Letters to the Editor
Salmon Migration

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In a previous paper (SAILA and SHAPPY, 1963) some of the observed behaviour of migrating salmon was summarized and some calculated statistics obtained from a Monte Carlo random walk were reported. It is gratifying to note that this work has prompted further consideration of the problem (PATTEN, 1964).

Our model was criticized because "it requires some highly restrictive assumptions in order to be applied." We now recognize that a clearer distinction should have been made between those aspects of the model which bear directly on the real world and those which are artificial and arbitrary and serve only to formulate a workable computer programme. The distance between the feeding ground and the natal stream as well as swim speed and maximum search duration all have natural counterparts, and the values used in the simulation were taken from the range of those available in the literature. Pessimistic values were chosen so that our conclusions could be deemed plausible from limited field studies. More accurate estimation of the parameters will be possible from future field work. The actual procedure followed by a salmon in conducting its migration is unknown and since we feel that sophisticated processes should not be postulated until the simpler ones prove inadequate, we suggested a slightly biassed random walk process. We never intended to imply belief that the migrant actually conducts itself according to the protocol used in the computer programme. The concepts of discrete steps, equiprobable choice of direction, and step length biassed in proportion to cardioid shaped figures are all artificial mechanisms chosen from a much larger set only for the purpose of specifying a non-ambiguous computer programme. Computed results, however, do compare favourably with reported returns. Therefore, it is not unreasonable to conclude that some form of random search having a homeward bias equivalent to that indicated in our paper can explain successful migration in salmon. We agree that some shape other than a cardioid type curve could have been used. Circles, ellipses, and parabollas were, in fact, considered. Because of the programming method used wherein a step vector is defined by an angle and a length, the rectangular coordinate system of ordinary vector notation was abandoned and the polar coordinate system was used. The parametric form of the cardioid type curve was found simpler and more versatile than the others considered. If the parameter, A, used in our paper is in the range $0 \leq A < 1$, there are no forbidden directions of movement as there are in the circular model suggested by PATTEN.

On the basis of available information, migrants which reach the coast do not return to sea but instead apparently search along the shore. This kind of

behaviour is different from the open ocean searching which is conducted in two dimensions. It follows naturally then that a different sort of model is required for coastal searching, a one dimensional model.

Coastal tag and recapture studies were reported for the coast north of the natal stream. Recaptured migrants were caught south of the release point and although this might indicate unerring choice of swim directions, we deliberately retained the random walk model (which allows northward swims away from home as well as southward swims toward home). A slight homeward bias was added to the northern coastal model. Also, no reported studies for the coast south of the natal streams were found. Therefore, the one dimensional random walk on the coast south of home was unbiassed.

Water temperature or characteristics of the shore at the extremities of the coast in the Arctic Circle and the tropics may well serve as reflecting barriers to orient the migrants toward home. The Alaskan coast extends westward into the open ocean and thus further reduces the chance of fruitless searching on the high seas. None of these effects were permitted in the model. As emphasized in our paper, these deliberately severe coastal models were designed to assure pessimistic estimates of return probability. This was done partly because the model neglects mortality as well as incomplete tag reporting and partly to emphasize the accuracy of biassed random searching.

As indicated in our paper, the model parameters were varied one at a time to satisfy ourselves that relative frequency of returns varied as expected. For example, increased duration of search was accompanied by increased returns.

The particular values used for the model parameters in nearly all the simulations were taken from the literature as described above. We set a goal of approximately 1/3 for acceptable return probability and continued the calculations to find the minimum bias that yielded the required return probability. A bias indicated by $A = 0.25$ seemed adequate but the larger bias indicated by $A = 0.3$ was reported in the summary and was used in the graphical illustration of bias in Figure 1. Thus of all the parameters used, only maximum step length was arbitrarily chosen for the particular model reported in the summary.

Except for the postulated sun compass, our open ocean model was kept completely devoid of all possible effects related to biological processes. It is known that salmon can perceive differences in water temperature, salinity, density, and pressure and that they are capable of olfaction and are affected by currents and possibly by visual and auditory stimuli. A model which postulates directed movements resulting from such effects requires greater justification than is available from observations to date. In fact, the success of our model suggests that some further investigations should be conducted to discover mechanisms which would explain the existence of a slight homeward bias rather than mechanisms which allow precise orientation or directed movement.

We also agree with PATTEN that increased accuracy of direction choosing on the part of a migrant fish may occur as it approaches progressively closer to home. For reasons given previously, this effect was not permitted in our model. However, the higher percentage loss which occurred on the coast in our model was not due to the severity of the coastal model. This loss is expected and is interpreted as a consequence of the fact that maximum search time is usually more than adequate for the open ocean search. If the feeding area were only 100 miles from the coast, the coastal percentage loss relative to the percentage loss at sea would be even higher.

The paragraph in PATTEN's paper following the label, "The Rational Decision Process" is a correct paraphrase of SIMON, 1957, p. 24. Also, PATTEN's four rational decision rules are almost identical to the rules given in SIMON, pp. 245–46. We question whether the model presented by PATTEN adapted from SIMON can be made to apply to the migration problem for reasons which follow. The reader is referred to SIMON, Chapter 15, pp. 262–65, in order to judge the validity of this assertion.

(1) SIMON's food-seeking organism is constrained to search along a tree-like space in which each "branch point" can be reached by only one path and can be left along an average of d paths[1].

In conversation Dr. SIMON has indicated a tree-like space was justified because his was a purely decisional model. It was not intended for spatial searching. In this type structure the organism can see an average of d points at a distance of one move away and d^ϑ points at a distance of ϑ moves away. In a two dimensional plane, the number of points visible at a distance of ϑ units varies in proportion to d times the square of ϑ. The probability of seeing a food pellet (or a point where $U = 0$ in PATTEN's use of the model) is considerably reduced when the variable ϑ is removed from the exponent.

(2) In SIMON's model the food pellets are distributed randomly and uniformly, i.e., it is equiprobable that any branch point contains a pile of food and this probability (10^{-4}) does not change as the search progresses. This condition is incompatible with PATTEN's own assertion (a likely one) that, "satisfactory behaviour alternatives are harder to find at sea than inshore."

Furthermore, in PATTEN's model the probability of finding a favourable branch point tends to zero, as the migrant wanders away from the path it travelled as a juvenile.

(3) PATTEN correctly names the four important parameters in SIMON's model and calls one of them "the maximum number of moves permissible" before "becoming irreversibly lost". This parameter, indicated by H in SIMON, represents "the maximum number of moves the organism can make between meals without starving." In SIMON's model, this parameter represents the maximum duration of search before the occurrence of a well defined condition, i.e., starvation. PATTEN's counterpart parameter measures an ambiguous condition. Even if we assume that migration is connected with a rational decision process, the migrant can be unaware of his position and orientation for nearly the entire migration season. If that migrant happens upon familiar territory (say the mouth of the natal stream) while it still possesses sufficient energy to swim upstream to the spawning grounds, then the condition of "irreversibly lost" vanishes.

This objection might be made clearer if the reader will recognize that the parameter, H, is not related to the total endurance of the migrating organism (175 days in our model). Note that after each meal, SIMON's organism is allowed another H moves. Analogously, after each move where the animal decides not to change direction $(U = 0)$ PATTEN's fish is allowed H moves during which to find another such point.

(4) We feel PATTEN's paper could have been less misleading if his use of terminology such as "probability of not becoming lost" was explicitly stated as being distinct from our term "return probability".

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[1] The original notation used by SIMON will be used throughout.

(5) The probability, Q, calculated by SIMON is that the organism will survive from meal to meal. PATTEN correctly indicated that return probability is calculated by raising Q to the K power where "K moves (are) required to reach the final destination" (We presume K is the *minimum* number of moves required.) PATTEN, however, did not give any indication of the magnitude of K. Note that as K increases, return probability tends to zero. Also note that no calculation of return probability is given.

SIMON'S Q, the probability of meal-to-meal survival is extremely sensitive to v since this parameter appears in the exponent of an exponent (equation 2·2 page 264 of SIMON). What evidence does PATTEN offer to show that $v = 3$ represents "a *small* (italics ours) capacity for rational search"?

It is not clear to us that PATTEN's model does indeed bear "rather more directly upon the search behaviour as it must actually be expressed in nature."

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Let me state immediately that my treatment of the Saila and Shappy model was not intended so much in criticism as in justification of a more behavioural approach. Some clarification was also felt desirable, and this was the reason for introducing vector notation, which shows explicitly how parameters influence the step vectors in both the sea and coastal phases of the simulated migrations. For example, that the northern case of the coastal search does not really possess a homeward bias (as asserted in the original paper and in the foregoing communication) is immediately apparent from my equation (5), where $Q/2$, the term introduced to provide the bias, is shown to influence the magnitude of a step but not its direction. This actually strengthens the authors' conclusion since the simulations were performed without benefit of a directional bias in the northern coastal case as well as in the southern.

It should be emphasized that the establishment of a small directional tendency as *sufficient* to give return probabilities comparable to those in nature says nothing of *necessity*. In other words precise navigation is not ruled out; only a broader class of possibilities is admitted for consideration than had previously been acknowledged. The rational decision model, based on the known facts of perception by salmon of numerous environmental variables, provides a behavioural framework for further investigations which is sufficiently general to accomodate both the precision navigation and the small bias hypotheses.

The following comments are reactions to the specific points raised above concerning applicability of the numerical extension of the decision model to migration problems. The discussion is largely academic, however, since I feel that SAILA and SHAPPY have already accomplished what can be accomplished with numerical approaches.

1. Equiprobable distribution of food heaps (or clues such that $U = 0$) was adhered to but is not required. This probability could be made a decreasing function of distance from shore to achieve greater correspondence with reality.

2. The condition "irreversibly lost" is not really more ambiguous than that of "starvation". The situation of a "lost" (not "irreversibly lost") salmon suddenly chancing upon familiar territory is analogous to that of a "starving" organism suddenly coming upon a food heap. The model contains provision for such a situation: It corresponds to a long run of $U = 1$ followed by a "strong" $U = 0$ ("strong" implying sharp reduction of ϱ and of members of $A \subset A^*$) and virtually deterministic homing.

3. The "probability of not becoming lost" was denoted by φ, whereas "return probability" was φ^K, K the number of moves required for a successful return. In the example, search time $(\hat{k} - \mu)$ was restricted to 100 moves. Thus, $0 \leq K \leq 100$. In the case where $\varphi = 0.9999$, the return probability for 100 moves would be $(0.9999)^{100} = 0.9908$, very high as originally stated. If $K = 1000$, the return probability would be $(0.9999)^{1000} = 0.9120$, still very high. The value μ (or ν) $= 3$ was regarded as indicative of a *small* capacity for rational search in the context of $(\hat{k} - \mu) = 100$; it would certainly be small in the case of $(\hat{k} - \mu) = 1000$.

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