^*)\bar{F}^* \\ \alpha^*(1 - \mu_F) & \alpha^*F(\epsilon) & 1 - \bar{\mu}_B^* + \alpha^*\bar{F}^* \end{bmatrix}. \tag{A26}$$

Proceeding as we did before, an ESS threshold x^* must obey

$$\lim_{\epsilon \rightarrow 0} \mathbf{v} \frac{\partial \mathbf{B}}{\partial \epsilon} \mathbf{u} \leq 0. \tag{A27}$$

Here $\mathbf{v} = (v_F, v_L, v_B)$ is the vector of reproductive values of the three types of mutant, given by a dominant left eigenvector of \mathbf{B} . In the limit, as $\epsilon \rightarrow 0$, the reproductive values tend to

$$v_F = 1 - \mu_F, \tag{A28}$$

$$v_L = \frac{F(x^*)}{\mu_B(x^*)}, \tag{A29}$$

$$v_B = \frac{\bar{F}(x^*)}{\bar{\mu}_B(x^*)}. \tag{A30}$$

As one would expect, as ϵ tends to 0, the reproductive values of mutant floaters and breeders tend to those of normal

floaters and breeders, given by, respectively, (A11) and (A12). The reproductive value v_L of an individual with a threshold quality territory is then just its expected LRS. The vector $\mathbf{u} = (u_F, u_L, u_B)$ is proportional to the frequency distribution of the three types of mutant in demographic equilibrium, given by a dominant right eigenvector of \mathbf{B} . As ϵ goes to 0, the vector elements tend to

$$u_F = \bar{F}(x^*) - \bar{\mu}_B(x^*), \tag{A31}$$

$$u_L = 0, \tag{A32}$$

$$u_B = \mu_F. \tag{A33}$$

These are, of course, the same as determined by (A6).

Applying the ESS condition (A27) yields

$$\beta'(0)(1 - \alpha^*)\mathbf{v} \begin{bmatrix} -(1 - \mu_F) & * & -\bar{F}(x^*) \\ (1 - \mu_F) & * & \bar{F}(x^*) \\ 0 & * & 0 \end{bmatrix} \mathbf{u} \leq 0. \tag{A34}$$

The second column of the matrix is irrelevant because by (A32) the second element of \mathbf{u} equals 0. The inequality is equivalent to

$$\beta'(0)(1 - \alpha^*)[(1 - \mu_F)u_F + \bar{F}(x^*)](v_L - v_F) \leq 0, \tag{A35}$$

which reduces to $v_L \leq v_F$ or

$$\frac{F(x^*)}{\mu_B(x^*)} = \text{LRS}(x^*) \leq 1 - \mu_F. \tag{A36}$$

To summarize, in view of (A25), x^* is evolutionarily stable against choosier mutants if $\text{LRS}(x^*) \geq 1 - \mu_F$, while we have just shown that x^* is evolutionarily stable against less choosy mutants if $\text{LRS}(x^*) \leq 1 - \mu_F$. Hence, x^* with $\text{LRS}(x^*) = 1 - \mu_F$ is the only ESS.

APPENDIX B

Optimal Acceptance Threshold under Strict Queuing

In this appendix, we verify that, under strict queuing, the optimal acceptance threshold can take any value between $1 - \mu_F$, the survival probability of a floater, and unity. To keep the analysis tractable, we make the simplifying assumption that queuers and territory owners have the same yearly mortality μ , independent of territory quality. Following Kokko and Sutherland, we let territory ownership correspond to position 0 in the queue. As argued above, queue lengths are in equilibrium if and only if

$$\alpha_i \text{LRS}_i = \text{LRS}_0, \tag{B1}$$

where LRS_i denotes the LRS at the territory quality where queue length increases from $i - 1$ to i and α_i represents the probability of ever obtaining the territory when in position i of the queue. We shall first show that when seasons are discrete, α_i is bounded above by $1/(1 + i)$, the corresponding probability in Kokko and Sutherland's continuous-time framework. This result allows us to prove that for the special case of a uniform territory quality distribution, in a stationary population without floaters the worst occupied territory can yield an LRS anywhere between 0 and $(n + 1)/(n + 2)$, where n denotes the queue length at the best territory. The worst territory can therefore have a value below $1 - \mu$, at which point floating is the better option. Since n can become arbitrarily large, the optimal acceptance threshold can have any value between $1 - \mu$ and unity.

Let us denote by p_{kj} the probability that an individual at position k in a queue will have position $0 \leq j \leq k$ in the

next season. This probability is given by the probability $1 - \mu$ that the individual survives, times the probability that exactly $k - j$ individuals of position $<k$ die. Hence,

$$p_{kj} = \binom{k}{k-j} \mu^{k-j} (1 - \mu)^{j+1}. \tag{B2}$$

The probability α_k of ever obtaining the territory when in position k equals the probability p_{kj} to reach position j in the next season times the probability α_j of ever obtaining the territory when in position j , summed over all j :

$$\alpha_k = \sum_{j=0}^k p_{kj} \alpha_j = \sum_{j=0}^k \binom{k}{k-j} \mu^{k-j} (1 - \mu)^{j+1} \alpha_j. \tag{B3}$$

Factoring out α_k from the right-hand side, α_k can be expressed in terms of the α_j ($j < k$):

$$\alpha_k = \frac{\sum_{j=0}^{k-1} \binom{k}{k-j} \mu^{k-j} (1 - \mu)^{j+1} \alpha_j}{1 - (1 - \mu)^{k+1}}. \tag{B4}$$

For a territory owner the probability of ever reaching its own territory is of course unity; that is, $\alpha_0 = 1$. The α_k for $k > 0$ are then easily computed iteratively. For example,

$$\alpha_1 = \frac{\mu(1 - \mu)}{1 - (1 - \mu)^2} = \frac{1 - \mu}{2 - \mu}. \tag{B5}$$

This quantity cannot exceed one-half, which means that the LRS of the first queuer behind the territory owner is less than one-half of the territory owner's LRS. In fact, it follows by induction that

$$\alpha_k \leq \frac{1}{1 + k}. \tag{B6}$$

To see this, suppose for $j = 0, \dots, k - 1$ that we have $\alpha_j \leq 1/(1 + j)$. Then

$$\begin{aligned} \alpha_k &\leq \frac{\sum_{j=0}^{k-1} \binom{k}{k-j} \mu^{k-j} (1 - \mu)^{j+1} [1/(1 + j)]}{1 - (1 - \mu)^{k+1}}, \\ &= \frac{1}{1 + k} \left[1 - \frac{\mu^{k+1}}{1 - (1 - \mu)^{k+1}} \right] \leq \frac{1}{1 + k}. \end{aligned} \tag{B7}$$

Clearly, we also have

$$\lim_{\mu \rightarrow 0} \alpha_k = \frac{1}{1 + k} \quad \text{and} \quad \lim_{\mu \rightarrow 1} \alpha_k = 0. \tag{B8}$$

The right-hand side of (B7) is identical to the value of α_k obtained by Kokko and Sutherland in their continuous-time framework. Hence, when seasons are discrete, the LRS at any position in the queue is always lower than the LRS at the same position in continuous time.

In a stationary population without floaters, the average LRS of territory owners must equal the average number of queuers per territory, denoted by \bar{k} , plus the territory owner itself; that is,

$$\frac{\bar{F}}{\mu} = 1 + \bar{k}. \tag{B9}$$

Let the worst occupied territory yield an LRS of F_0/μ , the best territory an LRS of F_{\max}/μ , and let the longest queue in the population have length n . In a population where queue lengths are in equilibrium, there will be n switch points, territory qualities where queue length increases by 1. The LRS F_i/μ at a switch point where queue length increases from $i - 1$ to i is given by

$$\alpha_i \frac{F_i}{\mu} = \frac{F_0}{\mu}. \tag{B10}$$

For a given combination of mortality rate μ and productivity F_{\max} at the highest-quality territory, the equilibrium conditions (B9) and (B10) determine the maximum queue length n and the productivity F_0 at the lowest-quality occupied territory. Now let us assume that F_0/μ is larger than $1 - \mu$. We claim that selection favors an acceptance threshold no larger than F_0/μ . To see this, suppose the acceptance threshold is larger than F_0/μ . In that case, some individuals would become floaters, which have an expected LRS of $1 - \mu < F_0/\mu$. Strictly speaking, F_0/μ is not an ESS because, as long as individuals always choose the best available queue or territory, individuals with an acceptance threshold lower than F_0/μ never end up on a territory with expected LRS smaller than F_0/μ . Hence, in populations in equilibrium, as long as $F_0/\mu \geq 1 - \mu$, there is no selection against individuals with an acceptance threshold lower than F_0/μ , and the acceptance threshold may drift to lower values than F_0/μ .

What remains to be shown is that F_0/μ can have any value below unity. For a given maximum queue length n , the maximum value of F_0/μ is clearly obtained when the best territory is the last switch point, that is, when $F_{\max} = F_n$. Equations (B9) and (B10) allow us to calculate n and F_0/μ . Figure 3 shows numerical solutions for exponentially distributed territory qualities. For uniformly distributed territory qualities, we can find an explicit solution. Rewriting (B9) as

$$\begin{aligned} \frac{1}{2} \left(\frac{F_0}{\mu} + \frac{F_n}{\mu} \right) &= 1 + \frac{\sum_{i=0}^{n-1} (F_{i+1} - F_i) i}{\sum_{i=0}^{n-1} (F_{i+1} - F_i)} \\ &= 1 + \frac{(n-1)F_n - \sum_{i=1}^{n-1} F_i}{F_n - F_0} \end{aligned} \tag{B11}$$

by (B10) and rearranging

$$\frac{F_0}{\mu} = \frac{2}{(1/\alpha_n) + 1} + \frac{2[(n-1)/\alpha_n] - 2 \sum_{i=1}^{n-1} (1/\alpha_i)}{[(1/\alpha_n) - 1][(1/\alpha_n) + 1]}. \tag{B12}$$

by (B8) as $\mu \rightarrow 1$, this tends to 0, and as $\mu \rightarrow 0$, this tends to

$$\frac{2}{n+2} + \frac{2(n-1)(n+1) - 2 \sum_{i=1}^{n-1} (i+1)}{n(n+2)} = \frac{n+1}{n+2}. \tag{B13}$$

By continuity, there is a small μ such that F_0/μ is near $(n+1)/(n+2)$. We can obtain any $n \geq 0$ by choosing an appropriate F_n ; hence, for sufficiently small F_n , we can get F_0/μ to be smaller than $1 - \mu$. We can also choose F_n sufficiently large such that F_0/μ can have any value smaller than unity but larger than $1 - \mu$. The optimal acceptance threshold can therefore have any value between $1 - \mu$ and 1.

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