Feedback Loop based Decision Making for the Rock Ant Temnothorax Albipennis

Lucas Saldyt

Abstract

Rock ants (Temnothorax Albipennis) display the captivating ability to choose optimally between nest sites in a partially decentralized, error correcting, and self-organizing process. Often, Temnothorax nests are fragile, which leads to frequent colony migrations where there are multiple options for a new nest site. This paper reviews and simplifies models of Temnothorax nest-decision making, and reduces them to a simple feedback loop. Then, this paper shows the dynamics of the decision feedback loop, and how it relies, in particular, on the ability of individuals to make accurate independent assessments, and remember which nests are superior to others.

Introduction

Ant nest choice is deeper than it may initially seem. First, the entire colony needs to cooperate during migration, which is a potentially risky task. In particular, because individual ants find new nests stochastically, there is potential for colony splitting when different ants select different nests (i.e. ant *a* leads half of the colony to nest 1, while ant *b* leads the other half of the colony to nest 2). However, there exist natural mechanisms to prevent this. Namely, the ants will wait until the number of ants at a target colony exceeds a threshold, known as the quorum threshold (which is very similar in principle to the threshold in a drift-diffusion model) [cite drift diffusion model]. Additionally, carrying of active ants will fix colony splits, if they occur, and reverse tandem runs are theorized to do the same [cite Pratt 2002].

The quorum threshold influences a more general and equally important principle, the principle of *graded commitment*. In nature, graded commitment has discrete levels based on different recruiting mechanisms: direct tandem runs (leading of other ants), transportations (carrying of other ants), and reverse tandem runs (leading of other ants, but in the opposite direction). Early work set out to describe the purpose and importance of each of these mechanisms, and this is discussed further along in the introduction. Tandem runs represent a lower level of commitment than transportations, because tandem runs allow ants to learn the route, and then asses the new site for themselves, while transports

do not allow route learning. So, it is the quorum threshold which allows the transitions between these two levels of commitment, and the quorum threshold is reached by a feedback loop based on individual assessments of the site's quality. The final agent-based model with show an abstract version of these dynamics, where it is easier to see the importance of individual assessment.

Summary (Mallon 2001)

Temnothorax Albipennis colonies generally have relatively small sizes, which makes errors more likely. However, ants are able to use graded assessment to make decisions efficiently even though their colony size is small. In the agent based model, it is easy to see how unlucky noisy assessment can send the decision feedback loop in the wrong direction.

Additionally, a small number of comparisons are actually made between two nest sites. Mallon 2001 publishes three experiments with $86\%, 46\%$ and 32% direct comparison, which indicates the presence of decentralized behavior. However, there is also good evidence that individual ants that have seen two sites know which is the better of the two.

With respect to quorum threshold, ants seem to use peer rate estimation to decide on the quality of a particular colony: instead of counting the number of ants at a colony, they estimate the total number from the frequency of ants (if many ants are seen over a brief period of time, then an ant knows that the current location has a large number of ants).

Summary (Pratt 2002, 2005)

Each recruitment mechanism has different advantages. Tandem running allows learning of the route to a nest as well as the deposition of pheromones along the route. Later in the decision process, ants switch to "transport" recruitment, where they literally carry other ants. This mechanism triggers when ants know that a destination nest has a large number of ants (is above the quorum, or threshold, which is estimated by encounter rate), and as discussed previously, this threshold acts as error-correction.

Faster recruitment to better sites allows decentralized optimal choice without direct comparison. In other words, when an ant encounters a good site, it recruits to that site

very quickly, which causes positive feedback when subsequent ants encounter and recruit to the same site. This can be seen in the population equations from Pratt 2002, where incoming ants depend on the number of recruiting ants.

Reverse tandem runs had no single explaining mechanism, but it was hypothesized that they either stimulated transport by idle workers, or fixed nest-splitting that would be more common in nature than in the lab. The quorum requirement seems to assist the ants in making optimal choices by acting as a general error correction mechanism — it delays decision making in case ants have chosen a sub-optimal nest, and this decreases the likelihood of colony splitting.

Summary (Granovskiy 2012)

Granovskiy 2012 simplifies many of the ideas in the previous 2005 agent-based model. It still has four macro-states: Exploring, Assessing, Canvassing (Leading), and Committed (Carrying). However, it is simplified each of them so that they contain only the substates: search and at-nest, as well as their respective specialized actions (tandem runs for the canvassing population, and transport and reverse tandem runs for the committed populations). Also, assessing ants can begin recruiting once they accept a nest.

Additionally, there is the possibility that any searching ant can be picked up and carried to a nest nest, and any ant can be led by tandem run. Otherwise, this model does not have any extra features from the 2005 model, but still seems to perform similarly.

Proposed Ordinary Differential Equation Model

The proposed model begins with an improved set of ordinary differential equations, based on Pratt 2002. It contains equations for five separate populations:

- S, the searching population (not at any nest)

- A_i, the assessing population at nest i

- L_i, the leading (forward-tandem-running) population at nest i

- C_i, the carrying (transport) population at nest i

- P_i, the passive population at nest i.

The model focuses on the following:

- Splitting the R_i population from S. Pratt 2002 into the L_i and C_i populations.

- Replacing the two switching equations $I()$ and $J()$ with dynamics switching between L_i and C_i based on a single switching equation $Q()$.

- Fixing unchecked growth in the original P_i equations.

- Allowing transport of various passive populations, which will allow a split passive population to be fixed.

- Adding transportation of the active searching population (but not the assessing, leading, or carrying populations).

Given N ants, where proportion p are active, the initial states are the following:

- $S = pN$

- $P_0 = (1 - p)N$

- $A_i, L_i, C_i, P_i = 0$

The original model used the following parameters:

μ_i	Likelihood of finding nest i
λ_i	Proportion led by leaders to i
ρ_{ij}	Switching rates between nests i and j
k_i	Acceptance probability for nest i
ϕ_i	Rate for carrying passive ants to nest i

The updated model builds on this list, but renames old parameters to make them more intuitive. Estimated values are from (Pratt 2002):

Name	2002	Value	Description (units = rate)
ϕ_i	μ_i	0.13	Finding nest i
λ_i	λ_i	0.033	Led by leaders to i
α_i	k_i	0.015, 0.02	Assessors who accept nest i
τ	ϕ_i	0.001	Uniform transport rate i

Parameter Descriptions

ϕ_i, previously μ_i, describes the rate at which search ants find nest i. Generally, this will be used to describe nests that are at different distances from the original destroyed nest.

λ_i describes the rate at which ants are led by leaders to nest i. Differences in λ_i would describe nests which were led to faster.

T is simply the quorum threshold, and is a free variable meant to be experimented with. Pratt 2002 found that a value between 8 and 30 was best.

α_i, previously k_i, describes the rate at which assessors accept a nest and begin recruiting. It is this parameter which allows a rapid positive feedback loop to occur, and this is largely responsible for optimal nest choice.

τ_{Pi}, previously ϕ_i is the rate at which passive ants are transported to nest i. However, this model introduces a few new parameters, based on the agent based models in [TODO: Gravinvosky?] and Pratt 2005. For instance, τ_{Si} describes the transport of searching ants. TODO: Should there also be transport of other active ants?

Proposed Equations and Descriptions

Searching population equation

The following equation describes the searching population, which starts as Np.

$$\frac{dS}{dt} = S * \sum_i \left[-\phi_i - \lambda_i L_i - \tau C_i \right] \qquad (1)$$

The first term, ϕ_i, describes ants that encounter new sites and enter the assessment population. $\lambda_i L_i$ describes ants being led to new sites and becoming assessors. L_i is included here because the presence of more leading ants will increase the rate at which ants are led to new sites (i.e. ten leading ants lead ants faster than a single ant). Therefore λ_i is proportional to L_i. τC_i describes ants that are transported to new sites. As with the previous term, τ is a rate per individual in C_i.

Assessing population equation

The following equation describes the assessment populations, which start at 0:

$$\frac{dA_i}{dt} = S * [\phi_i + \lambda_i L_i - \alpha_i A_i]$$
$$+ \tau \sum_{j \neq i,j} \left[C_i * (S + L_j + C_j + A_j) - C_j * A_i \right]$$
$$(2)$$

The first three terms match the first three terms of the search-population equation. $\phi_i S$ describes incoming ants that have found the nest themselves, $\lambda_i L_i S$ describes ants that were led to the nest i, and $\alpha_i A_i$ describes ants that accept a nest and begin recruiting. Lastly,

$$\tau \sum_{j \neq i,j} \left[C_i * (S + L_j + C_j + A_j) - C_j * A_i \right]$$

describes ants that were carried to i from other populations, or were carried away to nest j.

Leading population equation

The following equation describes the leading populations, which starts at 0.

$$\frac{dL_i}{dt} = \alpha_i A_i - Q(i)L_i - \sum_{j \neq i,j} \tau C_j L_i \qquad (3)$$

First, the function $Q()$, defined below, returns 1 if the nest i is above the quorum threshold and 0 otherwise. Therefore $1 - Q(i)$ is 0 when the nest is above the quorum threshold and 1 otherwise. So, when the nest i is above the quorum

threshold, only the terms $-Q(i)L_i$ and $\sigma_{L_i}L_i$ are active. $Q(i)L_i$ represents a movement of ants from leading to carrying. $\sigma_{L_i}L_i$ represents leading ants deciding to enter the search state. When the nest is below the quorum threshold, the first and third term are both active. $1 - Q(i)\alpha_i A_i$ describes assessing ants entering the leading populations after accepting a nest, and $1 - Q(i)Ci$ describes (potentially) carrying ants reverting to the leading state.

Carrying population equation

The following equation describes the carrying populations, which starts at 0:

$$\frac{dC_i}{dt} = Q(i)L_i - \sum_{j \neq i,j} \tau C_j C_i \qquad (4)$$

Similarly to the leading population equations, $Q()$ acts as a switch. When the nest i is above the quorum threshold, assessing ants will enter the carrying population directly through the $Q(i)\alpha_i A_i$ term and leading ants are converted through the $Q(i)L_i$ term. The term $(1 - Q(i))C_i$ describes ants that (potentially) revert to the leading state.

Passive population equation

The following equation describes the passive population dynamics. Initially, $P_0 = (1 - p)N$ and otherwise $P_i = 0$:

$$\frac{dP_i}{dt} = \sum_{j \neq i} [\tau P_j C_i - \tau P_i C_j] \qquad (5)$$

Essentially, the first term $\tau P_j C_i$ desribes ants being moved to site i from site j, while the second term describes ants being moved from site i to site j.

Quorum function

The $Q()$ switching function is defined as follows, and should be self explanatory. Potentially, (TODO) P_i population should not be counted (but in simulation, this is not a contributing factor):

$$Q(i) = 0, \text{if } \sum [A_i + L_i + C_i + P_i] \leq T$$
$$Q(i) = 1, \text{otherwise}$$
$$(6)$$

These equations do not account for reverse tandem runs, but could be modified easily to do so (especially once tandem runs are better understood).

Agent based model

The analysis of the above models led to the creation of a very simple agent-based feedback loop model. In essence, individual ants can make very accurate assessments of individual nests, and then recruit more quickly, based on the

strength of this assessment. This process creates a feedback loop, where better nests are assessed by more ants at a higher rate. The purpose of this model is not to replicate all of the events that occur in nature (such as the inividual tandem running or carrying actions), but instead to model the core dynamics of general distributed choice performed by intelligent agents.

Specific Implementation

Consider a model with N agents choosing between M items. Each agent has two properties:

1. A *commitment* strength, which is a floating point number that is initially zero

2. A *source* item, which is an integer representing the item that an individual agent considers optimal.

Each agent has two actions:

1. Recruitment to *source* item, triggered with probability c, which is the *commitment* strength of the agent.

2. Discovery of new items, triggered first with probability $1 - c$. Then a random (possibly weighted) item (or no item at all) is chosen to be encountered. Once a new item is found, *commitment* strength is updated if and only if the item is superior.

For instance, consider a simple scenario with two items that are both found at probability 0.013 per timestep, and have qualities of 0.02 and 0.015 respectively. Since agents start with no commitment strength, agents will trigger the discovery action. Once the discovery action is triggered, a multinomial choice is made, with the following chances:

- 0.013 chance of finding item 1.

- 0.013 chance of finding item 2.

- $0.974 = 1 - 2 * 0.013$ chance of doing nothing.

Suppose an agent encounters item 1. This agent's commitment strength is now updated to 0.02, and this agent now recruits to nest 1 with this probability. While simple, this model is able to explain the important behavior in Temnothorax decision making.

Results

Each of the above models was tested independently. Code is available online [1] so that results can be replicated.

---

[1] https://github.com/LSaldyt/temnothorax

ODE Results

Originally, Pratt (2002) investigated quorum threshold (T), but their model depends largely on two other parameters: α, for nest quality, and ϕ, for nest distance. Convergence time was explored as a function of these three parameters. Convergence time is defined as the number of timesteps taken to reach a population of 95% at the correct nest. A cutoff of 1000 iterations was used, such that a simulation running for longer than this was considered divergent (this is similar to how the mandelbrot set is calculated).

In each of the following population plots, the parameters are the same:

Name	2002	Value	Description (units = rate)
ϕ_i	μ_i	0.13	Finding nest i
λ_i	λ_i	0.033	Led by leaders to i
α_i	k_i	0.015, 0.02	Assessors who accept nest i
τ	ϕ_i	0.001	Uniform transport rate i
N	N	208	Total number of ants
M	M	3	Total nests (including original)
T	T	10	Quorum threshold

Pratt 2002 replications The following figures represent runs of the ODE population model published in Pratt 2002. The passive population equations have been fixed to prevent unchecked growth of passive populations. Since this section is only replications, more interesting results follow in the sections after it.

The model was implemented using the [TODO cite Python ODE] package. Population dynamics were split into passive population plots and active population plots. Model changes were made one at a time so that new models could be compared to older models in stages, so it was clear which changes were causing which effects.
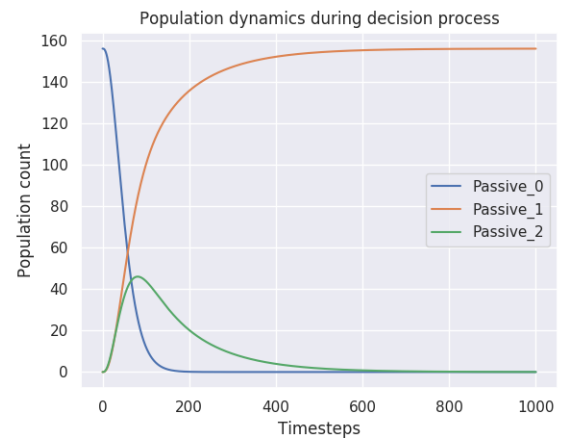

Figure 1:

Figure 1 shows a nest-splitting event, which is remedied roughly around 75 timesteps (An exact value is not crucial

here, because convergence times will be discussed later). Movement of passive ants happens fairly early, which is strange, but the quorum threshold is low in this example. After the nest splitting, the ants are able to correct and eventually choose the correct nest (Which in this case is nest 1, which has a quality of 0.02 instead of nest 2's quality of 0.015).
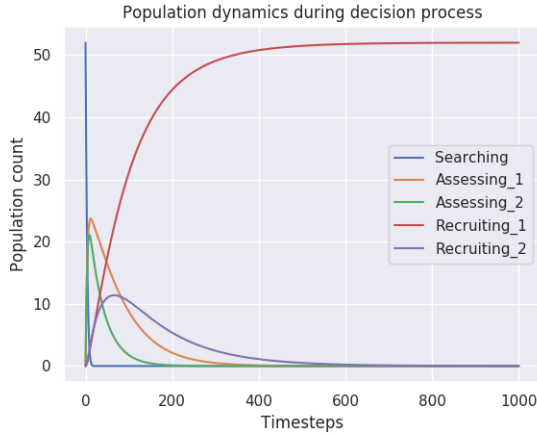

Figure 2:

Figure 2 shows a more complete picture of what is happening in this scenario. First, the searching population (blue) declines steeply, and ants encounter sites 1 and 2 in equal number. As ants enter the recruiting population, ants at site 1 begin to outnumber other ants. Eventually, the entire active population moves into recruitment for the superior site, site 1.

These dynamics are replicated exactly if the recruiting population is split into separate populations for leading and carrying. Plots showing this are omitted, because they are identical to the plots of the Pratt 2002 ODE model, since $R_i = C_i + L_i$ when the models are compared.

Updated ODE model Replacing switching dynamics in the Pratt 2002 model yields slightly different behavior, but this is explainable. Now, any carrying population can move any other population. This actually means that (in the model at least) carrying will happen in both directions, and the nest will potentially split under certain conditions. Under the parameters shown, this population does not split, however. In **??**, the effect of a quorum threshold can be seen. During roughly the first 40 timesteps, the passive population is constant. However, once quorum is met, passive ants are transported from nest 0 to nest 2 (Which is the superior nest in this experiment). This differs with the original model in that there is no nest splitting (under these parameters).

In the active population **??**, it can be seen where the quorum occurs, and how the dynamics change after this point. The leading population for the second nest (purple) all be-
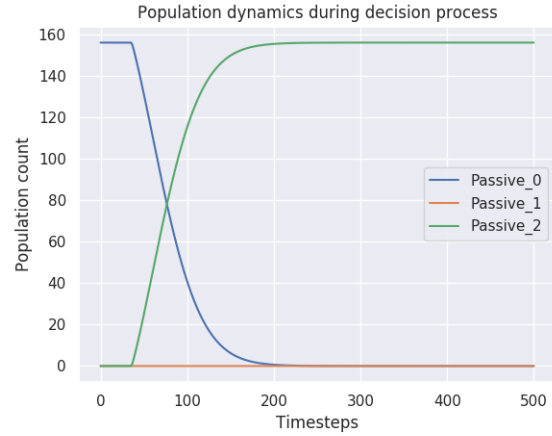

Figure 3:

come carriers (pink). This causes a change in the rate for assessors of nest 2 (green), which eventually lets the ants pick nest two.
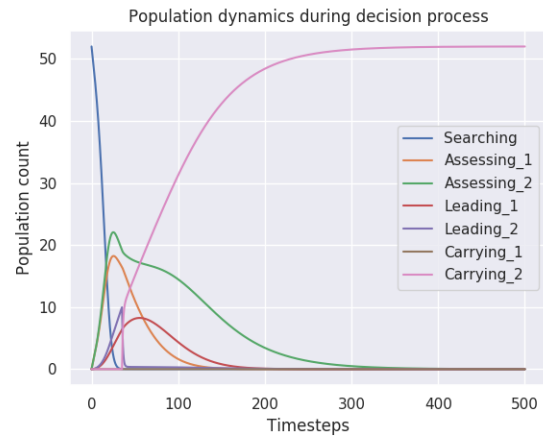

Figure 4:

With a different quorum threshold, temporary nest splitting can be reproduced. In figure 5, similar behavior to 1 occurs. Initially, there is a constant period before a quorum threshold is met. The quorum for nest 2 is met before the quorum for nest 1, and nest 2 is eventually chosen. The times and effects of the quorum's being met can be seen in the active version of this population graph, in figure 6.

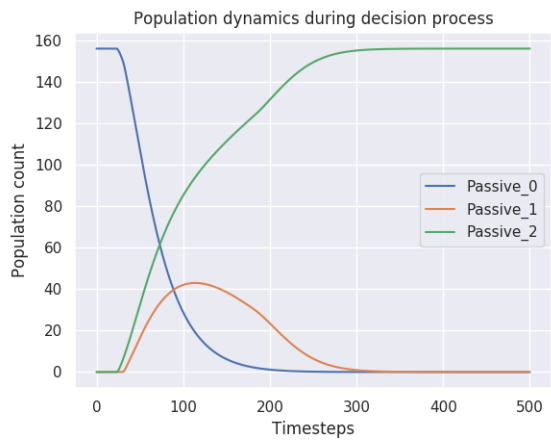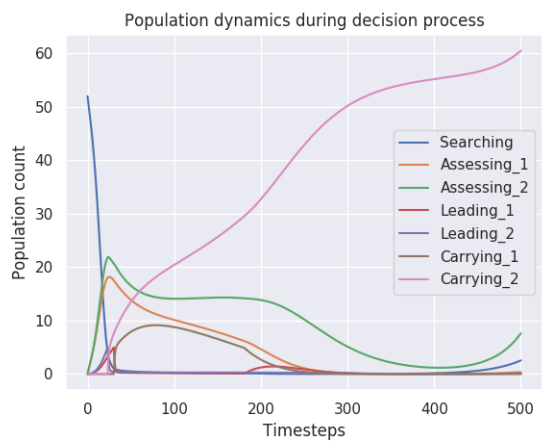**Convergence Time Results**

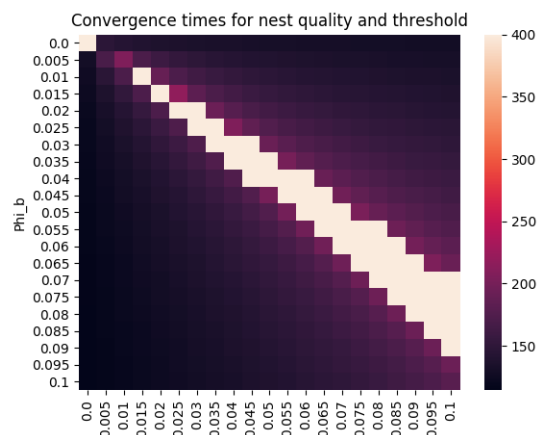**Agent Based Model Results**
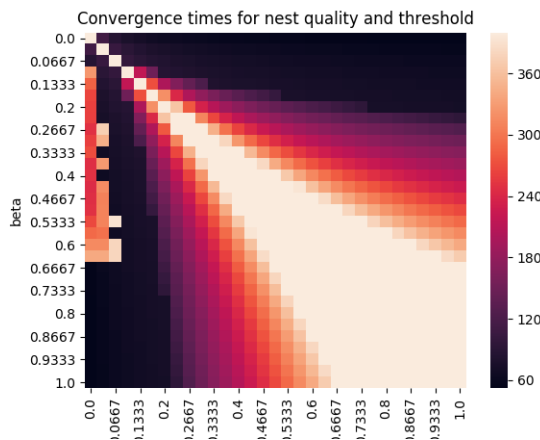
Bibliography

Figure 5:

Figure 6:

Figure 8:

Figure 7: