Birdsong dialect patterns explained using magnetic domains

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The songs and calls of many bird species, like human speech, form distinct regional dialects. We suggest that the process of dialect formation is analogous to the physical process of magnetic domain formation. We take the coastal breeding grounds of the Puget Sound white crowned sparrow as an example. Previous field studies suggest that birds of this species learn multiple songs early in life, and when establishing a territory for the first time, retain one of these dialects in order to match the majority of their neighbours. We introduce a simple lattice model of the process, showing that this matching behaviour can produce single dialect domains provided the death rate of adult birds is sufficiently low. We relate death rate to thermodynamic temperature in magnetic materials, and calculate the critical death rate by analogy with the Ising model. Using parameters consistent with the known behavior of these birds we show that coastal dialect domain shapes may be explained by viewing them as low temperature “stripe states”.

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I. INTRODUCTION

Under certain conditions physical systems of interacting particles form spatially ordered states. An old and famous example is the spontaneous magnetization of certain metals as they cool below the Curie temperature. The classic “Ising model” of this process also serves as a simple description of the appearance of order in social systems [1]. Whereas the directional alignment of neighbouring atomic spins within ferromagnetic materials produces an energetically favourable state, individuals in society find that aligning their behaviours with those of their neighbours can provide social benefits, or indicate the intrinsic fitness of the individual. In this paper, we introduce an ornithological application of this analogy.

Almost all birds sing or call. In some species these sounds are encoded in the DNA, while others learn [2]. From whom they learn and at what point in their lives varies: some birds fix their songs early in life, some continue learning throughout. Some learn from their parents and some from neighbours. Many song birds, but also some hummingbirds [3] and parrots [4], exhibit vocal dialects: the nature of their songs or calls varies geographically with well defined and sharp boundaries between dialect domains. Because the learning mechanisms and social behaviours of different species vary considerably, so the nature and dynamics of dialect domains is also rather varied. However, the fundamental ingredients of copying, set against randomizing influences such as dispersion and death suggest that an analogy to atomic alignment and thermal noise (or random motion) may be a useful way to understand the geographical distribution of birdsong dialects. In this paper we will show that such an analogy can provide analytical insight into field observations (in particular by Nelson [5]) of a particular species: the Puget Sound white crowned sparrow.

During the breeding season, Puget Sound white crowned sparrows occupy territories along the Pacific Northwest coast of North America, having flown 500-1900km from their wintering grounds in California [5]. Their songs may be analysed using audio spectograms, and the first such study (in 1977) of this species [6] revealed a number of distinct dialects, defined by the nature of their terminal trills, occupying well defined geographical regions along the coast. Subsequent studies have revealed the dialects illustrated on the map in Figure 1.

Male Puget sound white crowned sparrows are territorial, and adults returning to the breeding grounds typically reoccupy the territory they used the previous year and also sing the same song from year to year. Field observations and recordings suggest that male juvenile birds are able to learn more than one dialect in their hatching year, as they visit surrounding domains that are often separated by more than 100km [5]. When returning to the breeding sites in the following year these yearlings “overproduce” [9], initially singing more than one (typically two) dialects. The majority of existing adult territory holders arrive earlier than yearling males, so that when yearlings return and select an available territory, a number of neighbouring birds will be audible. Field observations and playback experiments [5] demonstrate that new territory holders who overproduce selectively discard dialects so as to match the majority dialect in their vicinity. Once a final selection has been made by a yearling, it sings the same song in subsequent years.

I hypothesized by ornithologists that the combination of overproduction and selective attrition gives rise to the observed dialect domains. We present a simple lattice model of this process which we use to quantify the conditions under which domains form. Using insights from the statistical physics of magnetism, we show that surface tension at domain boundaries and the formation of stripe states can be used to explain field observations of domain structure.

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II. THE MODEL

We represent territories as squares on a regular lattice, as in Figure 2. On the ground, the average distance between the centres of territories is \( \approx 115 \text{ m} \) [10]. Since dialects extend over considerable distances, then at the boundary between two domains, typically only two different songs will be sung by the majority of adults so the competition between dialects locally involves two choices. We therefore consider two adult song types, “up” \( \uparrow \) and “down” \( \downarrow \), thereby simplifying the analysis of our model. At the end of the breeding season, each site in our system is occupied either by a returning adult bird, or by a yearling who has settled upon his final song type, to be sung every following year until his death. Each year, each adult bird has a probability \( \alpha \) of failing to make it back to the breeding grounds after wintering in California. The average lifespan of a bird is \( \approx 2.5 \text{ years} \), which translates to a yearly death probability of \( \alpha = 0.4 \), if we approximate the lifespan as a geometric random variable. The process of repopulating the lattice each breeding season takes place in stages. In the first stage, all surviving adults reoccupy their previous territories as shown in Figure 2. Non-returning adults are represented by grey squares in Figure 2, and we assume that the population is stable so that all of these territories will be occupied by yearlings. We consider two possible processes of reoccupation:

A. Single phase reoccupation

In the first version of the model, we assume that yearling birds listen only to preexisting adults, and ignore each other. A (possible) justification of this assumption is that yearling birds will sing more than one dialect, therefore providing no clear signal to other birds. Under this assumption, when a grey site is repopulated, the yearling in that site can only “see” the adults around it. In this case we assume that, based on field observations [5], the yearling will match the majority of his adult neighbours. If neither dialect is in the majority then the yearling will chose between the two available dialects with equal probability. We consider two different possibilities:

FIG. 2. Schematic representation of the lattice model with single phase reoccupation. Adults song states are either “up” \( \uparrow \) or “down” \( \downarrow \). Grey squares represent territories vacanted due to the death of an adult bird. The heavy line traces the audible neighbourhood of the central site in the four neighbour version of the model. Question marks indicate yearling birds given equivocal information about local song type. States that are changed relative to the previous season are circled.
for the audible neighbourhood: the four nearest neighbour territories (outlined in bold for the central site in Figure 2), or the eight territories which form a square around each site.

B. Multiple phase reoccupation

Following the arrival of adult birds, the majority yearling birds then arrive within a window of approximately one month [5]. The median time to discard non-matching dialects is then 12 days, potentially allowing new territory holders to influence later arrivals. In the second version of the model, we explicitly account for the sequential arrival of yearlings. We divide the reoccupation into $n$ phases. At each phase, a fraction $1/n$ of the newly available sites are populated and each new territory holder settles on their final dialect before the next phase arrives. Subsequent phases are then able to make use of the songs of the earlier yearlings in deciding their adult song. In each case, the decision process is identical to the single phase model, except that newly arrived birds can “see” both the preexisting adults, and yearlings from previous phases. In the limit $n \to \infty$ we have the pure sequential model, when yearlings arrive one by one, mimicking the physical process of cooperative random sequential adsorption [11].

III. SIMULATIONS

A. Investigation of critical death rate

We consider first the single phase model on a square lattice where, initially, each site has equal probability of containing an adult bird of each dialect. Provided the death rate, $\alpha$, is sufficiently low, single dialect domains form and grow (Figure 3). As with the kinetic Ising model [12] evolving by Glauber dynamics [13], those parts of domain boundaries that are locally convex tend to shrink, whilst those that are concave tend to grow. The overall effect is one of smoothing boundaries due to an effective “surface tension” [12]. An intuitive explanation of the effect is that locally convex parts of dialect domain boundaries are more likely to contain sites that will have a majority of birds of the other dialect as neighbours during the next breeding season, as illustrated in Figure 4. The majority rule represents a non-linear response to local dialects. In contrast, a proportional response would be to align to a randomly chosen neighbour as in the voter model [12, 14], so that on average dialects would be chosen in proportion to their local frequency. The voter model does not lead to the formation of domains due to a lack of “surface tension” [14] and the importance of a nonlinear learning rule has recently been recognized in a non-spatial model [15] of bird dialects.

By increasing the death rate of adult birds, dialect continuity from year to year is reduced: a site which at the end of one year was surrounded by a majority of one dialect will be more likely, if the death rate is high, to be converted by random deaths into a site surrounded by a majority of the other, or one where neither dialect is in the majority. As a consequence there exists a critical death rate, analogous to the Curie temperature in ferromagnets, above which domains dominated by a single dialect cannot form. To discover the critical death rate we introduce a correlation length, $\xi$, for a square lattice of side $L$ with periodic boundary conditions. Let-
bours need to die in order to change the majority dialect
neighbour model, because a greater fraction of neigh-
borhoods need to die in order to change the majority dialect.

The critical death rate is considerably higher in the eight
neighbour model, because a greater fraction of neigh-
borhoods need to die in order to change the majority dialect.

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pand them. The probability that such states will form in
a rectangular system, starting from a randomized initial
condition, depends strongly on its aspect ratio. Higher
aspect ratios tend to produce multiple stripes, stretch-
ing across the short side of the system. The existence
of such “frozen” dialect states would provide a plausible
explanation for the structure of the Puget Sound white
crowned sparrow’s dialect domains, because their coastal
breeding grounds form a long strip. To investigate the
typical sizes of such domains in our dialect model we
have simulated the fully sequential version on a high as-
tance ratio rectangle (Figure 7). For large systems, when
domains become large, the dynamics of their boundaries
may be approximated with continuous curves and the ex-
plicit length scale of individual sites becomes irrelevant
[12]. In the absence of an absolute length scale only the
relative sizes of structures within the system are mean-
meaningful. We may exploit this scale free property of large
systems to compare the aspect ratio of stripe domains
in our simulation to those of real dialect domains. By
course graining the system of Figure 7 into 10 × 10 cells,
we estimated the aspect ratios \( AR \) of single domains to
lie in the range \( AR \in [0.6, 3.5] \) with mean and standard
deviation \( \mu(AR) = 1.4 \) and \( \sigma(AR) = 1.1 \). Distribution
maps [8] suggest that breeding territories of Puget Sound
white crowned sparrow spread \( \approx 50 \text{km} \) inland and com-
bined with the dialect distributions mapped in Figure
1, we predict that the aspect ratios of the real dialect
domains lie in the range \( AR \in [1.4, 3.3] \) with mean and
standard deviation \( \mu(AR) = 2.8 \) and \( \sigma(AR) = 1.6 \). The
similarity between the simulated and observed distribu-
tions supports our hypothesis that the observed domains
arise due to the processes modeled, and are stripe states.

IV. APPROXIMATION WITH KINETIC ISING
MODEL

Our analysis has made use of an analogy between di-
alect domains in bird populations and domains of aligned
spins in ferromagnets. We now make this connection ex-
plicit in the single phase case by deriving Ising models
with transition rates which match the expected transition
rates in our dialect system. This enables us to de-
rive an approximate relationship between death rate and
thermodynamic temperature. We also demonstrate how
phased arrival of yearling birds may be viewed as extend-
ing the distance over which nearby adult dialects can be
perceived.

A. Single Phase Reoccupation

Consider the four neighbour model. Letting \((x, y)\) de-
ote the nearest neighbours of site \((x, y)\) we define

\[
\psi(x, y) = \sum_{(x', y')} S(x', y'),
\]

where \( S(x', y') \in \{1, -1\} \) is the dialect at site \((x', y')\)
at the end of a breeding season. We now suppose that at
the start of the following season, site \((x, y)\) is vacant. The
yearling male occupying this site will not typically have
access to \( \psi(x, y) \) due to the non-return of one or more of
its neighbours. This disruption of information plays the
same role as temperature in the Ising model. We now
define the indicator function for the return of an adult
duck at each site

\[
R(x, y) = \begin{cases} 
1 & \text{with prob. } 1 - \alpha \\
0 & \text{with prob. } \alpha.
\end{cases}
\]

Using this indicator, we can compute the sum of the di-
alects seen by the new territory holder at \((x, y)\)

\[
\tilde{\psi}(x, y) = \sum_{(x', y')} R(x', y') S(x', y').
\]

The yearling will choose his dialect according to the sign
of this “noisy” version of \( \psi(x, y) \). We now define the step
function

\[
f(z) = \begin{cases} 
1 & \text{if } x > 0 \\
\frac{1}{2} & \text{if } x = 0 \\
0 & \text{if } x < 0.
\end{cases}
\]

Given \( \psi(x, y) \), the probability that he will choose the ↑
dialect is

\[
p_{\uparrow}(\psi) = \Pr[\tilde{\psi} > 0] + \frac{1}{2} \Pr[\tilde{\psi} = 0]
\]

\[
= E[f(\psi)]
\]

where the expectation is taken over all possible combina-
tions of vacated sites. For notational simplicity we have

FIG. 7. Evolution of the sequential four neighbour model
with \( \alpha = 0.4 \) on a 2000 × 50 lattice with wall boundary condi-
tions at long (horizontal sides) and periodic boundary condi-
tions at either end. Black (white) squares represent dialects
\( \uparrow (\downarrow) \). System is shown after 10 × \( 1.5^k - 1 \) iterations for
\( k \in \{1, 2, \ldots, 15\} \).
omitted the arguments \((x, y)\) of \(\psi\) and \(\tilde{\psi}\). To compute this expectation as a function of \(\alpha\) we note that the numbers \(N_{\uparrow}, N_{\downarrow}\) of birds with dialects \(\uparrow\) and \(\downarrow\) around site \((x, y)\) at the start of the breeding season (allowing for vacated territories), conditional on \(\psi\), are binomially distributed

\[
Pr\{N_{\uparrow} = u \cap N_{\downarrow} = v | \psi\} = \binom{\frac{u}{2}}{\frac{u-v}{2}} \binom{\frac{v}{2}}{\frac{u-v}{2}} \alpha^{u-v} (1-\alpha)^{v+u}.
\]

Noting that \(\tilde{\psi} = N_{\uparrow} - N_{\downarrow}\) we can compute the expectation in (8) as

\[
E[f(\psi)] = \sum_{u=0}^{\frac{2+\psi}{2}} \sum_{v=0}^{\frac{2-\psi}{2}} Pr\{N_{\uparrow} = u \cap N_{\downarrow} = v | \psi\} f(u-v),
\]

leading to the following expression for \(p_{\uparrow}(\psi)\)

\[
p_{\uparrow}(\psi) = \begin{cases} 
\frac{\alpha^2}{2} & \text{if } \psi = -4 \\
\frac{3\alpha^2 - 2\alpha^3 + \alpha^4}{2} & \text{if } \psi = -2 \\
1 - \frac{3\alpha^2 + 2\alpha^3 - \alpha^4}{2} & \text{if } \psi = 2 \\
1 - \frac{\alpha^2}{2} & \text{if } \psi = 4
\end{cases}
\]

As shown in Figure 8 \(p_{\uparrow}(\psi)\) takes the form of a smoothed discrete version of \(f(\psi)\). Now let us interpret dialect states at the end of each season as Ising spins, evolving under Glauber dynamics [13] at inverse thermodynamic temperature \(\beta\). In this case sites are selected one at a time uniformly at random from the lattice, and the probability that a selected spin will be set to the \(\uparrow\) state is

\[
\omega_{\uparrow}(\psi) := \frac{1 + \tanh(\beta \psi)}{2},
\]

which is also a smoothed discrete version of \(f(\psi)\). If we now choose \(\beta\) so that \(p_{\uparrow}(\psi)\) and \(\omega_{\uparrow}(\psi)\) match for \(\psi \in \{-2, 0, 2\}\), then any site on a domain boundary will have a probability of changing state the next time it is updated which is identical between the two models, given the value of \(\psi\). It is important to realize however that the simultaneous updates that take place in the dialect model introduce correlations between state flips which are not present in Glauber dynamics. Matching the values of \(p_{\uparrow}(\psi)\) and \(\omega_{\uparrow}(\psi)\), we find that

\[
\beta(\alpha) = \frac{1}{2} \tanh^{-1}(1 - 3\alpha^2 + 4\alpha^3 - 2\alpha^4).
\]

We may now make use of the approximate analytical relationship between death rate and inverse temperature to estimate the critical death rate in the dialect model. Equating \(\beta(\alpha)^{-1}\) to the exact critical temperature of the Ising model [18]

\[
\frac{1}{\beta(\alpha)} = \frac{2}{\ln(1 + \sqrt{2})}
\]

and solving for \(\alpha\), gives

\[
\alpha_c \approx 0.4178
\]

to four significant figures. Simulations of the correlation length \(\xi\) demonstrate that this method of prediction is remarkably accurate in the four neighbour case (Figure 5).

For the eight neighbour model, we redefine \(\psi(x, y)\) to be the sum of the eight dialects relevant to site \((x, y)\). In this case

\[
Pr\{N_{\uparrow} = u \cap N_{\downarrow} = v | \psi\} = \left(\frac{4 + \frac{\psi}{2}}{u}\right) \left(\frac{4 - \frac{\psi}{2}}{v}\right) \alpha^{8-u-v} (1-\alpha)^{u+v}.
\]

We let \(p_{8\uparrow}(\psi)\) represent the probability of a new territory holder choosing the \(\uparrow\) dialect in the eight neighbour model. Repeating the calculation steps above we find that

\[
p_{8\uparrow}(0) = \frac{1}{2}
\]

\[
p_{8\uparrow}(2) = 1 - 5\alpha^2 + 20\alpha^3 - 45\alpha^4 + 64\alpha^5 - \frac{115\alpha^6}{2} + 30\alpha^7 - 7\alpha^8
\]

\[
p_{8\uparrow}(4) = 1 - \frac{15\alpha^4}{2} + 24\alpha^5 - 34\alpha^6 + 24\alpha^7 - 7\alpha^8
\]

\[
p_{8\uparrow}(6) = 1 - \frac{7\alpha^6}{2} + 6\alpha^7 - 3\alpha^8
\]

\[
p_{8\uparrow}(8) = 1 - \frac{\alpha^8}{2}
\]

with \(p_{8\uparrow}(\psi) = 1 - p_{8\uparrow}(-\psi)\). Matching \(p_{8\uparrow}(\psi)\) and \(\omega_{8\uparrow}(\psi)\) for \(\psi \in \{-2, 0, 2\}\) we have

\[
\beta_8(\alpha) = \frac{1}{2} \tanh^{-1}(2p_{8\uparrow}(2) - 1).
\]
We define in the second and third rings. Sites in even higher rings of these first ring sites is decided by the states of sites in the set of nearest, next nearest, and next next nearest neighbour sites of a new territory holder with first, second and third ring dialect sums \( \psi_1, \psi_2 \) and \( \psi_3 \) will choose the \( \uparrow \) dialect. This probability can be computed exactly (see appendix) if we assume that all dialect arrangements within each ring, consistent with \( \{ \psi_i \}_{i=1}^{\infty} \) are equally probable. To quantify the importance of the second and third ring sites we have illustrated (Figure 10) the dependence of \( p_\uparrow \) on \( \psi_2 \) and \( \psi_3 \) when the first ring sites give equivocal information \( \psi_1 = 0 \). We see that the states of these outer-ring sites can change \( p_\uparrow \) by, at most, a factor of \( \frac{3}{2} \) when realistic death rates are assumed.

By selecting dialects uniformly at random from the lattice and updating them using the probabilities \( p_\uparrow(\psi_1, \psi_2, \psi_3) \), which may be viewed as a form of Glauber dynamics with appropriately chosen (by rather complicated) Hamiltonian, we obtain the correlation length estimates plotted in Figure 6. From this we see that the extended range interactions induced by the phased model, although weak, create a significant increase in the stability of dialect domains against death of adults.

V. CONCLUSION

Using field data on the behaviour and songs of the Puget Sound white crowned sparrow [5], we have developed a simple lattice model which may be used to explain the large dialect domains which appear along its coastal breeding grounds. We have shown that the destabilising effect of adult death, and the song matching behaviour of yearling males may be viewed as analogous, respectively, to thermodynamic temperature and spin-spin interactions in two dimensional magnetic materials. Pursuing this analogy we have shown how stable dialect domains may be viewed as stripe states with similar size distribution to observed domains, we have calculated the maximum death rate for which dialects will persist (\( \approx 60\% \)), and we have shown how phased arrival of new territory holders can significantly increase dialect stability through
an effective interaction beyond nearest neighbour territories. Birdsong dialects are widely observed and take a variety of forms [21]; we suggest that the analogy to ordering in physical systems may be usefully applied to other species and potentially to the study of observed and historical human dialect domains.

Appendix: Calculation of two phase probabilities

We show how to calculate the conditional probability that a new territory holder in the two phase model will choose the ↑ dialect given the first, second and third ring dialect sums ψ1, ψ2 and ψ3. We write this probability

\[ p_{r}(\psi_{1}, \psi_{2}, \psi_{3}) \equiv \Pr(\uparrow | \psi_{1}, \psi_{2}, \psi_{3}). \]

We adopt the site numbering in Figure 9. Let \( \vec{S} = (S_1, S_2, \ldots, S_{12}) \) represent the song states at the end of the previous breeding season, and let \( \vec{R} = (R_1, R_2, \ldots, R_{12}) \) be the indicators for returning adults at the start of the current season and \( \vec{r} = (r_1, r_2, r_3, r_4) \) be indicators of arriving yearlings in the first wave to the nearest neighbour sites of the origin. Let \( \vec{B} = (B_1, B_2, B_3, B_4) \) be a vector of Bernoulli variables \( B_k \in \{-1, 1\} \) which indicate song decisions in these sites in the case that returning yearlings are presented with equivocal information. We have

\[
\begin{align*}
\Pr(R_k = 0 \cap r_i = 0) &= \frac{\alpha}{2} & (A.1) \\
\Pr(R_k = 0 \cap r_i = 1) &= \frac{\alpha}{2} & (A.2) \\
\Pr(R_k = 1 \cap r_i = 0) &= 1 - \alpha & (A.3) \\
\Pr(R_k = 1 \cap r_i = 1) &= 0 & (A.4) \\
\Pr(R_k = 1) &= 1 - \alpha & (A.5) \\
\Pr(R_k = 0) &= \alpha. & (A.6)
\end{align*}
\]

We also define

\[
\begin{align*}
\psi_1(\vec{S}) &:= \sum_{k=1}^{4} S_k & (A.7) \\
\psi_2(\vec{S}) &:= \sum_{k=5}^{9} S_k & (A.8) \\
\psi_3(\vec{S}) &:= \sum_{k=9}^{12} S_k. & (A.9)
\end{align*}
\]

To compute the probability \( p_{r}(\psi_1, \psi_2, \psi_3) \) we condition on the central site being empty and consider the two possible stages at which a yearling bird can reoccupy it.

Case I: Central site reoccupied in the first phase

We define \( p_{1}(\uparrow | \vec{S}, \vec{R}) \) to be the probability (conditional on \( \vec{S}, \vec{R} \)) that the central site is in the ↑ state at the end of the season given that the yearling at the site returns in the first phase. We define

\[ X_0 := \sum_{k=1}^{4} S_k R_k \]  

(A.10)

then

\[ p_{1}(\uparrow | \vec{S}, \vec{R}) = I_{(X_0>0)} + \frac{1}{2} I_{(X_0=0)}, \]  

(A.11)

where the indicator function \( I_A \) of the event \( A \) is defined

\[ I_{A} = \begin{cases} 1 & \text{if } A \text{ occurs} \\ 0 & \text{otherwise}. \end{cases} \]  

(A.12)

Case II: Central site reoccupied in the second phase

We define \( p_{2}(\uparrow | \vec{S}, \vec{R}, \vec{r}, \vec{B}) \) to be the probability (conditional on \( \vec{S}, \vec{R}, \vec{r}, \vec{B} \)) that the central site is in the ↑ state at the end of the season given that the yearling at the site returns in the second phase. We define

\[ X_k := \sum_{i \in \{k\}} S_i R_i \quad k \in \{1, 2, 3, 4\} \]

(A.13)

where \( \{k\} \) denotes the nearest neighbours of site \( k \). The random variable \( X_k \) is the sum of all states around site \( k \) at the start of the season. The quantity that determines the fate of the central site is the sum of the states in sites \( \{1, 2, 3, 4\} \) at the end of the first phase. Let \( \{s_k\}_{k=1}^{4} \) (note change of case) be these states where \( s_k \in \{-1, 0, 1\} \). If \( R_k = 1 \) then site \( k \) is occupied by last year’s adult and \( s_k = S_k \). If \( r_k = 1 \) then the returning bird at site \( k \) is a yearling and bases its decision on \( X_k \). If \( R_k = r_k = 0 \) then the site remains empty so \( s_k = 0 \). Therefore

\[ s_k = R_k S_k + r_k [I_{(X_k>0)} - I_{(X_k<0)}] + B_k I_{(X_k=0)}. \]

(A.14)

We now define

\[ x_0 := \sum_{i=1}^{4} s_i, \]

(A.15)

then

\[ p_{2}(\uparrow | \vec{S}, \vec{R}, \vec{r}, \vec{B}) = I_{(x_0>0)} + \frac{1}{2} I_{(x_0=0)}. \]

(A.16)

Unconditional probability

Since the central site is equally likely to be filled in the first or second phase, then conditional on \( \vec{S}, \vec{R}, \vec{r}, \vec{B} \) we have

\[ \Pr(\uparrow | \vec{S}, \vec{R}, \vec{r}, \vec{B}) = \frac{1}{2} [p_{1}(\uparrow | \vec{S}, \vec{R}) + p_{2}(\uparrow | \vec{S}, \vec{R}, \vec{r}, \vec{B})]. \]

(A.17)
To compute the unconditional probability we define
\[ f_{R^r}(u, v) = \Pr(R_i = u \cap r_i = v) \] (A.18)
\[ f_{R}(u) = \Pr(R_i = u) \] (A.19)

The joint probability mass function of \( \vec{R} \) and \( \vec{r} \) is then
\[ f(\vec{u}, \vec{v}) := \Pr(\vec{R} = \vec{u} \cap \vec{r} = \vec{v}) \] (A.20)
\[ = \frac{1}{4} f_{R^r}(u_k, v_k) \prod_{k=5}^{12} f_{R}(u_k). \] (A.21)

We now assume that conditional on the values of \( \psi_1, \psi_2, \psi_3 \) all values of \( \vec{S} \) are equally likely. We let \( \mathcal{S} \) be the set of all possible values of \( \vec{S} \) and define
\[ A(y_1, y_2, y_3) = \{ \vec{S} \in \mathcal{S} | \psi_1(\vec{S}) = y_1, \psi_2(\vec{S}) = y_2, \psi_3(\vec{S}) = y_3 \}. \] (A.22)

Since all 16 values of \( \vec{B} \) are equally probable then
\[ p_{\uparrow}(y_1, y_2, y_3) = \frac{1}{16|A|} \sum_{\vec{S} \in A, \vec{u}, \vec{v}, \vec{B}} f(\vec{u}, \vec{v}) \Pr(\uparrow | \vec{S}, \vec{u}, \vec{v}, \vec{B}) \] (A.23)
where we have suppressed the arguments of \( A \) for notational compactness. To compute all such probabilities requires us to sum over \( 2^{32} \) combinations of song states \( \vec{S} \), arrival times \( (\vec{R}, \vec{r}) \) and decision variables \( \vec{B} \). Using a simple Python program running in parallel on five cores of an eight core workstation this can be achieved in approximately one day. An example of the result of this calculation is
\[ p_{\uparrow}(0, 0, 2) = -\frac{7\alpha^{11}}{512} + \frac{17\alpha^{10}}{768} - \frac{23\alpha^9}{768} + \frac{23\alpha^8}{384} - \frac{149\alpha^7}{1536} + \frac{17\alpha^6}{128} + \frac{19\alpha^5}{768} + \frac{23\alpha^4}{384} + \frac{5\alpha^3}{24} - \frac{\alpha^2}{48} + \frac{\alpha}{12} + \frac{1}{2} \] (A.24)

We have verified our analytical results using Monte Carlo simulations. We note also that further verification is provided by considering the cases \( \alpha = 0 \) and \( \alpha = 1 \). For example
\[ p_{\uparrow}(0, 0, 2)_{\alpha=0} = p_{\uparrow}(0, 0, 2)_{\alpha=1} = \frac{1}{2} \] (A.25)
consistent with the fact that in the limit \( \alpha \to 0 \), every yearling has four adult neighbours and so cannot be influenced by the outer rings, and when \( \alpha = 1 \) all information from the previous season is lost. For \( 0 < \alpha < 1 \), \( p_{\uparrow}(0, 0, 2) \) has a single maximum at \( \alpha = 0.5677 \).

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