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‘Mathematical exercise’ on a solvable stochastic control model for animal migration

H Yoshioka[1]

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Abstract

Animal migration is a mass biological phenomenon indispensable for comprehension and assessment of food-webs. So far, theoretical models to describe decision-making processes inherent in the animal migration have not been well established, which is the motivation of this research. It is natural to formulate the animal migration based on a stochastic control theory, which can describe system dynamics and its optimization in stochastic environment. To address this issue, a conceptual stochastic control model for the decision-making processes in animal migration is introduced and mathematically analysed. Its novelty is mathematical simplicity and the new theoretical, stochastic control viewpoint. Stochastic differential equations govern the animal population dynamics with gradual and radical migrations from the current habitat toward the next one. The population decides the occurrences, magnitudes, and timings of the migrations, so that a heuristic

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performance index is maximised. I derive a variational inequality that governs the maximised performance index and is exactly solvable. Its free boundaries govern the gradual and radical migrations. Despite the model simplicity, the exact solution is consistent with the empirical observation results of fish migration, implying its potential applicability to animal migration. The present model can be used for assessing fish migration.

Subject class: 92D25; 93E20; 90C39

Keywords: Animal migration; mixed stochastic optimal control; variational inequality

Contents

1 Introduction

Animal migration is a mass biological phenomenon driving food-webs [1]. Comprehension and assessment of animal migration is a key for management and conservation of ecosystems. Animal migration from a habitat to the next one is a consequence of decision-making processes among the population under stochastic environment [2]. It would therefore be reasonable to describe the animal migration based on some optimality principle that reflects the decision-making processes. Stochastic control theory [4] is a potential candidate for the above modelling purpose; however, to my knowledge, such an approach has not been examined so far or is still rare. This is the motivation of this research.

Here, I introduce a conceptual stochastic control model based on stochastic differential equations (SDEs) that govern animal population dynamics. The present model is rather simple and conceptual than detailed and mechanistic, but the derived results in this paper are consistent with the empirical observations as demonstrated later. The model focuses on migration of the population from a habitat toward the next one, which is assumed to arise as a consequence of an optimality principle to maximise a performance index. Both the gradual (slow and small-scale) and radical (rapid and large-scale) migrations [2, 8] are considered. The former is described with a regular control variable and the latter with a stopping time, both of which are simultaneously optimised. Here, the gradual migration means the migration in which a part of the population gradually migrates at a certain rate. The radical migration means the mass migration in which the most or all population migrates. The present model is therefore a mixed stochastic control model based on SDEs. Mixed stochastic control models have effectively been used in financial and economic research areas [4, 7]; however, its application to biological and ecological problems, especially animal migration, is rare. This paper thus presents a new mathematical approach to the migration. The dynamic programming principle ultimately reduces the problem of finding the optimal migration strategy to solving a boundary value problem of a degenerate variational inequality named Hamilton–Jacobi–Bellman (HJB) equation. The HJB equation is exactly solvable under certain conditions. Although this paper only addresses its mathematical aspects, some its practical implications are also provided.

2 Mathematical model

2.1 Stochastic differential equation

The mathematical setting in this paper follows that of Øksendal and Sulem [5, Chapter 4]. A system of SDEs that describes animal population dynamics in a habitat is presented. I assume that the population does not have reproduction in the habitat. I also assume that the population adopts a mixed strategy where gradual and radical migrations possibly coexist. The time is denoted as $t \geqslant 0$. The 1-D standard Brownian motion on the usual complete probability space is denoted as B_t. The time at which all the (remaining) population migrates toward the next habitat is denoted as $\tau \geqslant 0$. Here, τ is a stopping time adapted to a natural filtration generated by B_t. The model considers the problem such that the population possibly gradually migrates from the current habitat toward the next one in $0 < t < \tau$, and the remaining population radically migrates at the time $t = \tau$.

The total number of population in the habitat at the time t is denoted as N_t. The representative body weight of the animal at the time t is denoted as X_t. Here, N_t is considered as continuous not discrete for the sake of simplicity of analysis. The initial conditions are $N_0 = n \geqslant 0$ and $X_0 = x \geqslant 0$. Since the population is not reproductive, inspired by Yaegashi et al. [6], the SDEs that govern N_t and X_t are set as

$$dN_t = -(R + pu_t)N_t \, dt, \quad 0 < t < \tau, \tag{1}$$

which is the conventional exponential decay low of the population, and

$$\mathrm{d}X_t = X_t\left(r\,\mathrm{d}t + \sigma\,\mathrm{d}B_t\right), \quad 0 < t < \tau, \tag{2}$$

the simplest SDE of a growth phenomenon that preserves $X_t \geqslant 0$ [6], respectively. Here, $R > 0$ is the natural mortality rate, $p > 0$ is the maximum gradual migration rate, $r > 0$ is the intrinsic growth rate, $\sigma > 0$ represents the stochasticity involved in the body growth. The variable $u_t : (0, \tau) \to U = [0, 1]$ modulates the gradual migration rate where $u_t = 0$ means that there is no gradual migration at the time t. The total biomass of the population is $Z_t = N_t X_t$ with $Z_0 = z = nx \geqslant 0$. The conventional Itô's rule then leads to

$$\mathrm{d}Z_t = Z_t\left[(r - R - pu_t)\,\mathrm{d}t + \sigma\,\mathrm{d}B_t)\right], \quad 0 < t < \tau. \tag{3}$$

The variables to be optimised by the population are u and τ. The admissible set $\mathcal{T}$ of τ is the set of all adapted stopping times such that $\tau \geqslant 0$. The admissible set $\mathcal{A}$ of u_t is the set of all measurable functions u_t of the time $t > 0$ such that $0 \leqslant u_t \leqslant 1$, adapted to the natural filtration, and (1) has a unique strong solution for $t \geqslant 0$. The control u is assumed to be a Markov control, so that it is expressed as $u_t = u_0(Z_t)$ with some univariate function u_0. For the sake of simplicity of descriptions, u and u_0 are not distinguished in what follows.

2.2 Performance index

A performance index to be maximised by the population with an optimal couple $(u^*, \tau^*) \in \mathcal{A} \times \mathcal{T}$ is presented. The performance index $J = J(z; u, \tau)$ for $z \geqslant 0$ and admissible (u, τ) is set as

$$J = E^z\left[\int_0^\tau \frac{qZ_t^{1-\beta}}{1-\beta}e^{-\delta t}\mathrm{d}t + \int_0^\tau \frac{wu_t Z_t^{1-\beta}}{1-\beta}e^{-\delta t}\mathrm{d}t + \frac{q' Z_\tau^{1-\alpha}}{1-\alpha}e^{-\delta\tau}\right]. \tag{4}$$

Here, E^z represents the expectation conditioned on $Z_0 = z$, $\delta > 0$ is the discount rate (larger δ means that the population is more myopic), $q > 0$,

$q' > 0$, and $w > 0$ are the weight parameters, and $0 < \alpha < 1$ and $0 < \beta < 1$ are the sensitivity parameters. Smaller α or β implies larger sensitivity of the performance index on the population dynamics. Heuristically, smaller biomass, namely smaller body weight and/or smaller total population, is more fragile and more sensitive. I therefore assume the condition $\alpha < \beta$. The last term of (4) is replaced by 0 when $\tau \to +\infty$. Without any loss of generality, the parameter q' is set to be 1 in what follows. The performance index J contains the three terms. The first term is the profit gained in the current habitat during $(0, \tau)$. The second term is the profit by the gradual migration during $(0, \tau)$. The third term is the profit gained by the radical migration. The functional forms of the three terms are monomial types, which are chosen for tractability of the model. The functional form of J is heuristic and chosen for analytical tractability, but is potentially a minimal model that considers the effects of gradual and partial migrations. Although it is not explicitly considered here, from a biological viewpoint, it is natural to consider that J and its optimality principle arise as a result of evolutionary processes.

The value function $\Phi = \Phi(z)$ for $z \geqslant 0$ is defined as the maximised performance index J with respect to admissible $(u, \tau) \in \mathcal{A} \times \mathcal{T}$:

$$\Phi(z) = \sup_{(u,\tau) \in \mathcal{A} \times \mathcal{T}} J(z; u, \tau) = J(z; u^*, \tau^*), \; z \geqslant 0. \tag{5}$$

Hereafter, I assume the condition

$$r > R + p + \frac{\sigma^2}{2}, \tag{6}$$

so that $Z_t > 0$ for $t > 0$ when $z > 0$ almost surely, namely the population does not become extinct during $(0, \tau)$. In addition, I assume the necessary condition to make the value function Φ be locally bounded for $z > 0$

$$\lambda_1 = \delta - (1 - \beta)(r - R) - \frac{1}{2}\beta(1 - \beta)\sigma^2 > 0. \tag{7}$$

Indeed, without (7), the next inequality follows for $z > 0$:

$$\Phi(z) \geqslant J(z; 0, +\infty) = E^z \left[\int_0^\tau \frac{q Z_t^{1-\beta}}{1-\beta} e^{-\delta t} dt \right] = \frac{q z^{1-\beta}}{1-\beta} \int_0^{+\infty} e^{-\lambda_1 t} dt = +\infty. \tag{8}$$

2.3 Hamilton–Jacobi–Bellman equation

Application of the conventional dynamic programming principle to the value function Φ formally leads to the HJB equation

$$\min \left\{ \min_{u \in U} L\Phi,\ \Phi - \frac{1}{1-\alpha} z^{1-\alpha} \right\} = 0, \qquad z > 0 \tag{9}$$

subject to the boundary condition $\Phi(0) = 0$, where

$$L\Phi = \delta\Phi - (r - R - pu) z \frac{d\Phi}{dz} - \frac{\sigma^2}{2} z^2 \frac{d^2\Phi}{dz^2} - \frac{q + wu}{1-\beta} z^{1-\beta}. \tag{10}$$

The HJB equation (9) is a variational inequality of the non-linear degenerate elliptic type.

3 Main results

3.1 Exact solution

The HJB equation (9) is analytically solved and the candidate of the value function as its solution is presented in this section. For the sake of brevity of descriptions, the following quantities are introduced:

$$k_1 = \frac{1}{\sigma^2}\left(\frac{\sigma^2}{2}+R-r+\sqrt{\left(\frac{\sigma^2}{2}+R-r\right)^2+2\sigma^2\delta}\right) > 0, \tag{11}$$

$$k_2 = \frac{1}{\sigma^2}\left(\frac{\sigma^2}{2}+p+R-r+\sqrt{\left(\frac{\sigma^2}{2}+p+R-r\right)^2+2\sigma^2\delta}\right) > 0, \tag{12}$$

$$\lambda_2 = \lambda_1 + p(1-\beta)\ , \tag{13}$$

$$B_1 = \frac{q}{\lambda_1(1-\beta)} > 0, \quad B_2 = \frac{q+w}{\lambda_2(1-\beta)} > 0, \tag{14}$$

$$A_i = \frac{\beta-\alpha}{(1-\alpha)(k_i-1+\beta)}\bar{z}_i^{-(k_i-1+\alpha)} > 0 \text{ for } \quad i=1,\ 2, \tag{15}$$

$$\bar{z}_1 = \left[\frac{(1-\alpha)(k_1-1+\beta)q}{(1-\beta)(k_1-1+\alpha)\lambda_1}\right]^{\frac{1}{\beta-\alpha}} > 0, \tag{16}$$

$$\bar{z}_2 = \left[\frac{(1-\alpha)(k_2-1+\beta)(q+w)}{(1-\beta)(k_2-1+\alpha)\lambda_2}\right]^{\frac{1}{\beta-\alpha}} > 0, \tag{17}$$

and a critical quantity ω to categorise the type of the resulting optimal migration strategy

$$\omega = pq(1-\beta) - \lambda_1 w. \tag{18}$$

The condition $k_1 > k_2$ follows from a straightforward calculation. In addition, $\lambda_2 > \lambda_1$ follows from $\beta < 1$ and $p > 0$.

The proposition below provides a candidate of the value function as a (viscosity) solution to the HJB equation (9).

Proposition 1. *If* $\omega \geqslant 0$, *then the function* Φ_1 *that belongs to* $C[0,+\infty) \cap C^1(0,+\infty)$ *and* $C^2\left((0,\bar{z}_1)\cup(\bar{z}_1,+\infty)\right)$ *and expressed as*

$$\Phi_1(z) = \begin{cases} A_1 z^{k_1} + B_1 z^{1-\beta}, & 0 \leqslant z < \bar{z}_1 \\ \frac{1}{1-\alpha} z^{1-\alpha}, & z \geqslant \bar{z}_1 \end{cases} \tag{19}$$

satisfies the HJB *equation (9) except at* $z = \bar{z}_1$ *in the classical sense. In addition,* $u^*(z) = 1$ *for* $0 < z < \bar{z}_1$*.*

On the other hand, if $\omega < 0$ *and* δ *is sufficiently large, then the function* Φ_2 *that belongs to* $C[0, +\infty) \cap C^1(0, +\infty)$ *and* $C^2\left((0, \bar{z}_2) \cup (\bar{z}_2, +\infty)\right)$ *and expressed as*

$$\Phi_1(z) = \begin{cases} A_2 z^{k_2} + B_2 z^{1-\beta}, & 0 \leqslant z < \bar{z}_2 \\ \frac{1}{1-\alpha} z^{1-\alpha}, & z \geqslant \bar{z}_2 \end{cases} \tag{20}$$

satisfies the HJB *equation (9) except at* $z = \bar{z}_2$ *in the classical sense. In addition,* $u^*(z) = 0$ *for* $0 < z < \bar{z}_2$*.*

Proof: The proposition can be checked through a direct and elementary calculation except for the results $u^*(z) = 1$ for $0 < z < \bar{z}_1$ when $\omega > 0$ and $u^*(z) = 0$ for $0 < z < \bar{z}_2$ when $\omega \leqslant 0$ with sufficiently large δ. Here, only the result $u^*(z) = 1$ for $0 < z < \bar{z}_1$ is proven, since the other follows in a similar way.

According to the HJB equation (9), the optimal control $u^*(z)$ for each given $z > 0$ minimises the quantity

$$f(u) = u\left(pz\frac{d\Phi}{dz} - \frac{w}{1-\beta} z^{1-\beta}\right), \quad u \in [0, 1]\,. \tag{21}$$

Therefore, $u^*(z) = 1$ at $z > 0$ when

$$pz\frac{d\Phi}{dz} \geqslant \frac{w}{1-\beta} z^{1-\beta}. \tag{22}$$

A direct calculation shows that Φ_1 satisfies the inequality

$$pz\frac{d\Phi_1}{dz} - \frac{w}{1-\beta} z^{1-\beta} = A_1 k_1 z^{k_1} + \frac{\omega}{(1-\beta)\lambda_1} z^{1-\beta} \geqslant 0,\ 0 < z < \bar{z}_1 \tag{23}$$

when $\omega \geqslant 0$, which is the desired result. ♠

Since the sets $\omega \geqslant 0$ and $\omega < 0$ are disjoint, the function as a candidate of the value function Φ is defined as

$$\Phi_0(z) = \begin{cases} \Phi_1(z) & \omega \geqslant 0, \quad z \geqslant 0 \\ \Phi_2(z) & \omega < 0 \quad \delta \text{ is sufficiently large}, \quad z \geqslant 0 \end{cases}. \tag{24}$$

The verification theorem is a mathematical tool, which is useful especially when judging a candidate of exact solutions to a HJB equation is the value function or not. It turns out the the exact solution presented in Proposition 1 is the value function Φ according to the direct application of the verification theorem [5, Theorem 5.2] where the formal coupled stochastic process (t, Z_t) should be considered instead of Z_t. Furthermore, it can be analytically verified that the value function Φ is not a classical solution belonging to $C^2(0, +\infty)$ but a viscosity solution (appropriate weak solution) to the HJB equation (9) in the sense of Øksendal and Sulem [5, Definition 9.1]. It is sufficient to check the viscosity property at $z = \bar{z}_1$ when $\omega \geqslant 0$ and at $z = \bar{z}_2$ when $\omega < 0$ where Φ is not twice continuously differentiable. The following result shows a consistency between the value function and the HJB equation.

Proposition 2. *The function Φ_0 is the value function Φ. In addition, it is a viscosity solution to the* HJB *equation (9) that is continuous in $[0, +\infty)$ and satisfies the boundary condition $\Phi(0) = 0$.*

An important by-product of Proposition 2 is the following result that characterises the optimal timing τ^* of radical migration.

Proposition 3. *The optimal timing τ^* of radical migration is characterised with $\bar{z}_i$ as*

$$\tau^* = \inf\{t > 0; Z_t > \bar{z}_i\} \tag{25}$$

where $i = 1$ if $\omega \geqslant 0$ and $i = 2$ if $\omega < 0$ and δ is sufficiently large.

Thus, the animal migration is determined by the lack of twice differentiability of the value function.

In summary, the HJB equation (9) is exactly solved, and the couple of optimal controls (u^*, τ^*) was effectively characterised with its viscosity solution.

3.2 Practical implications

By Proposition 1, it is clear that $\Phi(z) \geqslant 0$ for $z \geqslant 0$ and $\Phi(z_1) \leqslant \Phi(z_2)$ for $0 \leqslant z_1 \leqslant z_2$. This implies the intuitively reasonable result that the population with a larger biomass would gain larger profit. This result would be correct for the population living in a habitat having a sufficiently high environmental capacity; however, it may not be so if the environmental capacity is small and internal competitions among the individuals in the population is not negligible.

Since parameter dependence of the threshold values $\bar{z}_i$ is known from (16) and (17), dependence of the radical migration on the environmental conditions can be investigated analytically. (16) and (17) show that the increase of q, namely the quality of the current habitat, increases the threshold value of migration. Since the SDEs (1) and (2) are not dependent on q, it is readily seen that τ^* increases almost surely as q increases. The exact solution therefore implies that the population, if there is no gradual migration, resides in the current habitat longer as the habitat quality increases.

A key in the present mathematical model is the sign of the quantity ω in (18) that governs the occurrence of gradual migration. The mathematical analysis results imply that $u^* = 0$ and $u^* = 1$ coexist when $\omega < 0$ and δ is not so large. It is important to note that (18) shows that $\omega \geqslant 0$ if q is sufficiently large, implying that the gradual migration would not occur when the habitat quality is sufficiently high. In this case, the population only radically migrates from the current habitat to the next one.

In practice, the parameters of the SDEs (1) and (2) can be directly estimated from biological observation data. On the other hand, the parameters in the performance index J would possibly be only indirectly estimated from qualitative observational data such as the occurrence of the gradual migration. Observing occurrence of the gradual migration would be helpful to restrict possible parameter values via the sign of the critical quantity ω. If the gradual migration is negligible, then observational data of the timing of radical migration can be effectively utilised for estimation of the parameters involved in J.

Finally, I examine consistency of the present exact solution with a real animal migration, focusing on the spring upstream (juveniles) and autumn downstream (adults) migrations of *Plecoglossus altivelis* (*P. altivelis*, Ayu): a major inland fishery resource in Japan having a one-year life history [7]. Hii River Fishery Cooperatives govern fishery resources in mid- and up-stream reaches of Hii River, Japan, serving as a habitat of *P. altivelis*. Personal communications among myself and officers and union members of the fishery cooperatives implied that *P. altivelis* in Hii River adopt firstly the gradual migration and then the radical migration in spring. The downstream migration occurs in a similar manner. Therefore, the present exact solution with the condition $\omega \geqslant 0$ is consistent with this empirical observation. This result implies that the analysis carried out in this paper is not purely a 'mathematical exercise' and that the exact solution would be a candidate for an mathematical tool for analysing the fish migration despite the model simplicity. Since we already have some of the biological parameters of the fish in Hii river [6], (18) will be effectively used for estimation of the other parameters in the upstream and downstream migrations. This will be addressed elsewhere.

4 Conclusions

A new solvable stochastic control model for animal migration is presented in Section 2, and the associated HJB equation is derived in this section as well. An exact viscosity solution to the HJB equation is found in Section 3, which turned out to be the value function in the same section. In Section 3, its parameter dependence is examined with an emphasis on fish migration as well. The mathematical analysis results demonstrated that the model from the new standpoint, although it is conceptual, is consistent with the empirical observations of fish migration.

Future research will address the problem where $u^* = 0$ and $u^* = 1$ coexist ($\omega < 0$ and δ is not so large). At this stage, it is not clear whether such a solution can be found analytically or not. Application of an appropriate numerical scheme, such as the verified finite difference schemes [3, 7], to the SDE equation is a possible option to resolve this issue. In parallel to the mathematical analysis, field observations of fish migration in a Japanese river will also be carried out. The observations will focus on spring upstream migration of P. altivelis. We will observe temperature and hydrological dependence of the fish migration. Whether this paper is truly a 'mathematical exercise' or not can be judged through its validation with field observations.

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Author address

1. **H Yoshioka**, Faculty of Life and Environmental Science, Shimane University, Nishikawatsu-cho 1060, Matsue, Shimane, 690-8504, Japan.
`mailto:yoshih@life.shimane-u.ac.jp`
orcid:0000-0002-5293-3246