Evolving an Agent-Based Model to Probe Behavioral Rules in Flocks of Cowbirds

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Abstract

Flocks of brown-headed cowbirds, *Molothrus ater*, self-organize social environments, which have strong impacts on social learning and behavior. To understand the rules underlying self-organization of the social environment, I develop an agent-based model of cowbird social association and evolve it to match observed patterns of association measured from real birds. The behavioral rules evolved in the model provide insight into the type of rules real birds use to organize their social environment. The evolved models successfully predicted both association patterns and additional related movement variables measured from a new flock of birds.

Introduction

Animal behavior often occurs embedded within the complex system of a group of interacting animals; however, traditional methods for elucidating behavioral rules include reductionist techniques that can destroy the very social environment necessary for the behavior of interest (Schank, 2001). Within the last decade, studying animal behavior within its natural, complex context has been enabled through use of agent-based models (Schank and Alberts, 1997; Powell et al., 1999; Schank and Alberts, 2000; Jackson et al., 2004; Bryson et al., 2007; Sellers et al., 2007). These models typically implement hypotheses about how individual animals move, make decisions, etc., and are then evaluated for ability to match emergent properties of situations they model, such as breeding productivity (Powell et al., 1999) or group decision making (Sellers et al., 2007). But this human-designed model building leaves open the possibility that other, non-considered scenarios could also match the observed behavior (Bryson et al., 2007). Schank and Alberts (2000) pioneered a method to address this issue: allowing heuristic search to optimize parameters of an agent-based model, thus reducing bias from pre-conceived notions. Here, I take this approach, developing an agent-based model, and evolving it with a genetic algorithm (GA), to elucidate general principles underlying behavioral rules used in social assortment of brown-headed cowbirds, *Molothrus ater*.

The brown-headed cowbird is an obligate brood parasite: females lay their eggs in the nests of other species, leaving the host species to raise their young. Because of this behavior, cowbirds were long thought to be exemplars of instinctual control of all aspects of social behavior, and in particular, mating behavior (Mayr, 1974). However, modern research revealed that cowbirds rely heavily on social learning for social interactions, including mating preferences and appropriate courtship behavior (King and West, 1989; Freeberg et al., 1995). This learning occurs when adult and juvenile cowbirds gather in large over-winter flocks (Friedmann, 1929; King and West, 1988).

These over-winter flocks have recently been shown to have strong self-organized patterns of social association based on age and sex (Smith et al., 2002). Furthermore, the make-up of the social environment surrounding a juvenile male within this self-organized pattern correlates with his singing behavior and courtship success (Smith, 2001; Smith et al., 2002), and experimentally induced differences in social environment in a flock can radically adjust many aspects of birds' future social and mating behavior (King et al., 2002; West et al., 2002; White et al., 2002a,b,c). Thus, the self-organized social environment provides the scaffold surrounding social learning in this brood-parasitic species.

However, the mechanism behind this self-organization is unclear: it must be assumed some preferential approach or avoidance occurs, but features such as specificity of preference and if all birds, or only some ages/sexes, drive the patterns, is unknown. To investigate mechanisms underlying such self-organization, I develop an agent-based model of cowbird social association, using a modified classifier system where movement is controlled by a set of interpretable rules. I evolve this model to match the self-organized association patterns seen in one group of birds, then use the evolved models to predict association patterns as well as other movement variables from a new group of birds.[1]

Agent-Based Model

Because the aim of this work is to gain insight into rules birds use to self-organize their social environment, I chose to model individual cowbirds as modified classifier systems

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[1]Model and GA created in C++ and available upon request.

(Holland et al., 1986; Booker et al., 1989). The if-then statements in the classifier are easily interpretable as choices made by a bird about its future behavior based on its current environment. The traditional classifier system was modified in two major ways for this agent-based model: (1) choice of classifiers was performed probabilistically based on strength to simulate the stochastic nature of animal behavior and (2) learning did not occur through reinforcement nor evolution of an individual agent's classifiers; instead, all parameters of the model controlling bird behavior, including classifiers, were evolved with a GA based on association patterns resulting from the interaction of multiple agents.

A model was characterized by the number of bird-agents of each of four possible age and sex classes (AM: adult male, JM: juvenile male, AF: adult female, JF: juvenile female) and model parameters controlling the behavior of each class.

Model Parameters

Two activity-state probabilities controlled probability of a bird becoming (1) active if inactive and (2) inactive if active. Only active birds moved in relation to their environment. This distinction allows modeling of situations where birds may be unresponsive to social environment, for example sheltering from weather or predators (Smith, 2001).

A list of classifiers governed each birds' behavior: when the environment matched conditions described by all five bits of an if-statement, the five bits of its then-statement directed a potential behavior (Table 1). The if-statement relates to the social environment: a bird was aware of neighboring birds if they were within 15 units; neighbors were near if within 5 units and far otherwise; neighbors' age and sex was noted; and if this neighbor had the same relationship in the last time step (old) or not (new). Eighteen distinct environmental conditions are thus represented; wild-cards in the if-statement enable a classifier to apply to multiple conditions. The near and aware distances mimic distances relevant to cowbirds: cowbird song degrades rapidly beyond 0.3 m (King et al., 1981), making it a socially relevant "near" distance (Smith et al., 2002); birds engage in social interactions from as far as 0.9 m, and social companions within this distance influence social learning (Smith, 2001).

The then-statement relates to birds' movement choices: whether to move or be still; if moving, to move in a directed manner related to a neighboring bird or randomly; and if moving directed, to move towards or away from the other bird. Additionally, two bits adjusted the overall activity state of a bird, making it active or inactive.

Finally, each classifier had an integer strength S which influenced the probability of its being chosen to perform.

These model parameters are what is evolved by the GA based on assortment patterns arising from individual agent-birds executing repeated classifier system cycles.

Bit	Interpretation of Value	
If	**1 (on)**	**0 (off)**
neighbor	aware of bird	no birds
distance	near	far
age	adult	juvenile
sex	female	male
time	new	old
Then	**1 (on)**	**0 (off)**
move	move	do not move
directed	move in relation to bird	move randomly
to	move toward	move away
inactive	become inactive	no change
active	become active	no change

Table 1: Interpretation of possible values in classifier statements. The if-statement could also include wildcards, which would match conditions corresponding to either value.

Classifier System Cycle

The agent-based model runs by each individual bird going through a classifier system cycle, consisting of: detect, match, select, and effect. Birds are modeled in an 90x90 unit artificial world; each bird is identified with its age (adult or juvenile) and sex (male or female), and a unique number. Before each cycle, each bird determines its activity-state based on its activity-state probabilities. All birds go through the cycle whether or not they are active.

Detect. Each bird populates a message board with messages in the same format as the if-statement of classifiers. A message is produced for every bird within its awareness distance, noting distance, age, and sex. The message is flagged with the neighbor's identifying number and compared to a list of messages from the previous time step: if identical conditions for this neighbor exist, the message is set as old; otherwise, new. If no other birds are in the individual's awareness distance, a single "no bird" message is produced, with wildcards in the distance, age, and sex bits, and the time bit reflecting whether lack of neighbors is new or old.

Match. Every message is compared to the if-statement of the bird's classifiers, and added to a matched set if all non-wildcard bits are identical. Classifiers in the matched set are flagged with the identity of neighboring birds; a classifier may be added to the matched set multiple times for different neighboring birds. If no classifiers match the message(s) on the message board, the matched set is empty.

Select. One classifier from the matched set is selected to perform; a classifier's probability of being chosen is equal to its strength's proportion of the total strength extant in the matched set. The classifiers in the matched set are ordered arbitrarily and contiguously assigned spans of integers equal

in size to their strengths; i.e., classifier c with strength $S_c > 0$ is assigned integers $\{A_{c1}, \ldots, A_{cS_c}\}$, where:

$$A_{c1} = 1 + \sum_{n=1}^{c-1} S_n$$

$$A_{cS_c} = S_c + \sum_{n=1}^{c-1} S_n$$

If $S_c = 0$, the classifier is assigned no integers. One classifier is selected when a random integer, chosen between 1 and the sum of all strengths in the matched set, falls within its assigned span. If the matched set is empty, a null classifier is passed to the next stage.

Effect. From the then-statement of the chosen classifier, a bird first determines any changes to its activity-state due to the active- and inactive-bits. The inactive-bit is processed first, such that the active-bit can "mask" the inactive-bit.

Birds that are inactive, have a null classifier, or an off movement-bit remain still. Active birds with an on movement-bit analyze the remainder of the classifier: if the directed-bit is off, they move 4 units in a random direction; if it is on, they move 4 units toward (on to-bit) or away (off to-bit) from the neighboring bird flagged on that classifier. If a "no bird" classifier has a flagged directed-bit, movement is in a random direction. If movement would take a bird out of the 90x90 world, they are stopped on the outside boundary.

Running the Agent-Based Model

A run of the agent-based model begins by creating the appropriate number of bird-agents of each of the four age and sex classes; each bird receives parameters specific to its age and sex. Birds are placed randomly in the 90x90 world, and 50 classifier system cycles are run to allow the birds to develop assortment. A further 300 classifier system cycles are run while the GA collects the data for its fitness function.

Genetic Algorithm

The GA evolves populations of agent-based models, storing parameters necessary to define a model in five chromosomes: one contains activity-state probabilities for all four age and sex classes; the remaining four contain the list of classifiers specific to each age and sex. Each classifier is stored as: 5 if-bits, 5 wild-bits which when on, make the corresponding if-bit wild, 5 then-bits, then a strength.

Fitness Evaluation

Model fitness is estimated as an average calculated from 200 runs (repetitions determined by power analysis). Fitness is based on match of association patterns to an ideal pattern, defined by proportions of near neighbor points (PNN) for each age and sex class with all others. PNN_{IJ} of class I with class J is calculated as in behavioral experiments

(Smith et al., 2002; White et al., 2002b) using points per bird (NN_{iJ}) as counts of near neighbor observations of bird i with bird j (NN_{ij}) normalized to size of class J (subtracting self when normalizing with own class):

$$\text{NN}_{iJ} = \frac{\sum_{j \in J} \text{NN}_{ij}}{|J \backslash \{i\}|}$$

$$\text{PNN}_{IJ} = \frac{\sum_{i \in I} \left(\text{NN}_{iJ} / \sum_K \text{NN}_{iK}\right)}{|I|}, K \in \{\text{AM, JM, AF, JF}\}$$

The NN_{ij} values are collected from the last 300 classifier system cycles of each model run: NN_{ij} is increased by 1 after every cycle for which bird j is near (within 5 units of) bird i. Fitness F of a model run is then calculated as:

$$F = 16 - \sum_I \sum_J \begin{cases} \left(\frac{\text{PNN}_{IJ}^{\text{ideal}} - \text{PNN}_{IJ}^{\text{measured}}}{\text{PNN}_{IJ}^{\text{ideal}}}\right)^2, & \text{PNN}_{IJ}^{\text{ideal}} > 0 \\ \left(\text{PNN}_{IJ}^{\text{measured}}\right)^2, & \text{PNN}_{IJ}^{\text{ideal}} = 0 \end{cases}$$

Evolution Process

A generation starts with 10 seed models, representing the 10 models with the highest fitness last generation, and 5 new random models (to maintain variation in the population). In the initial generation, the 10 seed models are also randomly generated. For random generation, values are chosen between: 0-1 for the 8 activity-state probabilities; 1-6 classifiers for each age and sex class; on/off for the 15 bits in each classifier; and integers 0-50 for each strength.

Each generation the 10 seed models mate to produce 35 offspring (see modification later). A mating produces one offspring from two models, each randomly assigned to be mother or father. Crossover occurs for each chromosome with a probability of 0.5 (otherwise, offspring receive mothers' chromosomes). In probability chromosomes, a crossover probability is chosen: the offspring receives the father's chromosome up to and including that probability and the mother's thereafter. In classifier chromosomes, a crossover classifier from both the mother and father and a crossover point within the classifier is chosen: the offspring receives the father's list of classifiers up to and including the crossover point in the chosen father's classifier and the mother's list after that point in her chosen classifier and thereafter. The offspring's list is truncated to 6 classifiers, to prevent overgrowth of classifier lists which was otherwise rampant. After crossover, point mutations occurr at each chromosome element with probability 0.01: probabilities add or subtract a value 0-0.2; classifier bits flip state; classifier strengths add or subtract an integer 0-3.

The 10 highest fitness models are chosen to seed the next generation. The GA is run for 40-50 generations.

Evolving the Agent-Based Model
Initial verification

Before evolving models to match movement patterns of real birds, models were evolved to a test situation of total own-
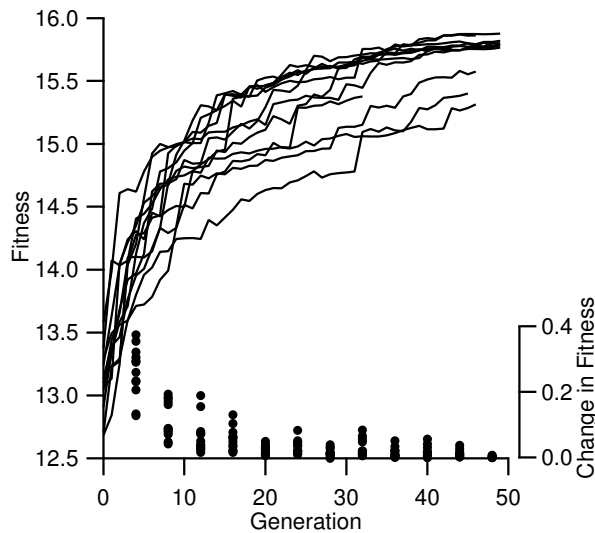
Figure 1: Fitness of best model for 12 runs of GA at each generation (lines) and change in fitness averaged every four generations (dots).

class association, i.e., $\mathrm{PNN}_{IJ} = 1$ for $I = J$ and 0 otherwise, in order to investigate behavior of the GA and model. Models were set up with 10 members of each age and sex class, and the GA was run 12 times to produce 12 models.

Genetic algorithm performance. The GA succeeded in increasing fitness of the models from their initial random starting points (Fig.1), reaching fitness mean=15.7±SE=0.06 of maximum 16. The average change in fitness each generation was significantly positive every four generations through generation 45 ($t_{9-11} \geq 3.4$, $P \leq 0.007$), and not thereafter ($t_5 = 1.9$, $P = 0.12$).

Evolved model performance. Evolved models showed desired assortment patterns, with birds gathering in small clumps of same age and sex class (Fig.2a,b). Perfect total assortment was not achieved, but evolved models reached about 0.8 PNN for own class and near 0 for others (Fig.2c).

Analysis of evolved parameters. To examine how evolution affected the models, evolved parameters were evaluated for their deviation from randomness.

There was no evidence of either directional selection on activity probabilities P ($|t_{47}| \leq 0.2$, $P \geq 0.8$, one sample t-test $H_0 = E(P) = 0.5$) or stabilizing selection for values of 0.5 ($|t_{47}| \leq 0.8$, $P \geq 0.5$, one sample t-test $H_0 = E(|P-0.5|) = 0.25$). However, the active-bit in the classifier was significantly more often on ($\chi_1^2 = 23.2$, P<0.0001). When not masked by an on active-bit, the inactive-bit was more often off ($\chi_1^2 = 31.8$, P<0.0001); when masked, there was no difference ($\chi_1^2 = 1.5$, P=0.2).
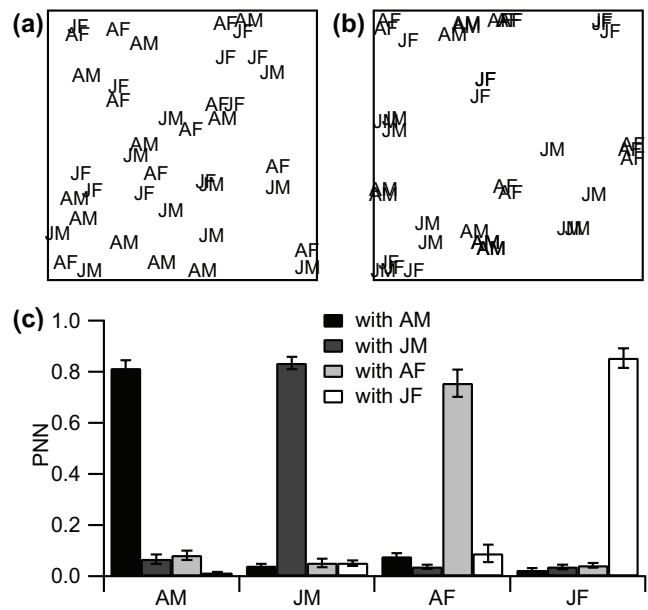

Figure 2: Evolution for total assortment. **(a)** Initial random placement of birds in world; **(b)** assortment at end of run following evolved rules. **(c)** PNN averaged over all 12 evolved models. Error bars represent standard error of the mean.

All bits in the remainder of the then-statement showed evidence of selection: the move-bit and directed-bit more often on ($\chi_1^2 \geq 33.6$, P<0.0001), and movements more often toward the other bird ($\chi_1^2 = 7.5$, P=0.006).

In the if-statement, all bits were more often wild than not ($\chi_1^2 \geq 9.7$, $P \leq 0.002$). When not masked by a wild, the time-bit was more often set to old ($\chi_1^2 = 10.4$, P=0.001); the age-bit to juveniles ($\chi_1^2 = 4.1$, P=0.04); and there was no difference in the rest ($\chi_1^2 \leq 3.4$, $P \geq 0.07$).

In order to determine if different strategies had evolved for remaining near one's class, classifier lists were divided into two groups: those which contain classifiers directing a move toward a neighbor of the same class in (1) more than half or (2) less than half of possible environmental conditions containing such a bird. Classifier lists in the second group more often simply had no classifiers at all that could respond to the same class (Mann-Whitney $U_{N=19,29} = 76$, P<0.0001), suggesting that the different behaviors were due to evolutionary constraints rather than different strategies.

Evolution to match real bird behavior

The agent-based models were evolved to match association patterns measured from real birds in Smith et al. (2002) during a subset of the Spring sample (22 Mar - 14 Apr); this consists of PNN for birds within 0.3 m and shows the typical stair-step pattern of increasing association with birds similar first in sex then age (Fig.3). The models were set up with 19 AM, 14 JM, 21 AF, and 16 JF to match age and sex distri-
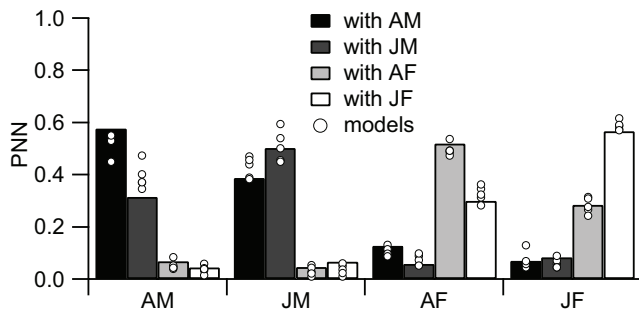
Figure 3: Association pattern from real birds used to evolve models (bars); association patterns from each of five evolved models, averaged over 100 runs (circles).

bution of the study. The basic GA was modified in response to initial tests' indication that constraints may be limiting evolution. The 5 new random models each generation may be too poor to contribute useful variation; thus the random models were mated to the 10 seed models to produce 10 of the 35 offspring, providing a mixture of proven and new elements. Five models were evolved to 49-52 generations. They successfully matched the desired PNN pattern (Fig.3) and averaged fitness 15.6±0.02, comparable to initial tests.

Interpretation of evolved models. As with the initial tests, the models showed neither directional nor stabilizing selection of activity parameters ($|t_{19}| \leq 0.2$, $P \geq 0.8$), but did show selection for on active-bits ($\chi^2_1 = 6.5$, $P = 0.01$). There was less evidence of selection in the remainder of the classifiers, with only neighbor, sex, and time-bits more often wild in the if-statement ($\chi^2_1 \geq 4.3$, $P \leq 0.04$), and move-bits more often on in the then-statement ($\chi^2_1 = 30$, $P < 0.0001$). This makes sense, as the behavior evolved for is not so directional nor easily defined as in the initial test. Rather than looking at individual bits across all classifiers, it is more instructive to examine the overall behavior produced.

In general, the evolved rules designated behaviors that increased chances of NN with birds of both ages of the same sex: such behaviors were moving towards or remaining still in response to the other bird (27% of all classifiers; 94% of those applicable to such situations, $\chi^2_1 = 24$, $P < 0.0001$). Behaviors which decreased chances of NN with opposite sex birds (moving away or randomly) showed a non-significant trend to be more common than behaviors increasing chances (20% all; 67% applicable, $\chi^2_1 = 3.6$, $P = 0.06$). Behaviors increasing or decreasing chances of NN with both same age and opposite age birds were present in approximately equal numbers ($\chi^2_1 \leq 0.2$, $P > 0.6$). Classifiers which responded to any bird, regardless of age and sex, were rare; most classifiers were specific to at least age or sex (87% of all classifiers, $\chi^2_1 = 59$, $P < 0.0001$), but rarely to both (27%, $\chi^2_1 = 23$, $P < 0.0001$). No model ever evolved a class with specific

rules in response each age and sex: all classifier sets included generalities. With one exception (JM in Run 1), all models evolved age and sex-based behaviors for all classes. All models evolved some classifiers which went against the overall pattern, for example, in one model juvenile males remained still in response to adults and moved randomly in response to juveniles. Thus, the rules evolved by the classifiers were characterized by a combination of partially specific responses; these tended to increase proximity to the same sex, decrease proximity to the opposite sex, and had mixed responses to different ages.

Evaluation of Evolved Models on New Data

The five evolved models were evaluated for their ability to predict association patterns plus additional behaviors not used for fitness evaluation – approach, response, and flight – in a new group of birds. These birds are the same as the JA condition in White et al. (2002b); I refer the reader to this publication for details of bird capture, housing, etc.

Behavioral data collection

Association patterns. I used near neighbor data collected by Dr Andrew King and Dr David White as part of White et al. (2002b); I calculated PNN for birds within 0.3 m for data collected between 13 Mar - 10 Apr, matching as close as possible the period for which the models were evolved.

Behavior samples. During the same time period, I collected behavioral focal samples: morning (0815-1145 hr) and afternoon (1215-1600 hr) 10 min focal samples on each bird every week for the four weeks, totaling 33.3 hrs observation. Observations were carried out in groups 3-5 times a week, and order of observation balanced across weeks.

During a focal sample, the following behaviors were recorded: approach (moving from a further distance to 0.3 m of another bird), response to approach (leave: moving further than 0.3 m from approaching bird; stay: remaining within 0.3 m), flight (take to the air by flapping wings), and landing environment (near: within 0.3 m of another bird; aware: within 0.9 m of another bird; alone: more than 0.9 m from any bird). Identity of other birds involved in these behaviors was noted. Note that these are not mutually exclusive behaviors: e.g., flights can also be approaches.

Comparison to models.

Data from models. Each evolved model was set up with 5 AM, 8 JM, 7 AF, and 5 JF, to match the make-up of the new group of birds. The same data as above was collected from 100 runs of each model, with the following conversions for the simulated world: near and aware distances were 5 and 15 units respectively; when a movement resulted in being within 5 units of another bird which had also moved that time step, it was only scored as approach if the movement was orientated $<90°$ either side of the other bird's original

location (i.e., an approach cannot be scored if moving away); and all movements were regarded as flights.

Comparison values. From each data set (real and models), 60 comparison values were calculated: 16 PNN among all age and sex classes; 16 proportion approach (PAP) values, calculated for all age and sex classes in the same manner as PNN, except using counts of approach (AP_{ij}) of bird i to j rather than near neighbor (NN_{ij}) observations; 16 proportion leave (PLE) values, calculated from counts of bird i responding with a leave (LE_{ij}) to bird j's approach (AP_{ji}):

$$LE_{iJ} = \frac{\sum_{j \in J} LE_{ij}}{\sum_{j \in J} AP_{ji}}$$

$$PLE_{IJ} = \frac{\sum_{i \in I} LE_{iJ}}{|I|}$$

and 12 proportion flight landing (PFL) values calculated from counts of bird i's flights (F_i) and landing environments E (L_{iE}):

$$PFL_{IE} = \frac{\sum_{i \in I}(L_{iE}/F_i)}{|I|}$$

Evaluation of model fit. Comparison values V_R from the real birds were compared to the distribution of 100 values V_M from each evolved model, to determine the fit of the model: if a two-tailed probability of the real value being drawn from that distribution (calculated directly as twice the proportion of V_M as extreme or more so than V_R) was less than α=0.05, the model was considered to not be a good approximation for that value.

The models showed themselves to be good fits to PNN, PAP, and PLE values, but not PFL values (Fig.4). For the first three value types, the model distributions were generally centered around corresponding V_R values, while for PFL the V_R values were in the tail of the distributions (Fig.4a,b). Correspondingly, over half of real PFL values were significantly different from the model, while very few of the other value types were (Fig.4c).

Discussion

An agent-based model of bird behavior was created and successfully evolved using a genetic algorithm to produce desired emergent properties of the system: association patterns of a group of birds. An initial test verified performance of the GA, which was subsequently used to evolve models to match association patterns measured from real birds. The evolved models matched not only association patterns from the situation for which they were evolved, but association patterns collected from a new set of birds. Additionally, they matched patterns of approach and response of the new birds, behaviors for which they were not directly evolved.

The initial test evolved for total assortment showed that the classifier system-based model was an appropriate choice
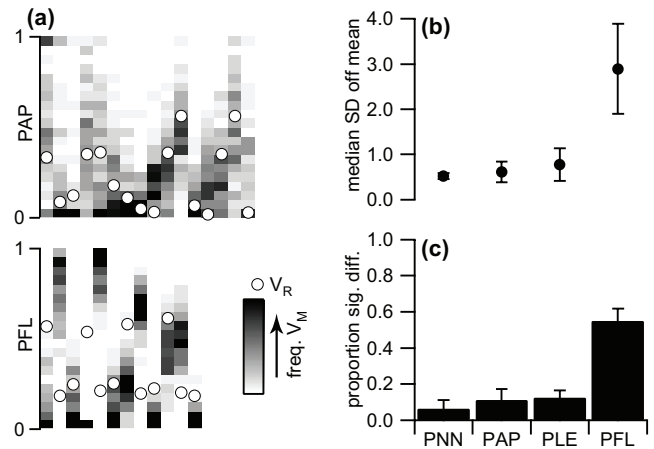

Figure 4: Fit of models to real data. **(a)** Example match of one evolved model's V_M distributions to real values for well matching (PAP) and poor matching (PFL) values. **(b)** Location of real values relative to model distribution shown by median number of standard deviations between V_R and mean V_M. **(c)** Proportion of V_R significantly different from model distribution. For **b,c**: mean across 5 evolved models shown; error bars represent standard error of the mean.

for modeling behavioral rules. The evolved rules were straight-forward and easy to interpret. The activity probability chromosomes appeared to have little impact, with the classifiers themselves controlling activity state; overall, it was more beneficial to be active, and thus able to respond to the environment. The classifiers evolved for directed movement towards other birds. It is possible that moving toward was favored over moving away as the movement distance was somewhat less than the near distance: moving away may not avoid an NN point next time step, whereas moving towards always maintained one. Classifiers made strong use of wildcards in the if-statement, allowing behavioral rules to apply to multiple conditions. When not wild, old conditions were more often coded for: this is sensible, as a condition still there from the previous time step may be more likely to remain, and thus be more useful to respond to. Any reason for the bias towards responding to juveniles is unclear; as this comparison was considerably less strong than all others, it is likely that it represents random variation. It is easy to see how rules coding for moving in response to the environment, particularly reoccurring conditions, and in a directed manner could create a strong pattern of association with similar birds. Also, when evolving for total association with only one class, use of wildcards enables birds to more efficiently respond to multiple conditions similarly.

There was no evidence of evolution of multiple strategies for achieving total assortment; instead, it appears evolutionary constraints were responsible for different responses to a bird's own class, in particular, never evolving applicable

classifiers. Thus, when evolving to match patterns of real birds, more variation was introduced by mating randomly generated models with the fittest ones.

The models evolved to real bird behavior successfully matched the association patterns for which they were evolved; this indicates these patterns do not require individual-based responses and can be produced using only age and sex-based rules. The models also matched association patterns of an entirely different group of birds, having a different age and sex distribution; this indicates the evolved association pattern is not tied to age and sex distribution, but is due entirely to the behavioral rules. Thus, these rules are generalizable beyond a particular model to other groups of birds, and so can provide insight into general principles underlying production of self-organized association.

By examining the five evolved models, we can postulate the following about behavioral rules of real birds. First, being able to become active in relation to the environment is key to production of self-organized behavior. Second, instead of requiring specific responses to all age and sex classes, general rules applicable across broad classes of birds (e.g., avoid males, be attracted to juveniles) can lead to assortment. Third, it is likely that all age and sex classes are actively involved in assortment: this is not only supported by repeated emergence in evolved models, but also by match of the models with other movements of real birds. Finally, existence of rules counter to the general pattern indicates that such rules can co-exist with assortment. This is particularly encouraging, as it is known that interaction of juvenile males with adult females–complete opposite classes–is highly important to social development of the juveniles (Smith et al., 2000; Smith, 2001; Smith et al., 2002). The models show that self-organized patterns of association can be maintained even with attraction between different classes of birds.

The above inferences could be tested by future behavioral or computer experiments. For example, behavioral choice tests could characterize attraction/avoidance to age and sex classes; observation could track birds' activity-states; simulations could be designed to match measured activity proportions but disallow response to environment, or only allow 1-2 classes to behave preferentially, and these simulations' effectiveness compared to the current model.

The evolved models were not only successful at predicting association patterns of a new group of birds; they also predicted other behaviors not included in the fitness function. In particular, the models were good fits for observed patterns of approaching other birds and the response to such approaches. These behaviors are key contributors to the self-organized association pattern; attraction and repulsion between birds is what drives with whom they associate. Thus, in evolving models to match a particular association pattern, I succeeded in creating models which match the mechanism producing these patterns. This success indicates the appropriateness of the formulation of the behavioral model and thus provides confidence for the generalizations to real birds.

Another type of behavior not included in the fitness function, proportion of flights to different proximities of other birds, was not well matched by the models. However, these flight behaviors are not contributors to association patterns: birds can land near other birds often or rarely, and maintain the same association pattern, as long as they approach particular classes in the same proportion. Thus, this behavior was independent of the criteria used for evolving the models. Additionally, the formulation of the model did not well reflect the range of potential flight behaviors: the model birds always moved a fixed distance, while real birds make flights of varying distances. This difference did not strongly impact association patterns: a flight of long distance when approaching or leaving could be approximated by several successive flights. However, this difference made certain types of flights, particularly to alone, less likely in the model.

That the models were successful at predicting association patterns for which they were evolved, as well as contributing behaviors, but not behaviors which could vary independently of association pattern, highlights both the limitations and strengths of this modeling approach. The models were designed with the intent of understanding rules underlying self-organized assortment. As such, they included parameters relating intuitively to such rules: behavior in response to neighboring birds. They were not designed to model patterns of flight behavior, and included no parameters for adjusting flight distance. When evolved to match association patterns, there was no reason for the independently varying flight behavior to have an impact, and the models did not accurately reflect these behaviors. However, the models were highly successful at the task for which they were designed: matching association patterns, predicting the behaviors which create these patterns, and thus providing insight into the mechanism behind self-organized social association.

The model is clearly a simplification of bird behavior, even in behaviors related to association patterns. Real birds exhibit behaviors related not only to age and sex of other birds, but to individuals; for example, birds exhibit consistent individual differences in their association behavior (Smith, 2001; Smith et al., 2002), and even "friendships" (spending large amounts of time with a specific individual). This model does not capture such individualized behaviors. Modeling individual differences, and allowing individual-specific behaviors, is an area of future investigation. It would be interesting to see if consistent patterns of individual difference emerged across evolved models, and thus perhaps be relevant to self-organization of association patterns.

Another potential area of future investigation corresponds well with the modeling framework used, classifier systems. Implementing learning of classifiers on an individual-agent basis could allow investigation of learning trajectories. For example, female feedback on singing behavior of males could be modeled, either on top of or distinct from the cur-

rent assortment model. Such a model could address whether the known JM-AF interactions are driven by males' learning or also require female attraction.

This work has shown that it is possible to use agent-based models as a tool to help understand animal behavior. With a question, what rules do birds use to produce their self-organized association pattern, and a model designed to provide intuitive answers, I was able to make inferences about the behavior of real birds. The use of a heuristic search method, the GA, moved the modeling exercise from one of validating a single hypothesized set of rules to one where I probed general principles of behavior. The five evolved models all had a different rules, and all successfully matched bird behavior, showing that there are many possibilities for the rule set. However, while it is not possible to say precisely what behavioral rules the birds use, the five evolved models provide independently generated hypotheses about such rules; thus, similarities across them point towards general principles that are likely to be true of any set of behaviors able to produce the desired association patterns, including those used by real birds. In sum, combining evolutionary algorithms with agent-based modeling can become a valuable tool, enabling study of animal behavior within the complex environments in which it naturally occurs.

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Evolving an Agent-Based Model to Probe Behavioral Rules in Flocks of Cowbirds

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Errata

p.564, column 2, paragraph 2, sentence 1 should read:

In the if-statement, age and sex were more often not wild and all other bits more often wild ($\chi_1^2 \geq 9.7$, P$\leq$0.002).

p.565, column 1, paragraph 2, sentence 2 should read:

There was less evidence of selection in the remainder of the classifiers, with only neighbor, sex, and time-bits showing selection in the if-statement ($\chi_1^2 \geq 4.3$, P$\leq$0.04), and move-bits more often on in the then-statement (χ_1^2=30, P<0.0001).