

# Egrets of a Feather Flock Together

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**Abstract** Group foraging and colonial formation in avian species are examined with an artificial life (alife) model using genetic algorithms (GA) and neural networks. Horn's classical model predicts that colonial birds are more successful than territorial ones in a patchy resource environment, and the reverse is true when resources are evenly distributed. The weak point of the model is confusion between colony formation and flock foraging and implicit assumption of perfect knowledge of resource distribution by foraging birds. The authors made an alife model that realized both flock foraging and colonial formation simultaneously during evolution in a patchy environment. The reference organisms were egrets, which make colonial nests in the breeding season and colonial roosts in the nonbreeding season. In the computer model, artificial egrets used the presence of other egrets as an indicator to locate resource-rich patches in a resource-clumped environment. On the contrary, egrets were less reliant on other individuals as a source of foraging information in evenly distributed resource conditions. Colonial nesting was also induced only in a patchy environment where the foraging efficiency was always higher than the evenly distributed condition. Local enhancement played an important role in achieving colonial and flock foraging.

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## Keywords

egret, local enhancement, flock, colony, heron, neural network

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## 1 Introduction

Group living is one of the most exciting themes in behavioral and evolutionary ecology [36, 12, 33]. The manner of group living ranges from a simple gathering of conspecifics to a systematic social assemblage shown in several social animals [47]. Territoriality is the alternative strategy that is also observed in a wide range of animal taxa. It also ranges from the individual to groups, and further social territoriality [4]. Contrasts between group and solitary living suggest some underlying mechanisms to cause the two strategies to diverge in the course of evolution.

There are two axes to consider in the observation of group living in nature. The first is colonial, or group formation for nesting or roosting. This axis is closely related to the reproductive and mating systems of organisms. The second axis is flock formation during foraging. The two axes may be further divided into two important aspects when we discuss the evolution of group living: predation and efficient foraging.

An antipredator hypothesis can be applied to both colonial and flock foraging. Group living provides selfish benefits to group members, such as the "dilution effect" and the "confusion effect" [23]. It also provides the "many eyes effect" [31, 32] or defensive activity against predators (e.g., mobbing). On the contrary, group living may make groups so conspicuous that predators can easily detect them. Trade-offs between benefits

and disadvantages of group living against predation have been discussed in many theoretical works (e.g., [30, 33]).

The other important aspect of group living is efficient foraging by coloniality and flock formation. Coloniality may provide an information center where roosting individuals exchange information about beneficial patches [13, 45]. On the other hand, flock formation provides “many eyes” for detecting prey and may bring a “beating effect” as observed in cattle egrets [37]. In some avian species, it has further evolved to systematic cooperative foraging as discovered in cormorants [28].

In this article, the authors discuss the evolution of group living with a focus on efficient foraging. Our reference organisms are egrets and herons (Ciconiformes: Ardeidae: *Egretta* spp.) that form heronries in breeding seasons and colonial roosts in nonbreeding seasons. The authors first review two conventional foraging models of group-living organisms in the light of resource distribution. Then the authors introduce an alife model that successfully lead to the simultaneous evolution of colonial and flock foraging by acquiring a simple behavioral rule, *local enhancement*. Finally the results of the simulation are compared with those of several other alife models.

## 2 Conventional Models for Group Foraging

### 2.1 Horn’s Model

Horn’s model [19] has been repeatedly cited to demonstrate the relationship between resource distribution and roosting strategy in avian species (cf. [8]). The model assumes a square universe of  $4 \times 4$  cells, or nodes, and each node is a candidate of a resource patch (Figure 1). Birds inhabiting the universe are assumed to perform central foraging from their nests or roosts. They have two choices: colonial or territorial roosting.

If resources are evenly distributed (upper panels in Figure 1), it is optimal for birds to make territorial roosts (small triangles) from which the individuals only visit four neighboring patches to minimize traveling costs (distance) for foraging. On the contrary, if the same amount of resources are concentrated in a single patch that moves around the universe (lower panels in Figure 1), the birds should form a single colonial roost (the large triangle) at the center of the universe. In general, the model predicts that birds are territorial if resources are evenly distributed. When resources are clumped and highly unpredictable, birds should form colonial roosts.

One weak point of Horn’s model is that both central and group foraging were simultaneously implemented at the beginning. In other words, birds in this model know exactly where resource patches would appear. Moreover, they know how to return to their roosts without wandering. The territorial foragers never explore resource piles in other territories.

The similar misleading simplification may also be seen in famous models of ant trail-making behaviors, which are frequently used as examples of “emergence” in alife studies (e.g., [14]). In those models, ants first start to forage randomly and then form pheromone trails after detecting resource piles. The ants can detect their colony perfectly, and thus return to their colony with relative ease. This efficient colony orientation is fairly unbalanced with their poor ability to find their resources at the beginning of the simulation.

Group foraging can be divided into two phases. At the first phase individuals form the center of their activities, such as a breeding colony and a communal roost. The formation of a colony or a roost ensures that these individuals execute central foraging. The second phase is the formation of flocks at foraging sites. Note that the scale is different between the two phases. The colonial formation is an event at a larger scale or a higher level phenomenon than the flock foraging. Sometimes these two phases are independently evolved, as in the case of the Diurnal Activity Center (DAC), which

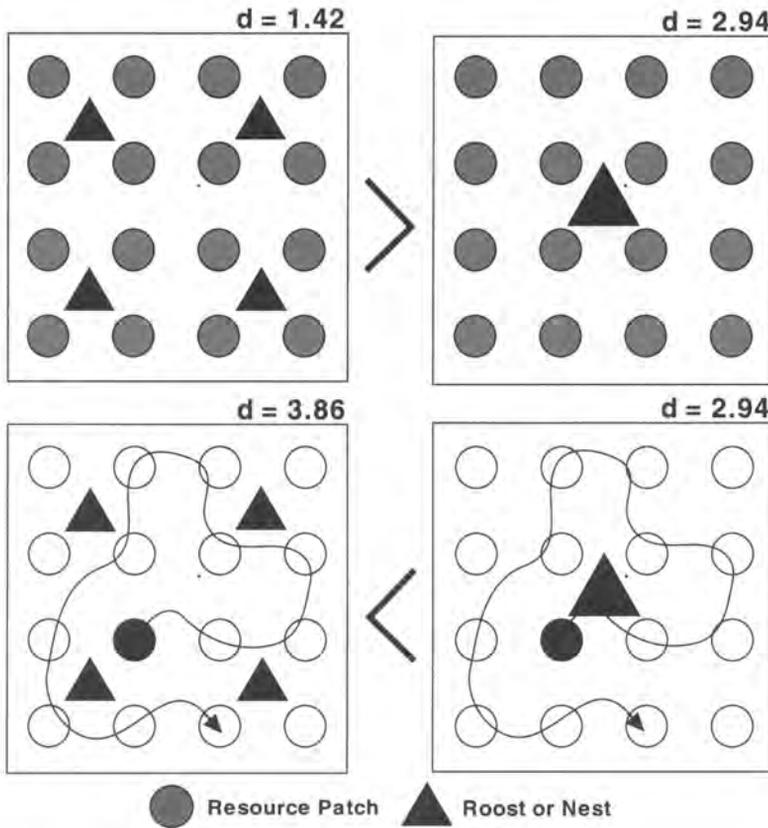


Figure 1. Horn's Model. Circles indicate the location of foraging sites. Triangles indicate the location of nests or roosts. The metric  $d$  is the mean travel distance for foraging from roosts.

was observed in European starlings [9]. However, in herons and egrets, it is likely that these two phases have evolved simultaneously.

## 2.2 Flock Foraging and Local Enhancement

Flock formation causes foraging efficiency in several ways, such as the beating effect, the many eyes effect, cooperative systematic hunting, and the copying of efficient foragers. The target statistics are the mean and the variance of an individual's intake within flock foragers. Flock foraging causes not only high mean values but also less variation in an individual's intake among flock members [11]. This low variability among flock foragers reduces the risk of a no-capture experience for each individual [38]. Several field studies showed that high mean and low variance of intake were achieved in avian species (e.g., [5, 6, 28]).

A key aspect is information parasitism among flock members. There are several ways to accomplish this parasitism, such as the information center strategy [5, 6], social learning, or copying the foraging tactics of skillful flock mates [38]. Among them, local enhancement is the simplest way in which foragers use the existence of other individuals as a key for finding beneficial foraging sites [39]. This simple rule is adopted in herons and egrets in nature [2, 44, 46].

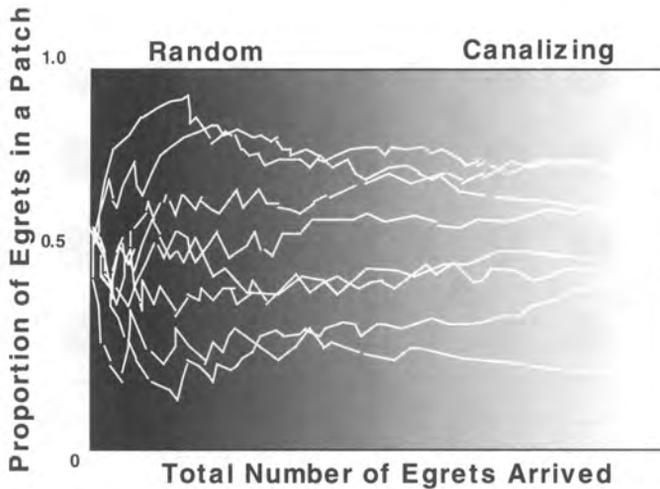


Figure 2. Poly-Eggenberger process.

Local enhancement can be expressed using the Poly-Eggenberger process [3, 43]. The formulation is as follows:

$$\Pr \left[ \bigcap_{j=0}^k (X_j = x_j) \right] = \binom{n}{x_0, x_1, \dots, x_k} \frac{\prod_{i=0}^k c_i(c_i + 1) \cdots (c_i + x_i - 1)}{c(c + 1) \cdots (c + n - 1)}$$

$$c = \sum_{j=0}^k c_j, \quad n = \sum_{j=0}^k x_j$$

where  $k$  is the number of patches,  $n$  is the total number of foragers arriving in the patches,  $c_j$  is the initial number of foragers in each patch, and  $x_j$  is the number of foragers added in each patch.

An assumption is made that there are only two patches that egrets choose for foraging sites. If there is no resource depletion in each patch, the change in the proportion of egrets at one site corresponds to a stochastic process described in the above formula. This process consists of two phases. The first phase resembles an ordinal random walk, but it soon changes over time to a specific canalizing phase (Figure 2).

If resource are clumped, the canalizing phase of the Poly-Eggenberger process continues to gather foragers until resources are completely depleted (the left panel of Figure 3). Poorer patches should be refused quickly, and egrets should be attracted more and more by those patches that contain other egrets. This process guarantees a high mean and low variance of an individual’s intake within flock members. On the contrary, if the resource is evenly distributed, the canalizing phase will seldom be achieved due to the frequent occurrence of resource depletion in each patch. Thus, the dynamics of foragers cannot be distinguished from a simple random walk (the right panel of Figure 3).

This mathematical formulation unfortunately becomes intractable in an analytical sense when resource depletion is incorporated. If a numerical calculation is the only way to solve this formulation, there is no advantage in pursuing this top-down

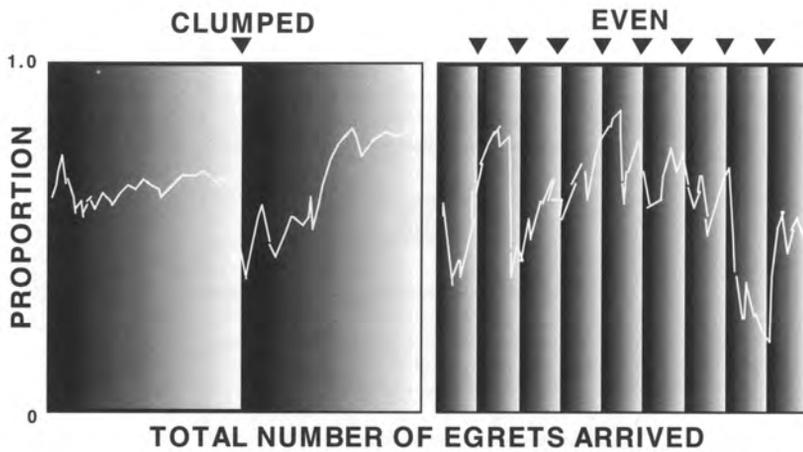


Figure 3. Poly-Eggenberger process with resource depletion.

Table 1. Relative Prey Abundance for Land Types

Land Type	PL	SW	PL SW	DW	DL	LF SW	LF
Value	3	2	3	0	0	4	3

approach. It cannot create alternative foraging behaviors because they have to be pre-specified at the beginning of the simulation. Our interest is not only to compare the benefits of alternative strategies, but also to foster those strategies in given environments.

### 3 Model: Wandering Egret Brains

The common problem of the above two conventional models is that they can only compare the evolutionary strength (e.g., in terms of Evolutionarily Stable Strategy (ESS)) of contradicting foraging strategies that are previously prepared or specified by the modelers. In real nature, foraging strategies should have emerged during evolution under given environments. Moreover, the above two models do not explain emergence of central foraging, per se. To achieve the simultaneous emergence of central and group foraging, the authors constructed an alife model to simulate foraging strategies of egrets equipped with self-reference neural networks.

#### 3.1 Foraging Arena and Egret's View

Artificial egrets forage in a habitat of 30 × 30 cells. Each cell is assigned one of seven types of land use. They are paddy land (PL), shallow water (SW), PL & SW, Deep Water (DW), Dry Land (DL), Lotus Field (LF), and LF & SW. These seven types of land use are commonly observed in the habitat of natural egrets and herons around Tsukuba, Ibaraki prefecture, in the middle part of Japan. The amount of prey in each cell is assigned by a random variable obeying  $\beta$ -distribution under a constraint that the total amount of the resource is 3,000. Each cell is then assigned an appropriate land type depending on the relative abundance of prey density (Table 1).

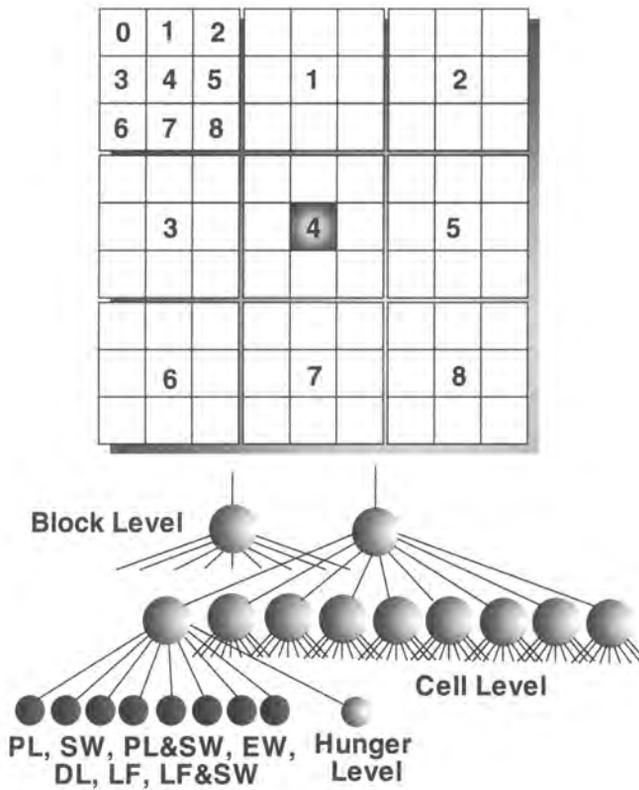


Figure 4. Egret's view and action network.

The prey amount in a cell decreases by a unit when the cell is foraged by an egret. If at least one egret is foraging in a cell, the cell is labeled as White Egret (WE) instead of the initial cell type. Thus, a foraging egret may choose from a total of eight cell types. Each egret can view  $9 \times 9$  cells around itself (Figure 4). The 81 cells are further divided into nine blocks, and each block consists of nine cells. A foraging egret is assumed to be standing or flying at the fourth cell in the fourth block (the shaded cell in the upper panel of Figure 4). There is no reflection at the edge of the arena, and an egret disappears from the arena if its  $9 \times 9$  view protrudes the edge.

### 3.2 Action Network

An individual egret has a three-layer action network for its foraging behavior (Figure 4). At the lowest level, there are nine nodes. Eight of them correspond to eight cell types (PL, SW, PL & SW, DW, DL, LF, LF & SW, and WE). Each node returns 1 or 0 depending on whether it matches the type of the patch at which the egret is looking. The ninth node receives the egret's hunger level as the input value. The hunger level is the amount of prey that the egret has obtained so far. The second layer of the neural network corresponds to each cell in a block of an egret's view. Every node has an identical nine-footed network. Each node at the top layer corresponds to each block of an egret's view.

Note that this network is quite different from ordinal multilayer neural networks. The important point is that the network is a simple assemblage of a nine-footed basal node (Figure 5). An intuitive image of this network is as follows. First a single-eyed

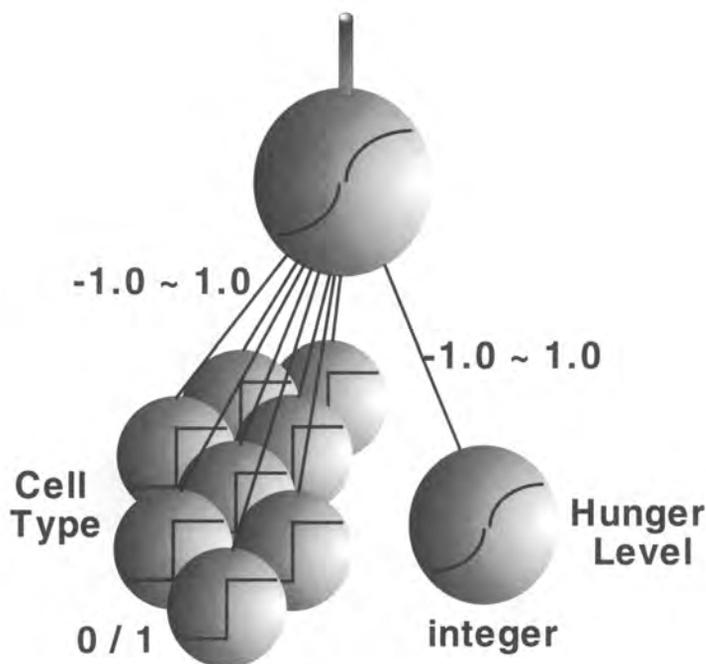


Figure 5. Structure of a basal node.

egret views 81 cells with its eye that consists of nine nodes. A total of 81 inputs are further subtotaled into nine blocks. Thus, the layers of this network simply correspond to a hierarchical view of egrets rather than the nonlinear propagation of input signals in ordinal neural networks.

### 3.3 Foraging and Reinforcement Learning

The weight of each path of the neural network is an important aid in the evolution of foraging behavior. Each egret has a set of nine bit strings, each of which encodes the weight value of each path in the nine-footed network. The weights are real values and are initially specified randomly with a range from  $-1$  to  $1$ . These values are later modified by GA operations in the course of evolution.

Ackley and Littman's approach [1] is applied to accomplish reinforcement learning of the foraging behavior. Other than the big action network consisting of 81 nodes, each individual has a small evaluation network that determines whether reinforcement learning is executed in each foraging bout. The structure of the evaluation net is the same nine-footed network as the lowest nodes in the action network (Figure 5).

Learning by egrets is performed as follows. An egret first looks around and puts down its action network on the 81 cells within its view. The action net quickly subtotaled return values from basal nodes. Then the egret chooses the block that returns the maximum output value. Next it chooses the cell that returns the maximum output within the chosen block and puts down its evaluation net on the cell. If the evaluation network is fired, the return value from the basal node of the action net is evaluated as the right answer. If the return value is positive, the desired target is set to  $1$ . If the return value is negative, the desired target is set to  $-1$ . Then the weights of the nine-footed basal node of the action net are rearranged to achieve the desired target as its return value by the backpropagation method (Figure 6).

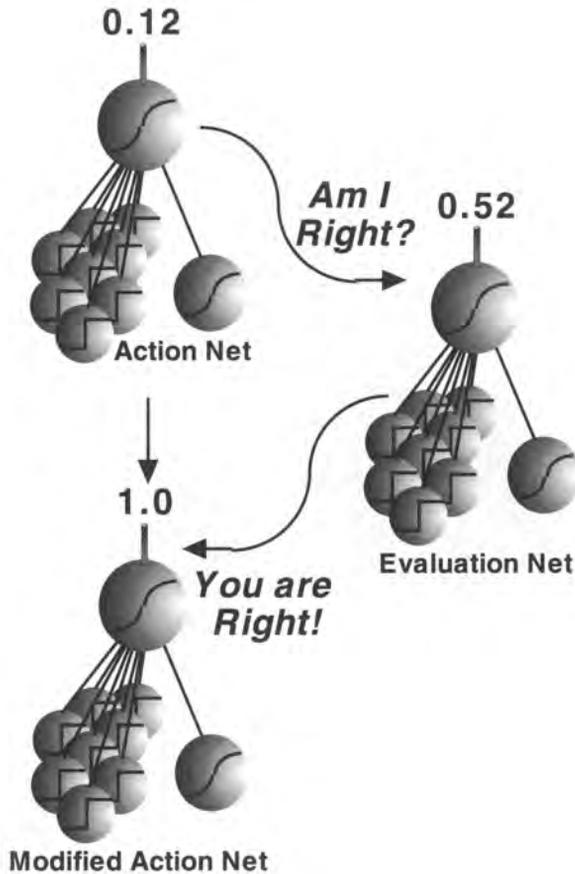


Figure 6. Reinforcement learning.

There are two important remarks. The first one is that all nine-footed basal nodes of the big action network simultaneously change their weights to nine paths. It means that after the reinforcement learning, an egret uses a modified eye for the following foraging. The second point is that the weight change of the paths is not inherited by the next generation. The offspring network weights are the same as those of parents without reinforcement learning if there is no mutation and crossing over.

The cell chosen by the action net is a candidate of landing. If the action net chooses the same cell in the next trial, then the egret lands on the cell and starts foraging. The egret gains a unit of reward if the patch contains some prey. In some cases, the egret does not land on the first chosen cell because the following reinforcement learning changes its preference and the action net does not choose the cell again.

### 3.4 Nesting

In addition to the action and evaluation networks for foraging behavior, each egret has another neural network for nest formation. The network structure is the same as the nine-footed basal node of the action net or the evaluation node. Egrets always have a positive motivation to make nests. Egrets try to seek nest sites every step after choosing candidate cells. Each egret puts its nest formation network on the selected cell. The

Table 2. Realized Frequency of Land Types

Land Type	PL	SW	PL SW	DW	DL	LF SW	LF
Clumped	0	0	0	410	465	25	0
Even	91	397	83	61	54	118	96

decision to form a nest is executed when the sum of the output from the nine-footed node of the nesting net exceeds 0.5.

If the nesting network is fired, the egret puts the net on 81 cells in its view and starts the hierarchical selection of a nest site in the same way that it picks up a candidate cell with its action network. No reinforcement learning was applied for the nest formation. The weights of the nine paths of the nest formation net are also modified by GA operations.

### 3.5 Reproduction

Hunger level is an integer value. The initial hunger level for each egret is five units and it decreases by one unit as time elapses. If the egret hits a prey, he gains five units. Its hunger level is multiplied by five if it returns to its own nest. Individuals that have a hunger level less than unity are eliminated from the foraging arena.

Each individual is constituted of three sets of bit-strings. Each set corresponds to the action, evaluation, and nest-making network, respectively. Each set is further constituted of nine sets of bit-strings that code the weight of paths in the nine-footed networks.

Egrets that make nest(s) are targets of GA operations. Each breeding individual is assumed to be an hermaphrodite. Although no egrets and herons are hermaphrodites in nature, this simplification is valid because no sex-related specificity is implemented in this model. Crossing over is applied among the breeding individuals and they exchange a part of bit-strings that codes the weights of the three networks.

The number of offspring for each individual depends on the hunger level of the mothers. Mutation occurs in the bit-strings of offspring at birth. Offspring start to forage at the nest where they were born.

### 3.6 Initial Settings

The initial population size was 400 individuals who were randomly distributed in the test fields. The crossing-over rate and mutation rate were always set at 0.9 and 0.5, respectively.

The clumped and evenly distributed resource patches were generated with  $\beta$ -random procedure to compare with Horn's model. A static but highly clumped distribution was adopted for the patchy environment instead of an irregularly moving resource-rich patch. The two parameters for  $\beta$ -function were both set to 0.001 in the resource-clumped condition. In the even resource distribution, the two parameters were set to two. Thus, the clumped and even distributions corresponded to the bath-tab and unimodal  $\beta$ -functions, respectively.

The realized frequency of each land type is shown in Table 2. Note that there were only three cell types (DW, DL, LF) in the clumped resource distribution. It was due to the random generator not producing values that corresponded with the other land types. On the contrary, all land types appeared in the even resource environment.

Four replications were conducted changing seeds for the random generator for each resource distribution. All other parameters, such as mutation and crossing-over rates, were common in each replication. Each run was performed for 10,000 generations.

## 4 Simulation Results

There was little variation in the results among the four replications for all aspects of the simulation. Thus, the results are credible despite the small sample size.

### 4.1 Nest Formation

Figure 7 gives a typical example of the change of nest distribution through generations in the clumped and evenly distributed resource arenas. Background patterns show resource abundance. Lighter shades indicate higher resource patches. The maximum and the minimum values are 300 and 0, and they are assigned pure white and pure black, respectively. When the resources were clumped (the left-side panels in Figure 7), egrets formed several large colonies as time elapsed. Note that the colonies were not always located at the resource-abundant cells. Moreover, the largest three colonies seldom changed their location throughout generations.

If the resources were evenly distributed (the right side panels in Figure 7), egrets never formed a large colony during 10,000 generations. Nests were dispersed all over the arena and there was no tendency to locate the nests at resource-rich cells.

In sections 4.2 and 4.3, all figures have the same implementation. For Generations less than 1,000, the resolution of the graphs is set to 10 generations. For 1,000 or more generations, the resolution was set to 100 generations. Thus, the graphs look busy during the first 1,000 generations and become calm in the following generations. All statistical analyses were conducted with the resolution of 100 generations.

### 4.2 Population Dynamics

Figure 8 depicts a typical example in the change of the total population size of foraging egrets in the two test arenas. The mean population size in the clumped resource condition almost always exceeded that in the even resource condition. The mean population size through generations was significantly larger in the clumped resource condition than in the even resource environment for all replications (mean for clumped = 316.419, mean for even = 228.004, nested ANOVA result was  $F = 325.351$ , d.f. = 7,  $p \ll .01$ ). Irregular fluctuations were observed in the population dynamics with the clumped resource field.

A typical example of the change of  $m^*/m$  of foraging and nesting egrets in the test field is observed in Figure 9. The  $m^*/m$  value in the clumped resource field was much higher than that in the even resource field (mean for clumped = 60.112, mean for even = 5.176,  $F = 3317.156$ , d.f. = 7,  $p \ll .01$ ). However, the tendency of foraging egrets to form flocks was not constant and was highly variable throughout generations under the clumped resource condition.

Figure 10 shows the number of landings by foraging egrets on each patch type. In the resource clumped field (upper panel of Figure 10), most egrets landed on the patch where other egrets were foraging (labeled as WE). The magnitude of the number of egrets landing on the WE cells was much higher than in the other cell types. The second best is LF, which was assigned the highest reward among the cell types.

The attractiveness of egrets was also prominent in resources that were evenly distributed (lower panel of Figure 10). However, the relative abundance of attractiveness was quite small compared with that observed in the resource clumped field. The second and following best cell types (LF, PL, LF & SW, and PL & SW) shared almost the same amount of relative abundance.

Egrets themselves were attractive while they made nests for breeding in the resource clumped patches (upper panel of Figure 11). However, the dominance of WE was not as strong as the attractiveness in foraging individuals. The second best was LF, which frequently predominated during 10,000 generations.

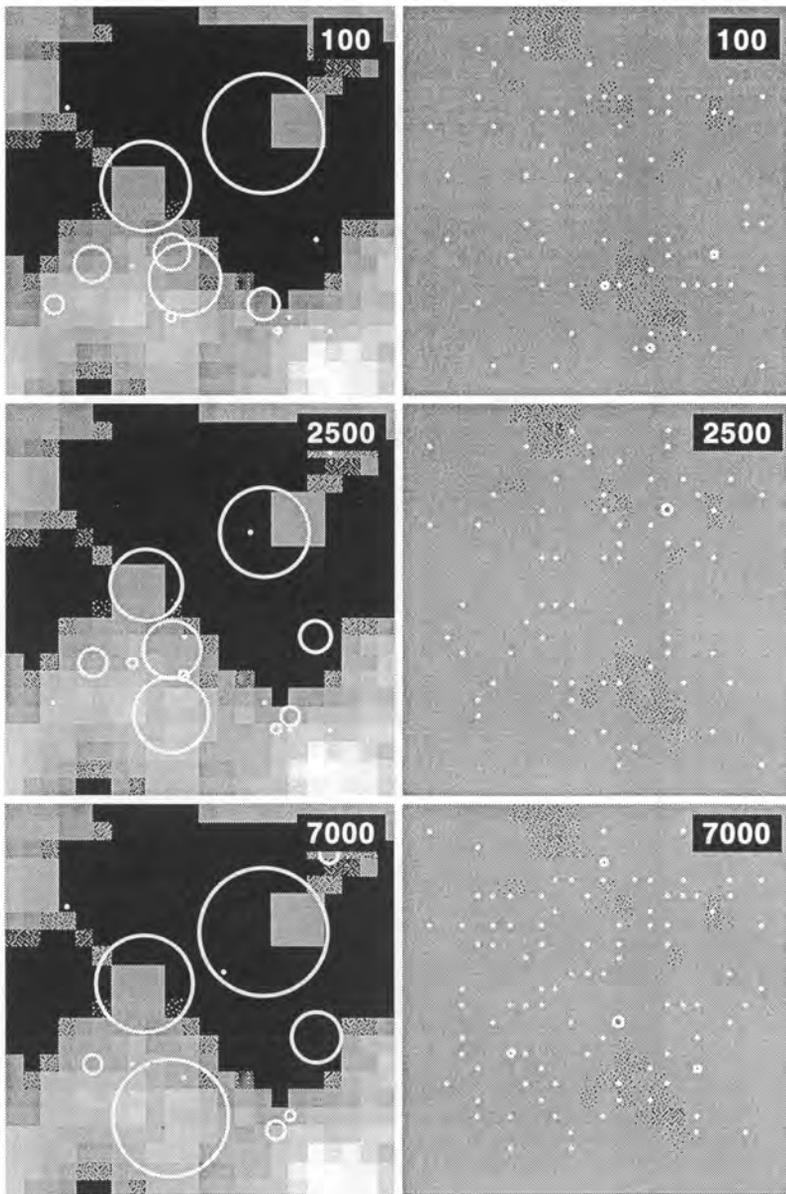


Figure 7. Distribution of nests.

Where resources were evenly distributed, the attractiveness of egrets decreased and the other patch types also attracted nesting egrets (lower panel of Figure 11). The attractiveness of each cell type changed frequently throughout generations.

### 4.3 Analysis of Action Network

Among the three networks implemented, the action net was used in every bout of foraging and nesting, and thus, should have recorded the most important footprints in the evolution of group foraging behavior.

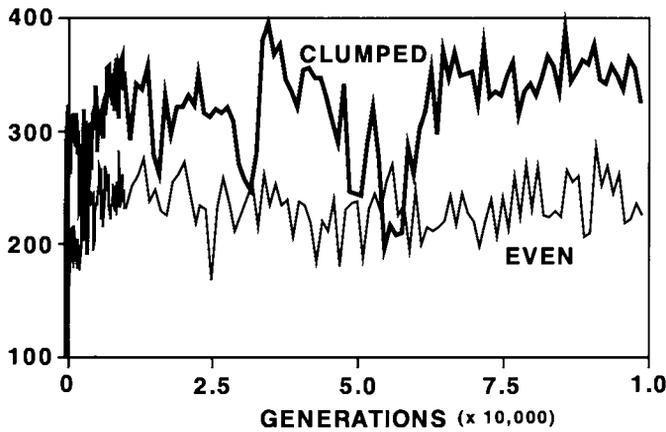


Figure 8. Total number of egrets.

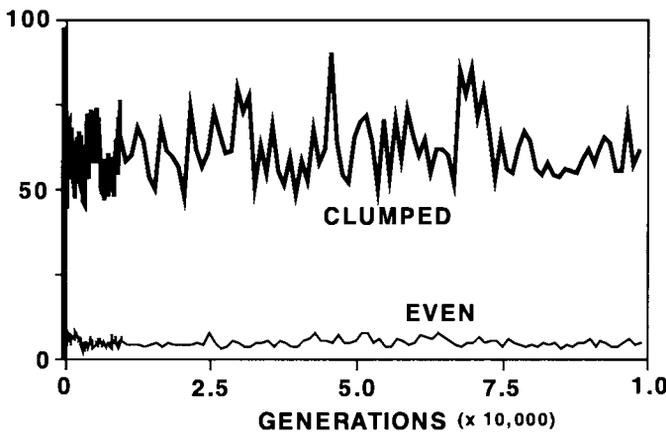


Figure 9.  $m^*/m$  of foraging egrets.

Figure 12 shows the changes in the mean weight for each path of the nine-footed basal nodes in the action network. In the resource clumped distribution (Figure 12), the weights for DW and DL were significantly negative throughout 10,000 generations (sign test,  $p \ll .01$ ) for three replications. On the contrary, weights for LF and WE were significantly positive (sign test,  $p \ll .01$ ). Weights for the other five land types showed neither positive nor negative tendencies. These weights had no correlation between each other.

When resources were evenly distributed (Figure 13), the weights for DW and DL were significantly negative and LF was significantly positive (sign test,  $p \ll .01$ ), as in the clumped distribution. However, the weight for WE did not significantly deviate from zero. Instead the weights for SW and PL & SW were significantly negative for three replicates (sign test,  $p \ll .01$ ). Correlations between these weights were very low and most of them were not significant.

Figures 14 and 15 show the change in the variance of weights for each path of the action network. When resources were clumped (Figure 14), variances were very low

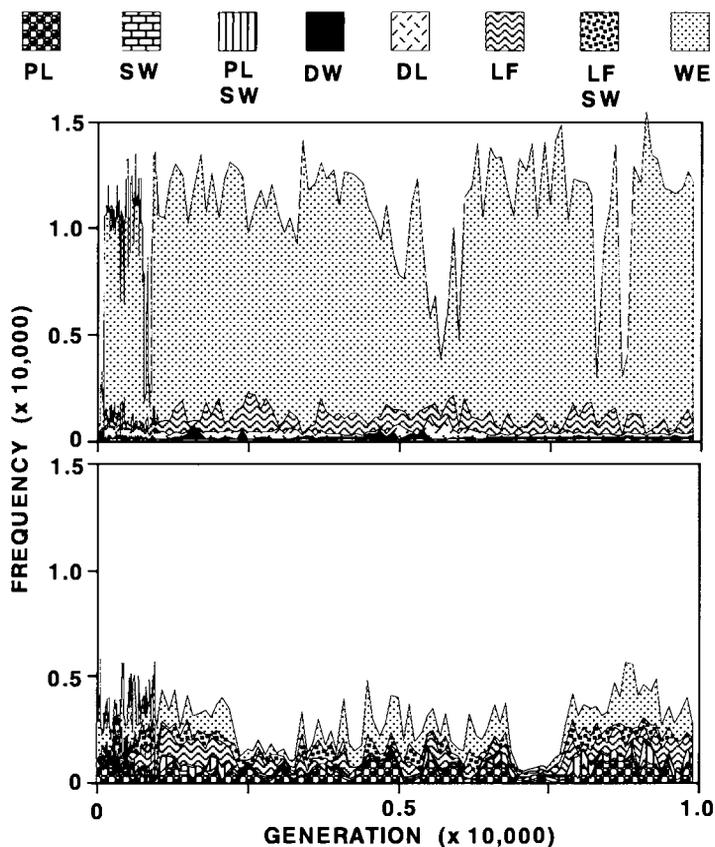


Figure 10. Number of egrets attracted by each cell type during foraging.

for those weights that showed significant deviations from zero (DW, DL, LP, and WE). On the contrary, when resources were evenly distributed (Figure 15), variances were relatively high, even for the weights that showed significant deviation from zero (see DW, DL, and LF).

### 5 Discussion

Our life simulation demonstrates that group foraging and coloniality emerged simultaneously in the patchy environment. The modeled egrets did not have prior knowledge as to which land type had rich resources nor how to change foraging strategies. The authors previously had implemented only simple stimuli from the land types, hunger levels, and random weighting values of neural networks.

#### 5.1 Foraging Behavior

The most interesting and important aspect of foraging behavior is the emergence of local enhancement. This simple and local rule was applied to foraging in the resource clumped environment (Figure 10). Even within an even resource environment, local enhancement was used to some extent (Figure 10).

In the clumped resource environment there were only four cell types. Among them, LF (Lotus Field) contained the maximum amount of prey. Figures 12 and 14 show

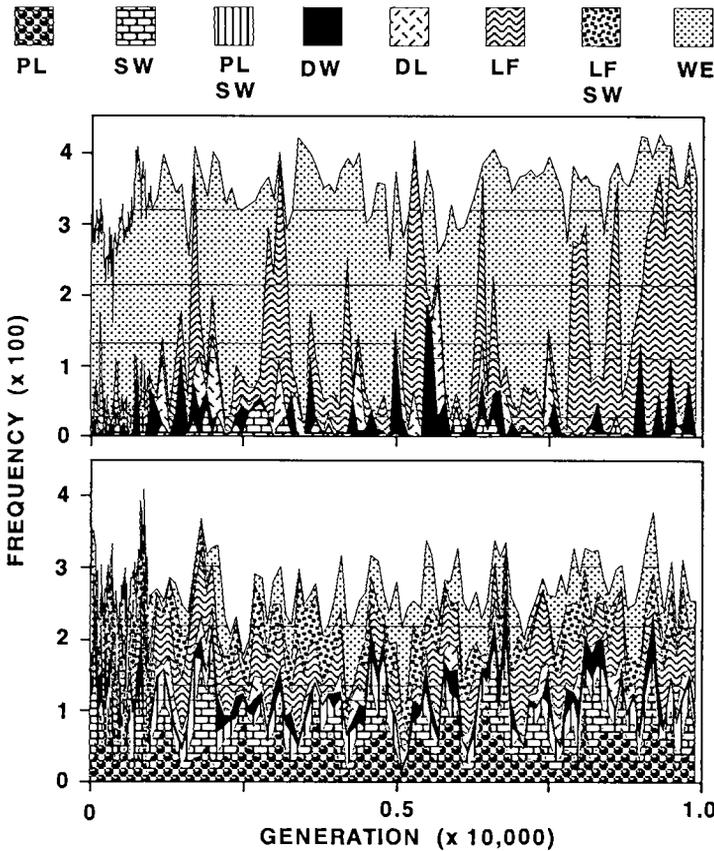


Figure 11. Number of egrets attracted by each cell type during nest formation.

that the weight for LF was nearly one with little variation during evolution. The mean weight for WE (White Egrets) had a greater degree of variance although this was still relatively small and remained positive.

On the contrary, the weights for DW (Deep Water) and DL (Dry Land) never exceeded zero. Thus, the artificial egrets have learned to discriminate good and bad paths using the proximate cue of existence of other egrets in their view. Note that the values for DW and DL came close to zero as generations passed. This may correspond to the shielding effect as discussed in [1].

Where resources were evenly distributed, the artificial egrets seemed to be confused by variable information on land types. They were thoughtful and landed much less frequently in any kinds of land types than in the clumped resource arena (Figure 10). However, they evaluated correctly that SW, DW, and DL were resource-poor types. The relative resource values for LF, PL, SW, PL & SW, and LF & SW were not so different from each other in the even resource condition. Even in this difficult situation, the egrets seemed to succeed in evaluating LF as the most favorable patch type (Figure 11).

One confusing result was that, even though the weight value for WE showed a negative tendency during the 10,000 generations, the egrets seemed to use the existence of others as a cue for landing during foraging bouts (Figure 10). This may be a result of complicated interactions with other stimuli; however, this consideration is beyond the scope of the crude analysis of the action networks employed in this study.

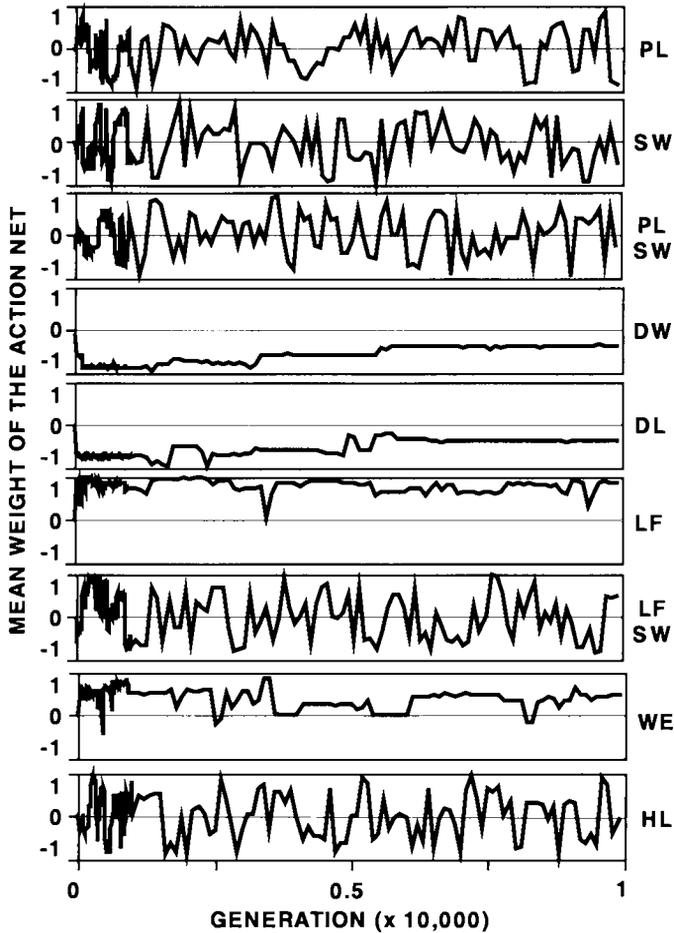


Figure 12. Mean weights for action net in the resource clumped condition.

## 5.2 Nest Formation

Local enhancement also played an important role in nest formation in the patchy environment. The cue of WE was most frequently used as the nesting stimulus (Figure 11). The results from nest distribution suggest that egrets did not always make colonies at the resource-abundant patches (Figure 7).

Moreover, the egrets were conservative about the location of large colonies. This may be simply because all the individuals that had evolved were those that survived and bred in the consecutive generations. Figure 8 demonstrates that the population size dramatically decreased and then rapidly increased at the beginning of simulations. Offspring starting their foraging game at their birth place were the survivors of bottlenecks at the early stage of evolution. In this sense, historicity might have played an important role. The relationship between bottlenecks and philopatry is also discussed in several avian species (e.g., [49]).

In an even resource environment, the existence of conspecifics did not work as a cue for nest formation (Figure 11). The number of nests was fewer than in the clumped resource condition, but the relative nest abundance against that in the clumped distri-

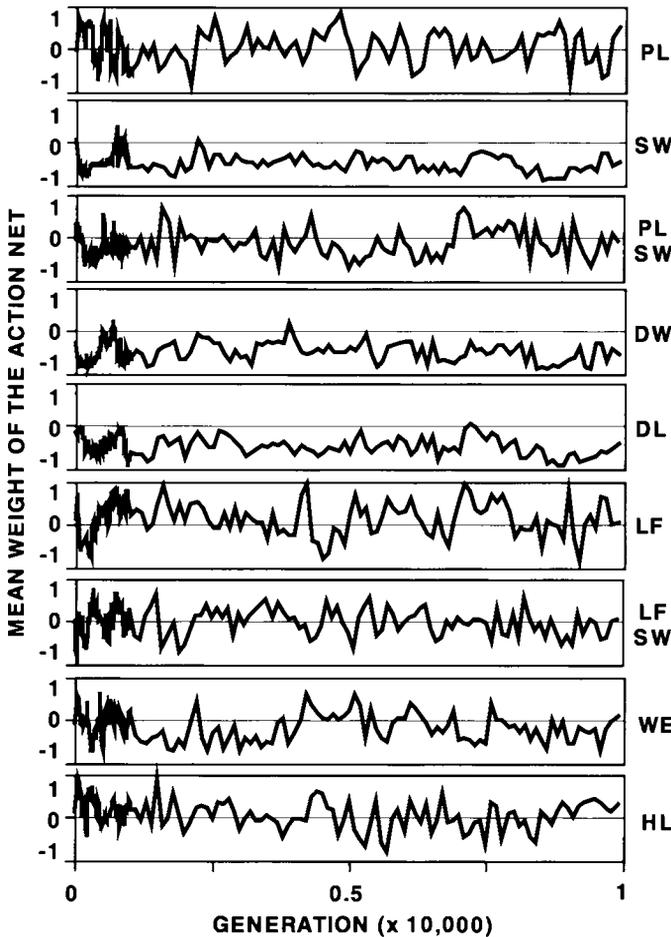


Figure 13. Mean weights for action net in the even resource condition.

bution was much higher than the landing frequency of foraging individuals (Figure 10). Figure 7 also suggests that there was no philopatry in the even resource environment.

**5.3 Information Transfer**

Evolution of coloniality is a controversial topic in behavioral ecology. The Information Centre Theory (ICT) is one of the candidates to explain the colony formation [5, 6, 13, 15]), which is also rejected in some studies (e.g., [27, 35]). In the present alife model, the colonies in the patchy environment were not information centers at all. Rather, information was transferred by simple local enhancement among wandering egrets at foraging sites. Of more interest is that artificial egrets sharing the same colony were often highly related at the “genetic” level. The preference of patch types coded in genetics might generate the leaving patterns that would support the ICT.

Local enhancement has both positive and negative aspects. If the target individual is foraging on a resource-rich patch, it guarantees efficient foraging for the followers. However, an excess of attractiveness accelerates the rate of resource depletion in the patch. Egrets moderately relied on the existence of other individuals where resources

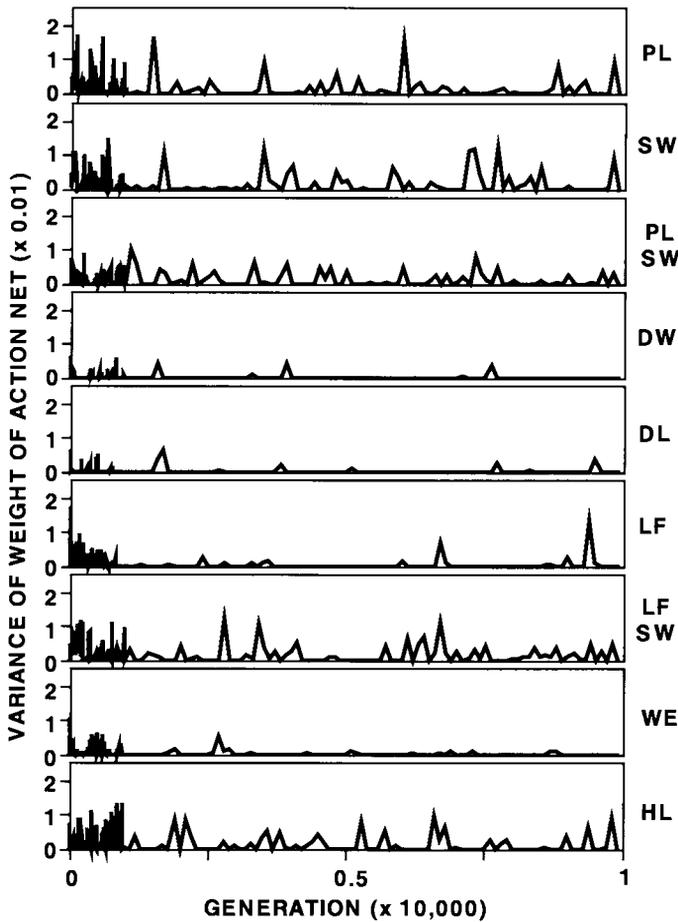


Figure 14. Variance of weights for action net in the clumped resource condition.

were evenly distributed. It is possible that the trade-off between the benefits and costs of social information had been resolved [40, 41].

**5.4 Flexibility and Robustness of Adaptive Behaviors**

Several key aspects require consideration in order to achieve the simultaneous realization of colonial and flock foraging, as developed in the present study. The first is the masking of the land value of patch types. Foraging egrets did not have prior knowledge of the actual resource abundance of each patch. In this sense, the present situation resembles the language acquiring game simulated by MacLennan [25]. The arbitrary matching of actual resource amounts and land types might cause highly fluctuating dynamics in local enhancement (Figures 10 and 11).

The second aspect is an egret’s viewpoint. The model adopted a hierarchical view consisting of 81 cells for each egret. The view enabled the efficient collection and abstraction of information at multiple scales of patches [22]. The number of view layers was fixed in the present model, but it may have been improved if the number of layers was adjustable to resource patchiness.

In order to force aLives to find their own answers to problems, it is necessary for models to be equipped with highly flexible meta-models, such as GA, Cellular Automata

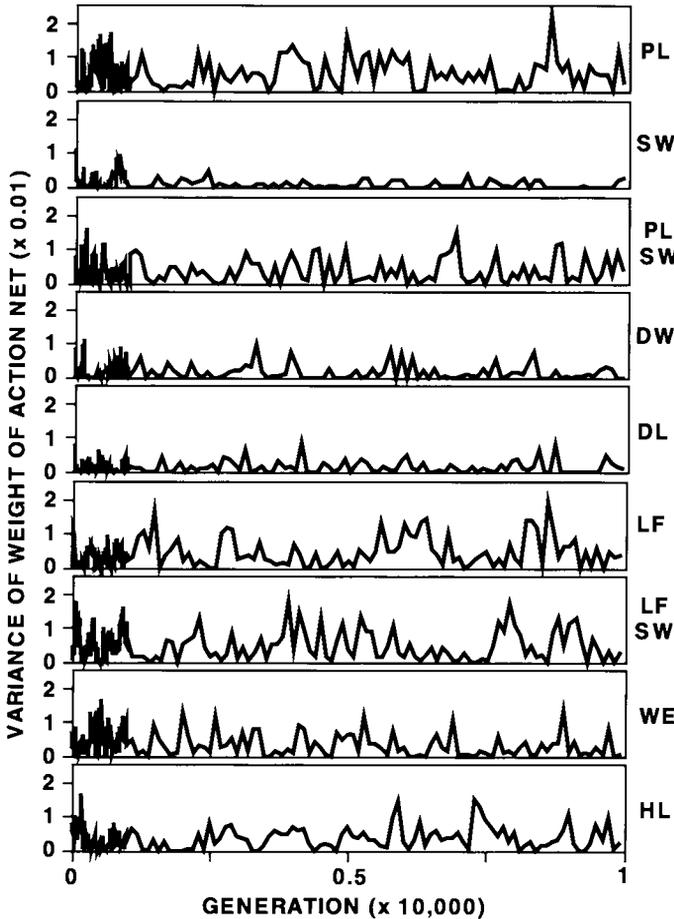


Figure 15. Variance of weights for action net in the even resource condition.

(CA), and neural networks. Combining these meta-models makes alive simulations a more powerful tool to investigate evolutionary processes (e.g., Lindgren’s IPD model [24], Ray’s Tierra [34], and Kauffman’s NK model [21]). Those meta-models are often used for creating open-ended simulations. The concept of open-endedness implicitly means that the systems are robust against changes in the environment. Robustness is achieved by obtaining a high variation in strategies and behaviors to respond to variable situations. Pleiotropy and epistasis in genetic codes are important to realize such robustness in evolving systems.

Models incorporating learning may behave differently from those predicted by optimal strategy models [29]. In the present model, neural networks equipped with GA played an important role in finding robust answers from a huge and complicated domain spanned by parameters.

There was a slight discrepancy between the prediction of Horn’s model and our simulation results. In Horn’s model, the territorial birds gain more in an even resource environment than in a clumped one. In the present model, the total gain was lower in even resource distribution. The answers obtained by iterated learning may not be the optimal answers for our foraging arena. However, the biological environment around artificial egrets changed rapidly and irregularly by interactions among patch qualities

and egrets. To live on in such a situation, egrets should behave robustly rather than optimally.

### 5.5 Territoriality, the Next Target

Many theoretical works and models have asked where birds make colonies and what size the colonies should be (e.g., [7]). Those discussing the relationship of resource distribution are modified version of Ideal Free Distribution models [10, 16, 17]. Birds in the models are fairly omniscient and know exactly where the resource patches are distributed.

Individual Based Models [20] are applied to construct general views of the evolution of coloniality (e.g., [48]). With the help of object oriented programming and artificial intelligence, the models create hypothetical individuals that behave like birds in the computer. The problem is the implementation of each individual. In those models, rules of the birds are all specified by the modeler and there is no emergence of colonial and flock foraging.

The present study succeeded in bringing forth colonial and flock foraging in a patchy environment. However, the artificial egrets could not bring forth territoriality. Territoriality and coloniality sometimes coexist in natural systems [26]. Several avian studies have showed that young birds prefer flock foraging, but the adults prefer solitary or territorial foraging [18, 42].

Among egrets and herons, the foraging behavior varies from species to species. Gray herons (*Ardea sinerea*) and great egrets (*Egretta alba*) prefer to forage in solitary, whereas cattle egrets (*Bubulcus ibis*) often forage in groups. Little egrets (*Egretta garzetta*) often forage in solitary and occasionally form flocks. In the middle part of Japan, these egrets form heterospecific colonies.

What is needed to implement such complex territoriality in the present model? Should putting another basal network and letting it control the repelling behavior against other egrets be considered? How many new neurons are necessary to achieve age-related and species-specific territoriality? In what way can we analyze results of interactions between multiple networks?

In making weak alife simulations, the most important thing that we have to remind ourselves is the elimination of extra information from the target objects. For example, several types of information, such as the absolute coordinate axis and the criterion of good patch, were excluded or masked in the present model. That information might be useful if we try to simulate animal behaviors in the light of the optimal theories or conventional kinetic models for prediction. However, in alife models, not the programmer but the aLives themselves have to seek and obtain what is good behavior in a given artificial world.

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