

Algorithms & Collective Decisions in Ants: Information Exchange, Numbers of Individuals & Search Limits

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1 Introduction

In order to explain the behaviour of social insects there has been a considerable amount of recent work which exploits self-organisation as its main behavioural principle¹⁻⁸. In particular this approach has been taken to explain the methods whereby ants forage for food.

One simple example of this is the choice over a simple branch between food sources either of differing quality or at differing distances or both. It is observed that in these simple cases the ants tend to choose the better food or the shorter path, when presented with the choice⁶⁻⁸. We should wish to know how the colony chooses between the possible paths offered to it.

Since the only information the colony has is that of the relative success of its foragers, we are interested in how it can make a choice of path? That is to say, what is the algorithm the colony is exploiting to make its decision.

We are not primarily concerned with the precise recruitment *mechanisms* employed by individual ants, such as the laying of pheromone trails. There has been a large amount of fine empirical work conducted to elucidate these mechanisms¹⁶⁻¹⁸, and we are aware of a great diversity of recruitment behaviour. We can reasonably expect that recruitment behaviours will evolve to support an effective decision making process. We of course acknowledge that a decision making process is an emergent property of the system, and may only exist when the ants possess the behavioural repertoire to implement it.

Consequently our algorithms are based on properties that individuals ants are known to possess. For instance we know that individuals may influence their nestmates to follow one path. We deliberately introduce no more detail than these essential properties: we assume only that ants may influence their nestmates, and do not specify a particular mechanism.

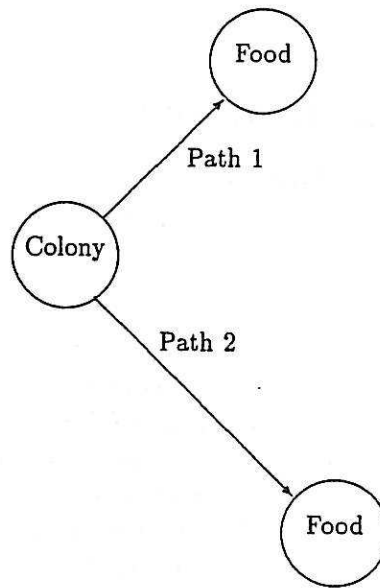


Figure 1: Conceptual model of path choice.

2 The Algorithms

2.1 Path Choice

The model is illustrated in fig. 1. Ants foraging from the nest may travel along either of two paths, which may be of different length. The food sources are considered equal, and have no effect on the decision process.

Ants leave the nest and select one of the paths. They travel along this path and back, and on return they influence their nest mates to take that same path. There is a global bias between the two paths which probabilistically determines which path the ants take. It is initially set at 50%-50%, so ants make a random choice. Returning ants update this bias by some value, in favour of the path they selected. After returning and influencing the bias, the ants leave again selecting a path probabilistically. The ants have no memory, and always act according to the current bias.

Ants will return faster from the shorter path, so the bias is likely to be updated in favour of the short path more often. Positive feedback will tend to take an unequal bias to fixation, 100%-0%, where all ants take the same path. Consequently there is a tendency for the colony to "choose" the short path. Random drift may however establish a bias in favour of the longer path, and the effect of positive feedback may lead to the colony choosing the longer path instead of the shorter path.

The algorithm is implemented in very simple C code, illustrated in fig. 2. This ensures accuracy and allows many replicates. We can vary several parameters:

- The number of ants foraging from the colony.
- The length of the two paths.
- The amount of *influence* each ant has on the global bias, when returning from a path. For any simulation, this is a fixed value: all ants always exert the same amount of influence.
- The rate at which ants initially leave the nest, or *release rate*. Foraging ants do not all leave simultaneously, though once they have left the nest they continue to forage.

```

#define TIME 0
#define DIR 1

/*definition of variables: */

int ant[2][1000],      /*array representing up to 1000 ants. Each has a
                       "time value" and a "direction value"*/
dist[2],              /*lengths of the two paths.*/
r,                    /*the value of "R" (time between ant releases)*/
influence,            /*the value of "I" (influence of each ant)*/
n_ants,               /*the number of ants*/
zero_fix,             /*number of times (in 1000 reps) path 0 is fixed*/
rep,                  /*replicate number*/
bias,                 /*bias towards path 0 (1..1000 rather than per cent)*/
t,i;                  /*loop counters*/

/*execution of a set of simulations: */

dist[0]=10;           /*path 0 has a fixed length of 10*/
for(dist[1]=10; dist[1]<=200; dist[1]+=5) /*increasing length of path 1*/
{ for(n_ants=1; n_ants<=200; n_ants+=5) /*increasing the number of ants */
  { zero_fix=0; /*initialise path choice counter*/
    for(rep=0; rep<1000; ++rep) /*produce 1000 replicates*/
    { bias=500; /*initialise path choice bias to 50%*/
      for(i=0; i<n_ants; ++i) /*each ant given: initial time value,
                              incremented in steps of r; direction
                              value of -1 when still in the nest*/

      { ant[TIME][i]= 1+(i*r);
        ant[DIR][i]=-1;
      }

      for(t=0; bias>50 && bias<950; ++t) /*proceed until bias is fixed*/
      { for(i=0; i<n_ants; ++i) /*each ant in turn*/
        { if( --ant[TIME][i]==0) /*Subtract one from ant's time
                                value. If zero it is about to
                                leave the nest*/

          { if (ant[DIR][i]==0) /*if it last took path 0...*/
              bias+=influence; /*... increase the bias*/
            else if(ant[DIR][i]==1) /*if it last took path 1...*/
              bias-=influence; /*... decrease the bias*/
            ant[DIR][i]=(bias<rand(1000)) ? 1:0; /*make a random path choice*/
            ant[TIME][i]=dist[ant[DIR][i]]; /*add path length to time value*/
          }
        }
      } /*all ants done*/
      zero_fix+=(bias>=950)?1:0; /*a path fixed*/
                                /*if path 0 was fixed, count it*/

    } /*1000 replicates done*/
  } /*end of increasing ants numbers*/
} printf(" %d %d %d\n",dist[1],n_ants,zero_fix); /*print out result*/
} /*end of increasing path length*/

```

Figure 2: The algorithm implemented in C. See Stickland *et al.* (1993) for full details.

For details of the simulations see Stickland *et al.* ⁹.

2.2 Food Source Choice

The model is similar to the path choice model (fig. 1), but the path lengths are equal. The quality of the food sources can be different.

Ants leave the nest, travel to a food source and back, and influence their nestmates. As with the path choice algorithm there is a global bias which the ants can update. The amount of influence the ants exert on the bias is *not* constant, but is determined by the quality of the food source they last visited.

Ants returning from the richer food source have a greater influence on the bias, and there is a tendency to move to fixation on the richer food source. Positive feedback will tend to take an unequal bias to fixation. Again, random drift may lead to fixation against the expected trend, with the colony choosing the poorer food source.

The algorithm is again implemented in very simple C code. Only two variables are required to investigate the behaviour of this algorithm.

- The number of ants foraging from the colony
- The values of the two food sources.

Full details are given in Stickland *et al.* ¹⁰

2.3 Path Choice with Different Food Sources

This algorithm combines path choice and food source choice. It is essentially the same as the path choice algorithm, except the food sources are of different quality. When an ant returns from a path, the influence it exerts on the bias is determined by the quality of the food source it visited.

We place the richer food source at the end of the longer path. This presents the colony with a conflict of interests: it may choose the short path *or* the richer food source. Full details are given in Stickland *et al.* ¹⁰

3 Behaviour of the Algorithms

The implementation of the algorithms allowed us to explore their behaviour over a very wide range of parameter values. For instance the values we used for *release rate* covered a range between two extremes: when many ants left the nest before any ant had time to return, and when one ant might make several round trips before another ant left the nest at all.

For any single set of parameters, 1000 replicates were run to completion (95% confidence limit of ± 32 .) The performance of the algorithm is expressed as the number of replicates in which one path, or food source, was chosen. A complete analysis is given in Stickland *et al.* ⁹⁻¹⁰.

3.1 Path Choice

Over a wide range of conditions the ant colony would show a strong tendency to select the shorter path. The graph in fig. 3 shows a sample set of simulations, with a range of path lengths and numbers of ants.

Several points are apparent from the simulations. The short path is more likely to be chosen when:

- the difference between path lengths is large
- there are many ants foraging
- the release rate is high

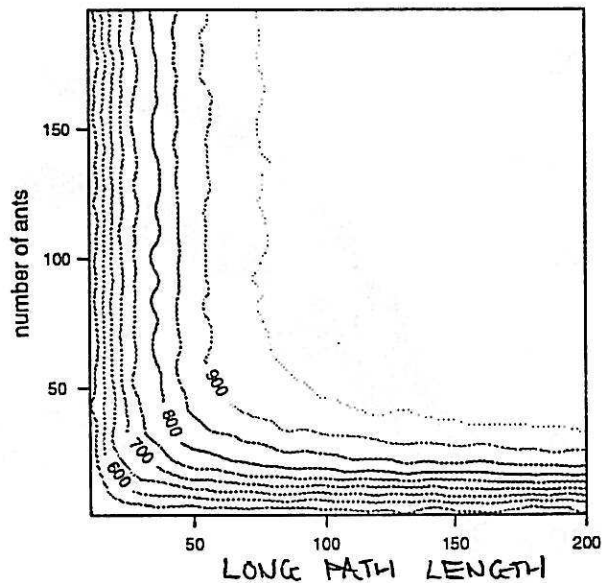


Figure 3: Success of path choice algorithm. The graph is three dimensional, contours representing the number of replicates (of 1000 total) in which the colony finally chose the short path. The path length shown is the long path: the short path is fixed at length 10. The length is the number of time steps required to make one return trip. In this example the release rate was set for one ants to leave the nest every 25 time steps. The ants exerted an influence of 2% on the global bias upon returning. See Stickland *et al.* (submitted) for details.

When the influence exerted by ants is high, this will usually increase the chance of the colony choosing the short path. When the release rate is slow, however, one ant may make several trips (and update the bias several times) before other ants complete any trips. One ant will initially choose a path randomly and is subject *only* to positive feedback as a selection force. If it has a high influence it will have a large random effect on the bias, which can lead to the long path being chosen.

3.2 Food Source Choice

The ant colony shows a very strong tendency to select the rich food source, as illustrated in fig. 4. The range of simulations makes it clear that the rich food source is more likely to be chosen by the colony when:

- the absolute values of the food are low (ants have a low influence)
- the food sources are of very different quality
- there are more ants foraging

We also recorded the number of time steps each simulation took to run to completion. The time taken is very much greater when the food quality values are low, but only when there are few ants. Clearly for small colonies there is a trade off between speed and accuracy when selecting a food source.

3.3 Path choice with different food sources.

The behaviour of this algorithm is more complex to investigate. There is a conflict between selecting either the short path or the rich food source: unlike the other two algorithms, there is

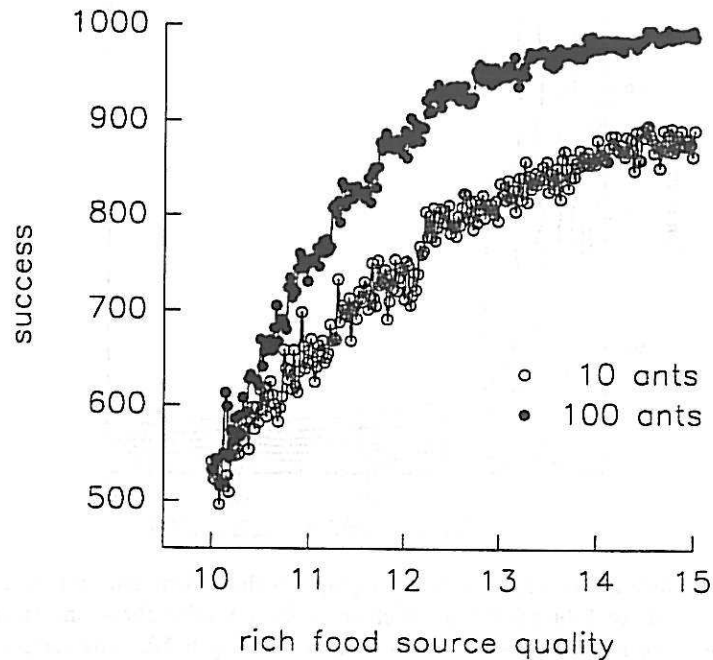


Figure 4: Success of the food choice algorithm. The graph shows the number of replicates (of 1000 total) in which the colony chose the richer food source. The food quality shown is the rich food source: the poor source is fixed at the value 10.

no clear expectation of what is the “right answer”, against which to measure success.

To investigate this algorithm we estimate the *equiprobable path length ratio*. This is the path length ratio at which the tendency to select the rich food and the tendency to select the short path are exactly balanced. It can be identified by finding the path lengths at which the each path is chosen in 500 of the 1000 replicates. Clearly the equiprobable path length ratio will vary according to the parameter values (see fig. 5).

The equiprobable path length ratio increases when the difference between food source values is increased. This is clearly because the tendency to select the richer food source will also be greater. However, the equiprobable path length ratio will reach a maximum value. We call this the *search limit*.

The search limit represents the point at which no further increase in food value will be detected by the colony. The richer food source is too far from the nest for the foragers travelling to it to return quickly enough to influence the bias. This is a property which emerges from the nature of the information exchange in the system.

A large search limit indicates that the colony will choose a path predominantly according to the food source quality. A low search limit indicates that the colony chooses predominantly according to path length. The search limit tends to be large when:

- ants exert a low influence on the bias when returning to the nest
- the release rate is slow

A further property is that when there are very few ants present the colony will almost invariably choose the richer food source. There is a minimum number of foraging ants necessary to detect which path is shorter. This minimum number is reduced when the food quality is high (returning foragers exert a large influence on nest mates).

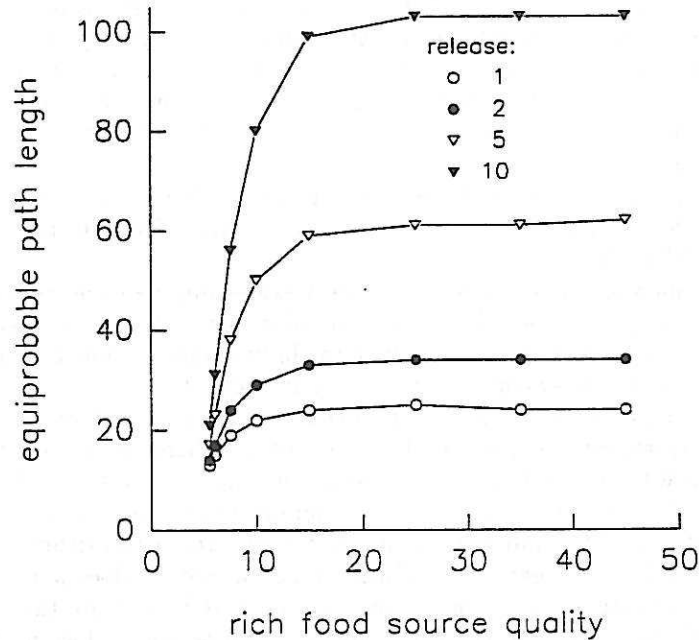


Figure 5: The equiprobable path length ratio, over a range of food quality values. The poor food source is fixed at 5. The release arte values are the number of time steps between foragers first leaving the nest.

4 Conclusions

These algorithms illustrate that a choice between paths or food sources can be made collectively. The individuals involved need act in only a very simple manner, making no comparative judgements when exerting influence on nestmates.

We consider three parameters determined by the nature of the ant colony: the number of foragers, the release rate from the nest, and the influence that foragers exert on their nest mates when returning. These not only determine the effectiveness of path choice and food source choice, but have a complex rôle in the more realistic model with unequal path lengths and unequal food sources. The combination will determine whether food quality or path length predominates in the colony's choice, and will also determine the size of the emergent search limit. They can be viewed as supporting a *foraging strategy*.

A large number of foragers will increase the effectiveness of any algorithm within limits. When the path lengths and food sources are both unequal, the food quality will predominate the colony's choice if there are very few ants. The size of the colony will be the main factor dictating the number of foragers. The requirement for a viable foraging strategy may determine the colony size, though this may be limited by the environment.

A slow release rate will reduce the effectiveness of the path choice algorithm. However when unequal food sources are introduced, a slow release rate will result in a large search limit. If too many ants leave the nest at once, the colony will have already have chosen the nearest food source before foragers can return from the other source. Even if this source is much richer, the foragers will not now recruit to it.

The influence ants exert on nestmates will be determined by the recruitment behaviour employed. There is a great diversity of recruitment behaviour, which we might expect to be the product of natural selection. The influence exerted by foragers may determine whether the colony

makes a choice predominantly of path length or food quality, and the size of the search limit. Foragers of several species have been observed to respond differently to food of different type and quality, and alter their response according to the state of the colony when starved¹¹⁻¹⁴.

The behaviour of the food choice algorithm indicates that there is a trade off between accuracy and speed of choice of a food source, and that this can be controlled by the influence exerted by ants. Since this is a product of recruitment behaviour, ant foragers should be able to control this trade off in response to different food types: they could recruit quickly to short lived food sources by exerting a high influence, or gain an accurate assessment of the quality of more permanent food sources by exerting a low influence.

The importance of colony size should be stressed. This will determine the number of foraging ants, and may also have a large influence on the release rate. These factors will determine the foraging strategy of the colony.

Slight variations numbers of foragers, individually exhibiting the same behaviour, will produce different foraging strategies. This might result in colonies of different size exploiting a slightly different ecological niche, despite the similarity of the individuals. The distinction between similar individual behaviour and similar colony behaviour is important.

The foraging strategy of the colony will also change as it ages and grows, if the recruitment behaviour of the foragers remains constant. If the recruitment behaviour of the foragers changes as the colony grows, the foraging strategy might remain constant. Alternatively, changing recruitment behaviour might produce a complex progression of foraging strategies as the colony ages.

The search limit illustrates an important point about these algorithms. It is an emergent feature, which derives from the nature of information exchange. It does not derive from optimal foraging. Fewell's observations of *Pogonomyrma occidentalis*¹⁵ indicate that the energy budget of foragers is unlikely to influence their behaviour. A rich food source beyond the search limit of a colony might be ignored even if it represented the best balance of energy against time, risk or the energy required in foraging. The colony will not detect this piece of information about the environment.

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