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ABSTRACT

The sequential search strategy is a prominent model of searcher behavior, derived as a rule by which females might sample and choose a mate from a distribution of prospective partners. The strategy involves a threshold criterion against which prospective mates are evaluated. The optimal threshold depends on the attributes of prospective mates, which are likely to vary across generations or within the lifetime of searchers due to stochastic environmental events. The extent of this variability and the cost to acquire information on the distribution of the quality of prospective mates determine whether a learned or environmentally canalized threshold is likely to be favored. In this paper, we determine conditions on cross-generational perturbations of the distribution of male phenotypes that allow for the evolutionary stability of an environmentally canalized threshold. In particular, we derive conditions under which there is a genetically determined threshold that is optimal over an evolutionary time scale in comparison to any other unlearned threshold. These considerations also reveal a simple algorithm by which the threshold could be learned.

1. Introduction

The environment changes continually and, on an evolutionary time scale, these changes can impose selection pressures that alter the optimal expression of phenotypes or behavior. Behavioral plasticity, the ability of an animal to alter its behavior in response to changes of environmental conditions, is expected if the environment shifts appreciably across generations or within the lifetime of an individual, whereas costs incurred to learn appropriate responses to environmental stimuli may favor less pliable, environmentally canalized behavior when the environment is relatively static [reviewed by 1–5]. In this paper, we address issues related to how environmental stochasticity influences the control of female mate choice decisions in the context of a prominent model of searcher behavior.

The *sequential search strategy*, the model that we use to address this issue, has an extensive history in the field of economics [reviewed by 6,7]. Janetos [8] and Real [9] introduced this strategy as a potential rule by which females might sample and choose among prospective mates and numerous empirical and theoretical papers related to their

ideas followed [reviewed by 10]. The solution of the model is a fixed, optimal threshold criterion against which the quality of prospective mates is compared. The threshold is invariant in the original formulations of the model because females were presumed to sample males from a known, static distribution of prospective mates that either does not change across generations or is somehow learned perfectly by searchers each generation [11]. This assumption is clearly unrealistic and the impact of uncertainty about this distribution on mate choice decisions has been explored in a variety of contexts [11–19]. For instance, Hutchinson and Halupka [16] explored the performance of threshold-based decision rules when males are distributed in patches that differ in their composition of prospective mates and Collins et al. [11] compared the performance of fixed and learned thresholds under conditions in which the distribution of males from which females choose varies spatially or temporally across generations.

In this paper, we are concerned with the stability of an environmentally canalized, genetically determined threshold when environmental stochasticity causes perturbations of the distribution of prospective mates across generations of searchers. The existence of an evolutionary stable fixed threshold was tacitly assumed in various comparisons made by Collins et al. [11] and here we establish general conditions under which this assumption is justified. These considerations reveal, in addition, a simple algorithm by which the threshold could be learned.

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2. The model

In this section of the paper, we provide a brief description of the search process and the assumptions used to derive the solution to the sequential search strategy, where the quality of a prospective mate—the to-be-realized fitness gain to a searcher—is revealed by inspection of a phenotypic *indicator character* [reviewed by 20,21]. The model can be applied when either sex is considered to be the searcher, but for simplicity we suppose that this role is played by females. Wiegmann et al. [22] formulate the model in detail [see also 23].

Females pay an expected cost $c > 0$ to sample a prospective mate and inspect his expression of a phenotypic indicator character X, where X is bounded on the interval $[0, \infty)$. The cumulative distribution of X is F, which is presumed, for now, to be known by searchers. Prospective mates are sampled randomly and sequentially from F. The time horizon over which females search is unlimited and males are assumed to mate indiscriminately. Hence, the number P of prospective mates that can be sampled by a female is unrestricted and the phenotypes of males in any encounter sequence $\{X_1, X_2,..., X_P\}$ are independent and identically distributed.

The acceptability of an encountered male is determined by a comparison of his expression of X to a threshold criterion T. The indicator character of a sampled male is related to the to-be-realized fitness gain to a searcher by a function u, which is presumed to have a finite mean and to be continuously differentiable with respect to X. (For simplicity, $u(0) \geq 0$ and $du(x)/dx = u'(x) \geq 0$ are also assumed.) A female who adopts a particular threshold criterion t terminates search and mates with the first prospective mate in a sequence of encounters whose phenotype is $X \geq t$. This male is invariably the last prospective mate encountered in the sequence $\{X_1, X_2,..., X_P\}$ because when the time horizon for search is unrestricted the threshold is fixed and an unacceptable, previously encountered male is never later accepted.

The quality of an accepted male is $u(X_P)$ and the cost paid to sample P males is cP, where both the quality of a mated male $u(X_P)$ and the cost to sample a prospective mate c are measured in units of fitness to a searcher. Hence, the net fitness return to a searcher is $u(X_P) - cP$. The expected net fitness return v to a searcher who employs the threshold t is

$$v(t) = \frac{\int_t^\infty u(x)dF(x)}{1 - F(t)} - c\left(\frac{1}{1 - F(t)}\right). \tag{1}$$

The first term on the right-hand side is the expected quality of a male whose expression of X equals or exceed t and the second term is the cost to sample a prospective mate multiplied by $1/(1 - F(t))$, the number of males that a female expects to sample to find an acceptable mate when the threshold t is used as the criterion against which males are evaluated.

The optimal threshold criterion t* satisfies

$$u(t^*) = v(t^*). \tag{2}$$

In other words, the optimal phenotypic threshold is the X that causes a searcher to be indifferent between the acceptance of an encountered individual, which would yield a net fitness gain u if she mated, and the prospect of continued search, which would yield an expected net return v [7,9]. Substitution of $u(t^*)$ for $v(t)$ into (1), rearrangement and integration by parts leads to an expression of the solution that we will use throughout this paper, namely

$$c = \int_{t*}^\infty u'(x)[1 - F(x)]dx \tag{3}$$

[18,22]. The last important model property relates to the conditions under which a female will sample prospective mates. A female will search for a mate provided that c is less than the mean male quality μ because she

otherwise has no incentive to engage in the search process. In particular, her expected net gain if she engages in search is negative whenever $c > \mu$.

The cumulative distribution of the male indicator character X, namely F, is more realistically expected to fluctuate from generation to generation and in the next section of the paper we establish sufficient conditions for the evolutionary stability of a genetically determined t* to perturbations of F.

3. Evolutionary stability of a genetically fixed threshold

The optimal threshold t* is a function of the distribution F. If t* is continuous with respect to F, then under some conditions, which we will establish, it is stable to generational perturbations of F. In particular, we shall establish conditions on perturbations of F across generations that allow an unlearned, genetically determined t* to be optimal over an evolutionary time scale in comparison to any other genetically determined threshold.

Imagine a sequence of distributions $\{F_n\} = \{F_1, F_2, F_3, ...\}$ of X on the interval $[0, \infty)$ for which u has finite mean $\mu_n > c$, where $\{F_n\}$ is an evolutionary sequence of distributions, experienced over a sequence of n generations of searchers, that converges, as will be specified, on F. For each F_n there is an optimal threshold criterion t_n^*. If these threshold criteria converge on the optimal threshold t* under F, then t* is optimal over the evolutionary sequence $\{F_n\}$. Thus, our objective is to establish conditions on $\{F_n\}$ which imply that t_n^* converges on t*.

Theorem 1. *If* F_n *converges to* F *uniformly on the interval* $[0, \infty)$ *of X and* u *is bounded on* $[0, \infty)$, *then* t_n^* *converges to* t*.

Proof. It cannot be true that $\{t_n^*\}$ is unbounded. Imagine that the subsequence $\{t_{n_i}*\}$ of $\{t_n^*\}$ tends toward infinity. Then

$$
\begin{aligned}
c &= \int_{t_{n_i}^*}^\infty u'(x)\Big[1 - F_{n_i}(x)\Big]dx = \int_{t_{n_i}^*}^\infty u'(x)\Big[1 - F(x) + F(x) - F_{n_i}(x)\Big]dx \\
&= \int_{t_{n_i}^*}^\infty u'(x)[1 - F(x)]dx + \int_{t_{n_i}^*}^\infty u'(x)\Big[F(x) - F_{n_i}(x)\Big]dx \\
&\leq \int_{t_{n_i}^*}^\infty u'(x)[1 - F(x)]dx + \int_{t_{n_i}^*}^\infty u'(x)\Big|F(x) - F_{n_i}(x)\Big|dx \\
&\leq \int_{t_{n_i}^*}^\infty u'(x)[1 - F(x)]dx + \sup u(x) \cdot \sup\Big|F(x) - F_{n_i}(x)\Big|.
\end{aligned}
\tag{4}
$$

The first term on the right-hand side approaches zero as i increases to infinity because u has a finite mean with respect to F. The second term converges to zero because F_{n_i} converges uniformly to F. This contradicts the assumption that $c > 0$. The sequence $\{t_n^*\}$ must consequently be bounded.

The Bolzano–Weierstrass Theorem then assures us that $\{t_n^*\}$ converges to some number [24]. Suppose that $\{t_n^*\}$ converges to the limit S, where $S \leq t^*$. Then for i sufficiently large

$$
\begin{aligned}
0 &= c - c \\
&= \int_{t_{n_i}^*}^\infty u'(x)\Big[1 - F_{n_i}(x)\Big]dx - \int_{t*}^\infty u'(x)[1 - F(x)]dx \\
&= \int_{t_{n_i}^*}^{t*} u'(x)\Big[1 - F_{n_i}(x)\Big]dx + \int_{t*}^\infty u'(x)\Big[1 - F_{n_i}(x)\Big]dx - \int_{t*}^\infty u'(x)[1 - F(x)]dx \\
&= \int_{t_{n_i}^*}^{t*} u'(x)\Big[1 - F_{n_i}(x)\Big]dx + \int_{t*}^\infty u'(x)\Big[F(x) - F_{n_i}(x)\Big]dx.
\end{aligned}
\tag{5}
$$

The second integral converges to zero as i increases to infinity. The Dominated Convergence Theorem applies to the first integral, with the integrable dominating function u(t) [25]. The conclusion is that

$$0 = \int_S^{t*} u'(x)[1 - F(x)]dx. \tag{6}$$

Because u strictly increases with X and $F(t^*-) < 1$, this can happen only if $S = t^*$. An analogous argument yields the same conclusion for the

situation in which $S \geq t^*$, which proves that every convergent subsequence $\{t_{n_i*}\}$ converges to t^*.

The boundedness condition on u can be relaxed, as we now show, if a more stringent convergence condition is imposed on $\{F_n\}$.

Theorem 2. *If F_n converges to F in the sense of $L^1(u'(t)dt, [0, \infty))$, then t_n^* converges to t^*.*

Proof. The proof is similar to the proof of Theorem 1. If there is a subsequence $\{t_{n_i*}\}$ that tends toward infinity, then

$$c = \int_{t_{n_i}^*}^{\infty} u'(x)\left[1 - F_{n_i}(x)\right]dx$$
$$= \int_{t_{n_i}^*}^{\infty} u'(x)[1 - F(x)]dx + \int_{t_{n_i}^*}^{\infty} u'(x)\left[F(x) - F_{n_i}(x)\right]dx \qquad (7)$$
$$\leq \int_{t_{n_i}^*}^{\infty} u'(x)[1 - F(x)]dx + \left\|F(x) - F_{n_i}(x)\right\|_1.$$

The final expression on the right-hand side approaches zero as i increases, which contradicts the assumption that $c > 0$. Thus, the sequence $\{t_n^*\}$ is bounded.

Now suppose that the bound on $\{t_n^*\}$ is S, where $S \leq t^*$. Then for i sufficiently large

$$0 = \int_{t_{n_i}^*}^{t^*} u'(x)\left[1 - F_{n_i}(x)\right]dx + \int_{t_{n_i}^*}^{\infty} u'(x)\left[F(x) - F_{n_i}(x)\right]dx. \qquad (8)$$

The second integral converges to zero as i increases to infinity. The first integral can be zero only if $S = t^*$. A similar argument yields the same conclusion for the situation in which $S \geq t^*$, which proves that $\{t_n^*\}$ converges to t^*.

Another trade-off takes us to the next sufficient condition for the convergence of thresholds. Let the mean quality of males associated with distribution F_n be $\mu_n = \int_0^\infty u(x)dF_n(x)$. The convergence of means, together with a much weaker mode of convergence in $\{F_n\}$, then suffices for $\{t_n^*\}$ to converge to t^*.

Theorem 3. *If F_n converges to F pointwise, and μ_n converges to μ, then t_n^* converges to t^*.*

Proof. The proof is again structurally similar to that used in Theorem 1. If there is a subsequence $\{t_n^*\}$ that tends toward infinity, then

$$c = \int_{t_{n_i}^*}^{\infty} u'(x)\left(1 - F_{n_i}(x)\right)dx$$
$$= \int_{t_{n_i}^*}^{\infty} u'(x)(1 - F(x))dx + \int_{t_{n_i}^*}^{\infty} u'(x)\left[F(x) - F_{n_i}(x)\right]dx \qquad (9)$$
$$\leq \int_{t_{n_i}^*}^{\infty} u'(x)(1 - F(x))dx + \left|\mu_{n_i} - \mu\right|.$$

The final expression on the right-hand side approaches zero as i increases, which contradicts the assumption that $c > 0$. Thus, the sequence $\{t_n^*\}$ is bounded.

Now suppose again that $\{t_n^*\}$ is a convergent sequence with limit S, where $S \leq t^*$. Then for i sufficiently large

$$0 = \int_{t_{n_i}^*}^{t^*} u'(x)\left[1 - F_{n_i}(x)\right]dx + \int_{t_{n_i}^*}^{\infty} u'(x)\left[F(x) - F_{n_i}(x)\right]dx. \qquad (10)$$

The second integral is bounded by $|\mu_n - \mu|$, which converges to zero as i increases to infinity. This forces the first integral to zero, which can happen only if $S = t^*$. An analogous argument yields the same conclusion for the situation in which $S \geq t^*$. The conclusion is again that $\{t_n^*\}$ converges to t^*.

Theorem 4. *If $\int_A u(x)dF_n(x)$ converges to $\int_A u(x)dF(x)$ for every measurable subset A of $[0, \infty)$, then t_n^* converges to t^*.*

Proof. This proof follows the proof that we used to establish Theorem 1. The Generalized Dominated Convergence Theorem is applied to the sequence of measures $u(x)dF_n(x)$ (or, from integration by parts, the measures $u'(x)[1 - F_n(x)]dx$) and the sequence of indicator functions for the sets $[t_n^*, \infty)$. The latter are dominated by the unit constant function and the argument proceeds as in Theorem 1.

Finally, it is straightforward to illustrate why t^* is optimal over an evolutionary time scale in comparison to any other environmentally canalized, genetically determined threshold whenever conditions on F are sufficient for t_n^* to converge to t^*.

Corollary 1. *If t_n^* converges to t^*, then $v(t_n^*)$ converges to $v(t^*)$.*

Proof. This statement follows directly from the fact that u is continuous (and independent of F) and the fact that $v(t_{(\cdot)}^*) = u(t_{(\cdot)}^*)$. Hence, the expected net fitness return associated with t^*, namely $v(t^*)$, is higher than the expected return associated with any other determined threshold and t^* is evolutionarily stable against perturbations $\{F_n\}$ that converge, as we characterized, on F.

4. Learned thresholds

Thus far we have imagined that the threshold criterion is environmentally canalized and our concern was with the evolutionary stability of t^*. Now we present a continuity result that applies specifically to situations in which a threshold is learned by searchers within a generation through their experiences with a single distribution F that has an associated optimal threshold criterion t^*. The result that follows provides a sufficient condition—and a simple algorithm—for a searcher *with no prior knowledge* of F to learn a threshold that converges on t^*.

Imagine that a female observes a sequence of male phenotypes $\{X_n\}$ before search is initiated, where each X_i is an independent and identically distributed sample from F. Define the sequence of *empirical distribution functions* $\{F_n\}$ constructed from the realized sequence of encounters $\{X_n\}$ as

$$F_n(x) = \frac{1}{n}\sum_{i=1}^{n} I_{[X_i, \infty)}(x), \qquad (11)$$

where

$$I_{[X_i, \infty)}(x) = \begin{cases} 1, & \text{if } X_i > x \\ 0, & \text{otherwise} \end{cases} \qquad (12)$$

is the indicator function of $[X_i, \infty)$. Notice that each F_n is itself a random variable.

Theorem 5. *If $\{F_n\}$ is the sequence of empirical distributions, then t_n^* converges to t^* with probability 1.*

Proof. The Glivenko–Cantelli Theorem ensures that $\{F_n\}$ converges uniformly with a probability of 1 to F [26]. Let Y_n be the random variable $u(X_n)$ for every n. The Law of Large Numbers provides that

$$\frac{Y_1 + Y_2 + K + Y_n}{n} \to E(Y) \qquad (13)$$

with probability 1 as n approaches infinity. This is equivalent to the statement that

$$\int_0^\infty u(x)dF_n(x) \to \int_0^\infty u(x)dF(x) \qquad (14)$$

as n approaches infinity. The assertion now follows by application of Theorem 3.

5. Discussion

The optimal threshold under a sequential search strategy is expected to vary across generations of searchers when environmental conditions perturb the distribution of male quality [11,16]. In this paper, we established conditions on perturbations of this distribution that permit the evolutionary stability of an environmentally canalized phenotypic threshold. In our formulation of the problem we supposed that each generation of searchers experiences a somewhat different distribution of prospective mates. In practice, the evolutionary time scale over which our results can be applied will depend on the magnitude of environmental perturbations across generations, where the perturbations are non-catastrophic and, over an evolutionary time scale, non-directional. The convergence conditions that allow for an optimal fixed threshold should be simple to establish in a typical evolutionary simulation that involves hundreds or thousands of generations. The convergence conditions that we derived effectively specify when environmentally induced perturbations of the distribution of male quality permit a particular environmentally canalized phenotypic threshold to outcompete all alternative genetically determined thresholds.

How uncertainty about the distribution from which males are sampled influences mate choice decisions has been explored in a variety of other contexts [11–19]. The sequential search strategy has been compared, for instance, with other search strategies under conditions in which males are distributed in patches and there is inter-patch variability in the quality of prospective mates [11,16]. The expected net fitness return to searchers that apply a fixed threshold is, not surprisingly, reduced when search is confined to a single patch and the mean quality of males varies considerably among patches. The results derived from this scenario might similarly apply to conditions in which the mean quality of prospective mates varies across generations of searchers if we construe patches as generations. The evolutionary dynamics of environmentally canalized thresholds in patchy environments should, however, differ to some extent from cross-generational dynamics because when variability occurs across generations all searchers in a particular generation experience the same distribution of prospective mates [11].

Collins et al. [11] developed a genetic algorithm to compare the performance of a learned threshold to a fixed threshold, where the mean quality of prospective mates varies spatially or temporally across an evolutionary time scale of many thousands of generations. They found that a learned threshold is most advantageous when there is high variability of the mean quality of males among patches or generations and that the relative performance of learned and fixed thresholds depends on the variability of male quality within patches or generations. The existence of an optimal, genetically determined threshold was tacitly assumed in some of their comparisons of learned and fixed thresholds. In this paper, we established conditions under which this assumption is justified, conditions on the distribution of male quality that permit the evolutionary stability of a genetically determined phenotypic threshold. Importantly, the results that we established do not depend on any particular parametric restrictions on the male indicator character, like normality, or simple shifts of the mean male phenotype across generations.

Learned acceptance thresholds generally yield a higher expected fitness return than environmentally canalized thresholds when searchers experience high uncertainty about the quality of prospective mates and the cost to gather and process information on the distribution of male quality is small. Bayesian rules, like the one applied by Collins et al. [11], are often used to model the dynamics of a learned threshold, where searchers are presumed to have some prior knowledge of the distribution of male quality [13,14,27,28; but see 15]. The convergence conditions that we established for the persistence of an environmentally canalized phenotypic threshold revealed a simple algorithm by which a searcher with no prior knowledge of the distribution could, in principle, learn a threshold that converges on the optimal threshold.

The functional relation between the male indicator character and male quality was assumed to be invariant under the conditions that we established for the evolutionary persistence of an optimal, genetically determined phenotypic threshold. This relationship can, however, also shift across generations as a consequence of environmental stochasticity. The approach we used could be similarly applied to establish conditions on the evolutionary stability of an optimal fixed threshold when the fitness function is likewise perturbed.

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