Birds use self-organized social behaviours to regulate their dispersal over wide areas : evidences from gull roosts.

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Abstract

Direct and video observations indicate that flocks of black-headed gulls exhibit simple rules for disposition, orientation and movements of individual birds, even in dispersed foraging groups.

Characteristics of at least some of these rules may be linked to the daily dispersal flights between nocturnal roosts and diurnal feeding areas. Every day, these flights distribute tens of thousands of gulls over thousands of square kilometers. They are organised in vast, stable and oriented networks with roosts at nodes. These dispersal networks are comparable to vast automata networks with the transition functions acting nightly at roosts .

At these roosts, birds do not sleep, but perform impressive mass movements. These movements are autocatalytically generated, using the same simple rules as for diurnal flocks. All the features of these movements are linked to the spatial structure of the local network. We therefore suggest that these mass movements contribute to the transition functions of the dispersal network.

Counts of gulls indicate that they regulate their daily dispersal according to both the total amount of birds to be distributed and the resource availability. We suggest that our model of two interacting complex systems, autocatalytic mass movements as transition function of the dispersal network, is able to account for this regulation.

The course of this paper will lead us from the simple rules structuring diurnal flocks of gulls *(I. Simple rules structure flocks)* till the global complexity of the distribution of tens of thousands of them over wide areas *(IV. Dispersal regulation : the global complexity).* These rules will be linked to this complexity through the spatial structure of daily moves *(II. From dispersal network to automata network)* and the nocturnal roosting(*) behaviours *(III. From mass movements to the transition function).*

The construction of this model is based on many field data. The aim of this paper is not to attest the accuracy of these results, this will be done elsewhere and concerns more directly behavioural ecologists. The aim of this paper is rather to construct a new hypothesis based on a wide background of field realities.

I. SIMPLE RULES STRUCTURE FLOCKS.

Every day in winter, black-headed gulls *(Larus ridibundus)* disperse over wide areas to feed. They could explore vast feeding-areas of cities and countries or stand on localized feeding-spots, like rubbish tips or sewage stations. On these stable and localised food sources birds usually arrive in the morning and could spend the whole day till the go-back to the roost. For logistic reasons, only these stable patches have been investigated.

Three main "simple rules" will be explored: the inter-individual distance, the facing direction and the choice of this direction.

Rule 1 : Inter-individual distance.

Data were collected on the water purification station of Diepenbeek. During ten days, videofilms of black-headed gulls flocks were made. The lenght of one or several gulls were mesured on a still picture, and this length was used as unit to measure distances between the feet of the gulls this unit is called "Lr".
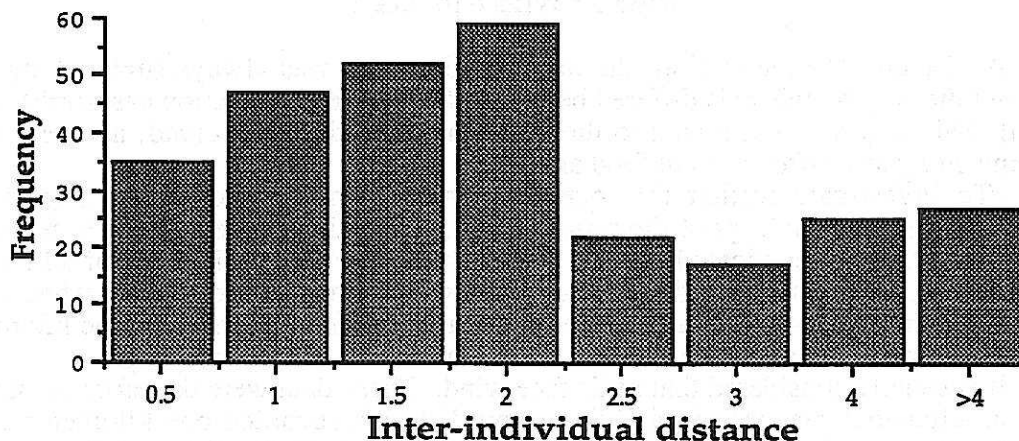

Figure 1. Frequency of inter-individual distances at landing (Lr units).

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* The roosting behaviour is the behaviour of gathering for the night, usually in some particular places. These assemblies can gather numerous birds and are generally monospecific. In non-breeding season, most of the birds species use roosts. Despite this frequency and numerous publications both its mechanism and function remain mysterious.

In 52% of the landings, gulls landed at 1 - 2 Lr of another gull (average: 2.266 (n=302)). Landings closer than one Lr (i.e. gulls almost or completely touched one another) were often unstable (prop unstable= 0.6857 (n=35)), the average distance of unstable landings is 0.67 Lr. Reactions on the unstability were performed almost always immediately (Proportion= 0.9394, n=33): the owner or the newcomer moved up, or they started some kind of fight. We have no evidence that gulls actively reduce distances if they are too large. In a group with stabilized distances, birds did never react (n=92) if another bird flew away, although he increased the interindividual distance of his neighbours by his departure.

Rule 2 : Fly off, landing and facing direction.

To mesure the direction the birds choice to face a set of eight directions was used (N,NE,E,SE,S,SE,W,NW).

For each of the ten days one direction was used in 42%-78% of the low flights and diving (proportion prefered direction=0.5849 $\pm$ 0.1090, n=7). Birds flying in any other direction than the prefered one, tended to turn in flight when landing, even up to 180°, or immediately (<1seconds) after landing. Therefore, this direction was even more pronounced for landings than it was for flying (proportion:0.563 (n=1167) versus 0.6469 (n=371) P=0.0022). Foraging dives at the best feeding-place happened fewer when the facing direction is opposed to the stream direction (0.8783 (n=433) vs 0.2083 (n=42) P<0.0001). The facing direction choice could thus imply a foraging cost for the birds.

It is clear that these two first simple rules structure the group as an uniform entity. One aim of this structuring is surely to react to environmental stimulus as a whole. An example is the sudden taking wing of a resting group because of a predator arrival. A minimal interindividual distance and a common fly off direction are needed to avoid collisions, as well as for keeping the mass impressiveness of the all group.

But beyond these simple group behaviours, the structuring of a group could also give it some emerging self-organisational properties. It will be explored with the nocturnal mass mouvements within the third section of this paper. But simple questions could yet lead us to a further level of complexity. One of these is *"which direction do the birds choice to face ?"* .

Rule 3 : Where to face ?

At the purification station, the prefered direction was always (n=9) along one axis, but the way on this axis differed between days (prefered direction east (n=5), west (n=4)). This way was not linked to the basin in which the gulls dived, neither was it determined by any differences in food amount.

To investigate further this question, the facing direction of resting groups (n=405) in the surroundings of the refuse tip of Mont-Saint-Guibert has been recorded nearly daily during the winter 1990-91. For each day (n=78), all the birds of all resting groups (16 possible sites recorded) choice exactly the same direction. Even when some groups were in the bottom of a 50 meter deep quarry, while others were one kilometer away in an open field and still others ones on a lake three kilometers away.

It is usually considered that birds face wind. These data were therefore compared with simultaneous records of wind force and direction recorded one kilometer away from the center of the area explored. The difference between the direction choosen and the wind direction differs widely from zero (mean = 120°; Wallon,1991).

Our data show also clearly that birds face mostly two opposed directions, the two ways of one axis (figure 2). The choice of the way varies from day to day but could remain quite stable for longer periods (Wallon, 1991).
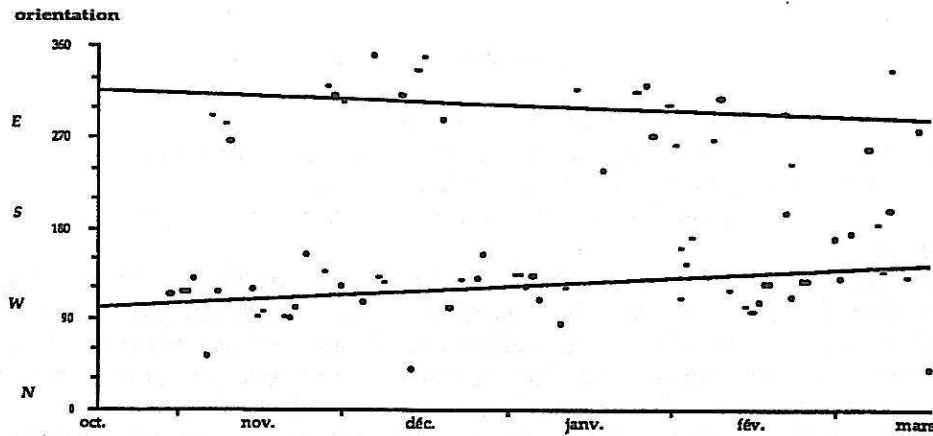
Figure 2. Successive choices of facing direction for the resting flocks at Mont-Saint-Guibert (1990-91). The mean difference between both lines is 180°.

Sutch pattern of the both sides of one axis has been confirmed by records in different feeding regions and appears to be widely generalised. But the axis choosen differ from one region to another. The mapping of these axis indicates that they point to the roost or, more precisely, that they are parallel to the local pattern of fly routes to the roost. This correlation is of great interest for us because it links the simple rules to a wider level of complexity: the daily dispersal network.

II. FROM DISPERSAL NETWORK TO AUTOMATA NETWORK.

Daily movements between feeding-sites and roosts could be as long as 200 kilometers. Few is known about the spatial structure of these journeys but they are generally considered implicitly as converging to a centrally placed roost from the surrounding areas all around. The birds are supposed to go to the nearest roost, selecting the shortest travel. At these roosts, birds will arrive from all directions.

Even if this scheme is always present as the background of most hypothesis about the function of communal roosting in birds, it has scarcely been tested and never been based on any field data.

Methods

In order to test this sheme for black-headed gulls, various kind of datas have been collected during four consecutive years (1989-1993).

1. Direct observation of arrivals and departures at different roosts and their surroundings. **2.** Follow-up of flying flocks from feeding-sites till roosts and from roosts to feeding-sites. **3.** Analysis of old enquieries (Unpublished datas AVES, 1964) about the fly routes in the same region. **4.** Simultaneous counts of arrival fluxes on many different roosts . **5.** Capture, marking and recoveries of birds individually marked with reflective "back-marks" (n=502). **6.** Trakking of radio-tagged birds (n=2).

The detailed results of these various methods could not be given here (De Schutter, In prep). We will only present the general features of the pattern of fly routes constructed from all these results. These features are confirmed in many roosts of different regions in Belgium. They will be explained for evening gathering routes; the morning routes are the same with, of course, a reversed flight way. As example, figure 3 presents the map of the main evening fly routes in a part of central belgium (Brussels and north Brabant).

Dispersal network

The following features could be pointed out.

All the birds leave every feeding area in only one direction. They join a roost following roughly this direction. *(methods 1, 2, 4 & 6)*

Routes never cross but join together or, more rarely, split before the roost. *(method 2)*

Birds arrive on roosts from maximum two close directions*(methods 1 & 5)*. The roost is, therefore, not centrally but marginally placed regarding to the feeding areas drained. And the roost joined is therefore not always the nearest one. In particular, birds close to a roost but on the side opposed to the reaching routes will fly much longer journeys to reach a further one in the right direction.

Birds could pass over a roosting site, or leave it, in order to join a further roost. It is always done in one unique direction, opposed to the arrival ones. These passes-over are generally observed in the early evening. By this way, birds coming from a given feeding-site could spend the night on different roosts. *(methods 1, & 4)*

Old enquieris about fly routes as well as our study during four consecutive years indicate that they remain very consistent from year to year and over a long period of time. *(methods 1, 2 , 3 & 4)*

The follow-up and recoveries of marked individuals indicate that birds are not faithfull neither to feeding-sites, nor to roosting-sites. Diurnal movements between feeding areas induce changes in roosting-sites for the next night. Also at night, mostly during the first part it, direct exchanges exist between roosts. *(methods 5 & 6)*
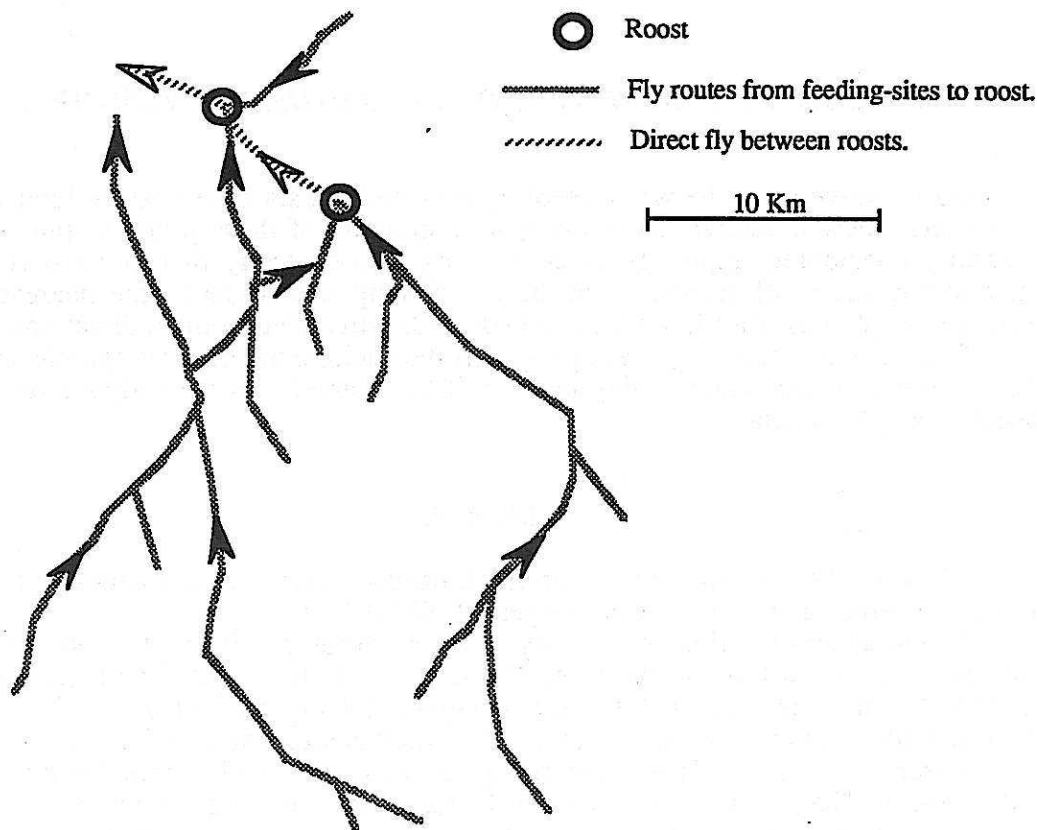

Figure 3. Main fly routes and roosts in the area of north Brabant (central Belgium).

In stead of a radiating pattern with a centrally-placed roost, we have got in fact a vast directed network with interconnected roosts at nodes, using precise rules of arrangement (figure 3). We will call it the "dispersal network". This dispersal network is both very stable in its spatial pattern and very unstable in its members composition.

Automata network

Directed networks of automata and neurons have demonstrated their ability in creating emergent organizational properties. One main idea of this paper is that the dispersal network could act in the same way and could organize the distribution of the birds over their diurnal areas.

We can isolate the routes linked to one roost as in figure 4. This figure easily recalls the neuron sheme with the ramification of the entering dendrits, the roost as cell body and an outgoing axon reaching further roosts. But this metaphor of the roost as a neuron is not valid; the main output of a roost is not the birds passing over it and continuing by the "axon" to reach other roosts. The real output is the morning departure of birds reaching their feeding-sites.
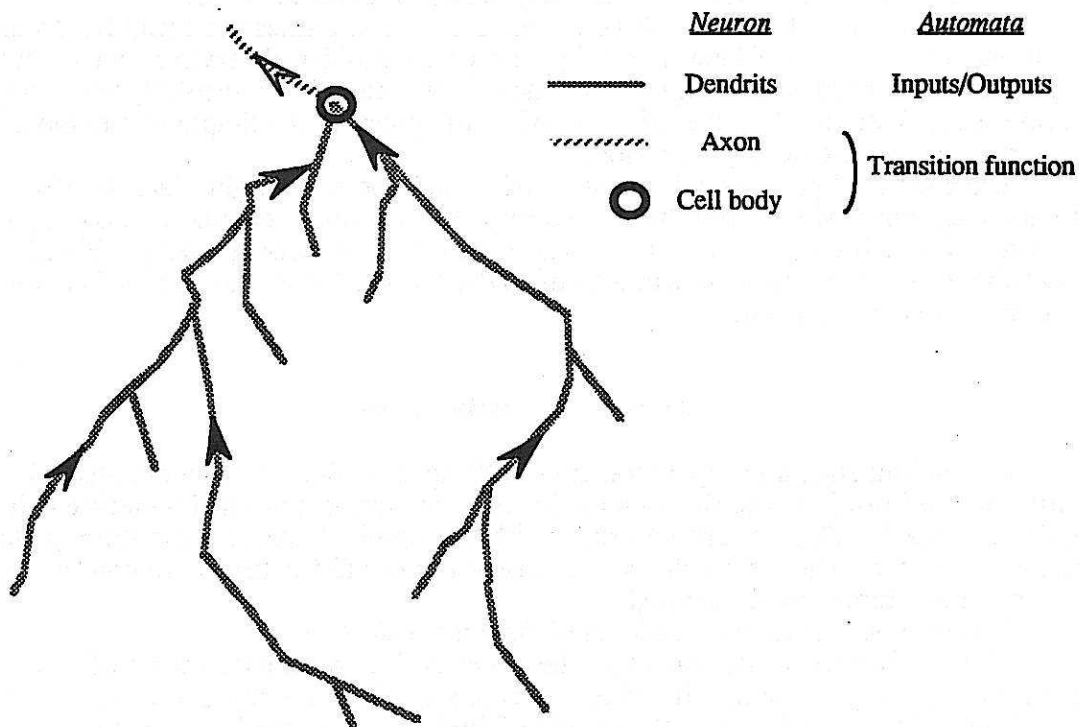

	Neuron	_Automata_
————	Dendrits	Inputs/Outputs
·········	Axon	Transition function
O	Cell body	

Figure 4. The main fly routes reaching and living the roost of the Nekkerspoel.

Therefore we will use another model called "automata" where the fly routes between feeding-sites and roosts carry both the inputs in the evening and the outputs in the morning. Inputs and outputs are temporaly separated and can not interfer(*). The transition function of this "roost-automata" is computed nightly, at roost. This transition function is in charge of transforming the dispersal for the next day.

Direct exchanges between roosts are not considered as outputs by this model. They are in fact included as inherent parts of the transition function. They permit a change in the amount of birds to be redistributed from each roost through the morning outputs.

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* To fit completely an automata network to the dispersal network this temporal dimension could be represented as a third spatial dimension. Along this third dimension the number of two dimensional network layers corresponds to the number of days considered.

The next section *(III.)* will explore the likelihood of the night-time behaviours to ensure any transition function. The last one *(IV.)* will adress how widely changes from one day to the next could result from such a function.

III. FROM MASS MOVEMENTS TO THE TRANSITION FUNCTION

Untill now we are neither able to discriminate the variables, nor to define the rules of any transition function managing the redistribution of birds from a roost. We can only show how nightime behaviours are likely to insure any transition function. A transition function links inputs to outputs through computed changes. Different features of the gulls nights will therefore be considered in order to check how much they are likely to relate input to output through any integrative process.

Only the basic features will be exposed here, sometimes too roughly. Nearly a thousand of hours have been spent by one of us (GDS) observing and recording sleepless black-headed gull nights. All these hours have been absolutly necessary to define these features. So, even if some of them appear quite simple and evident it is important to notice that they were not !

Black-headed gulls usually roost on lakes and pools. At night black-headed gulls do not sleep but perform very impressive mass movements separated by short pausing periods. We will first discuss the pauses, then the movements patterns. Finally, the mechanic of these movements will lead us to discuss the "roost - transition function" as a complex system in itself.

Pauses: the resting sheet.

If standing still, a group of roosting gulls appears like a very elongated, sharply cutted and uniformly white sheet on the black water surface; we will therefore call this group a "sheet". This pattern contrasts with the rough shape of a the diurnal flocks resting on water. The three rules which structure diurnal flocks *(I)* are conserved but they are much more strictly applied.

Uniformity: a strict inter-individual distance (rule 1)

The uniformily white aspect of the sheet is due to an extremly uniform inter-individual distance. The density of birds is constant from the middle to the margin of the sheet, which could gather thousands of birds and be one kilometer long. This creates a surprisingly sharply cutted margin to the shape of the group. This inter-individual distance could vary in time. It will never been shorter than 1 Lr unit, with a mean of 2.5 Lr (n= 91, st.d.=1,49). When the sheet stands still for a long time (>1 hour) the interindividual distance seems to increase progressively and uniformly. Probably because of asymetrically compensated "brownian" moves.

Face together (rule 2)

As for diurnal flocks, all the members of a resting sheet sit parallel and face together exactly the same direction. This rule can only be transgressed if the inter-individual distance is great ($\geq$ 3.5 Lr) and if the sheet stands still for a while.

Face along the network axis (rule 3)

As for diurnal groups the choice of the direction to face is stable. It also consist of a single choice between the two opposite ways of one axis. This rule is more much strictly followed nightly and the relation between this axis and the dispersal network has always been confirmed.

Ovally elongated shape (rule 4).

A resting sheet is always very elongated and usually ovally shapped. The mean breath on lenght ratio is 9.5 (n=15). The long axis of this oval is in fact the one used for the facing choice.

Therefore it is in fact the local network pattern which determinates both the facing direction and the shape of a resting sheet (rules 2, 3 & 4). This has been

confirmed on different roosts. On some sites, we have studied the local network pattern before any observation of the night sheet. It has therefore been possible to made predictions about both shape and facing direction. These predictions were always confirmed.

Mass movements : the moving sheet

Resting sheets are rarely still for a long time. Inside the sheet, impressive mass movements are generated. Hundreds of them were followed and sketched or recorded on video tapes. It is impossible to consider here the diversity of these impressives and complex mass behaviours. Figure 5 gives a simplified description of an idealized movement.

0'00"   5'00"
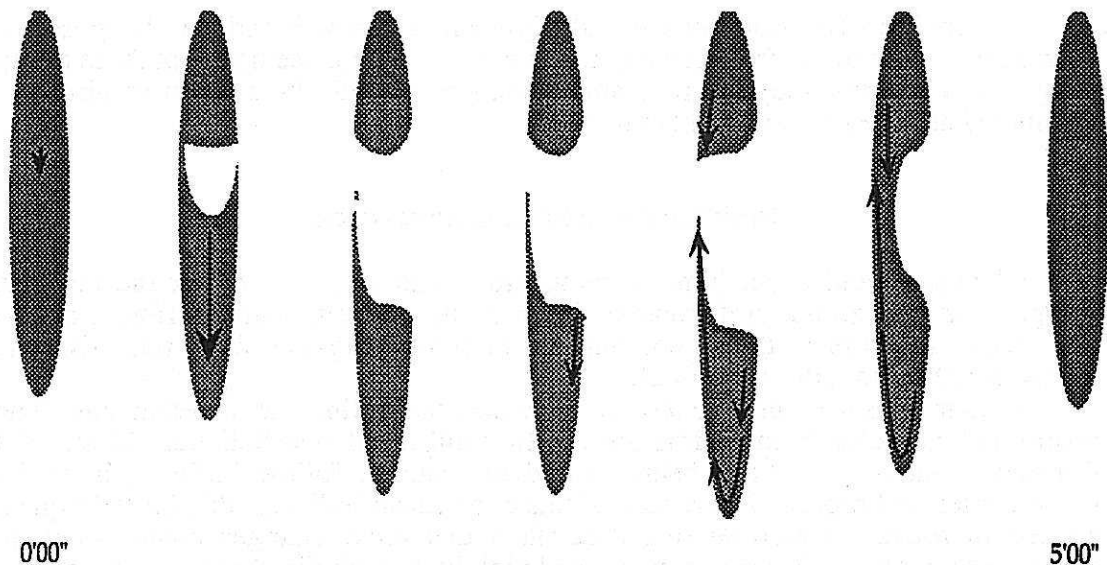
Figure 5. Simplified example of nocturnal mass movement.
Occuring with (tens of) thousands gulls.

The movement start with a group of birds swimming together speedly in one direction. This move is infectious and could sweep till the most part of the sheep. These moves divide the sheet in two smaller sheets. And after a stabilization, they tend to recover their original unity. These moves are performed along the sheet elongation axis. We could therefore describe such move as a division of the sheet perpendicular to the network axis. All the spatial features of these moves are in fact correlated to the spatial structure of the local network.

An auto-catalytic transition function

The impressivness of the scene comes from the uniformity of the group moving as a whole, sometime at very high speed. Inside these mouving groups, each bird has never more than 1 Lr inter-individual distance.

These moves are induced from one bird to his neighbour. This infectious process is linked to the inter-individual distance. When the distance between one moving bird and his resting neighbour decreases till a minimum (< 1Lr) it induces the resting bird to "flee" and move in the same direction and at the same speed. The mechanic of these movements has been experimentally tested inside roosting sheets with a stuffed gull placed on a remote-controlled small ship.

This mechanic is clearly an auto-catalytic process generating amplification of small moves. It has been proposed that groups using such auto-catalytic mass

movements get abilities for collective decision making, pattern formation or general structuring, that far exceed the ones of isolated individuals (Deneubourg and Goss, 1989).

As these moves are spatially correlated with the local dispersal network patterns, it could be proposed that any collective decision would concern this network, i.e. the output-input spatial structure.

We therefore suggest that these auto-catalytic mass movements contribute to the transition function of the roost.

IV. DISPERSAL REGULATION : THE GLOBAL COMPLEXITY.

A transition function occuring at night on roosts will induce changes in the distribution of the birds, from one day to the next. We shall see here that these changes really occur and that they are regulated according to both the amount of birds to be distributed and the resource availability.

Individual marking: changes occur.

Changes could occur both in composition and size. To check the individual composition of a group, birds must be individually marked. Three different methods have been used to mark them : combination of colour rings (n= 694), reflective back-marks (n=502) and radio-tags (n=2).

Colour rings were used to test the individual faithfullness to a feeding-site. These results indicate clearly that birds are not faithfull at all (De Schutter, 1987, 1988). Reflective back-marks have been created in order to follow individuals on both feeding-sites and roosts. The results of this experiment indicates that birds frequently change of roost. Radio-tagging data show that these changes could occur both diurnally through the dispersal network and nightly through direct roosts exchanges.

These results show that changes in the distribution of the birds occur widely from one day to the next. But they do not address the question of the regulation of these changes. Do these changes occur "randomly", or are they managed? The study of the variations in the amount of birds at different sites will address this question.

Roosts : regulation according to the amount to be distributed.

It is logistically impossible to counts simultaneously tens of thousands of birds dispersed over areas of thousands of square kilometers. But during the night all those birds are gathered in few roosting sites. As the roost distribution is directly linked to the diurnal distribution, this question of the regulation of birds dispersal, has been explored through the analysis of roosts counts.

The number of birds present on both roosts of the surroundings of Mechelen (central Belgium) has been counted frequently during two consecutive winters (n= 30, 45) and nearly every night for the two next ones (n= 78, 85). We have tested the "predictability" of these curves. A curve beeing predictable if its value is quite stable or if its occur non-randomly (i.e. if the probability of a given event is a function of the outcome of the preceeding one, this could be tested with run up and down tests; Sokal & Rolf, 1981).

The results indicate that the evolution of the total number of birds present on both sites, as wel as their sum, evolves in a completely unpredictable way. Neither stability, nor any peridiocity, could be identified within these curves (figure 6).
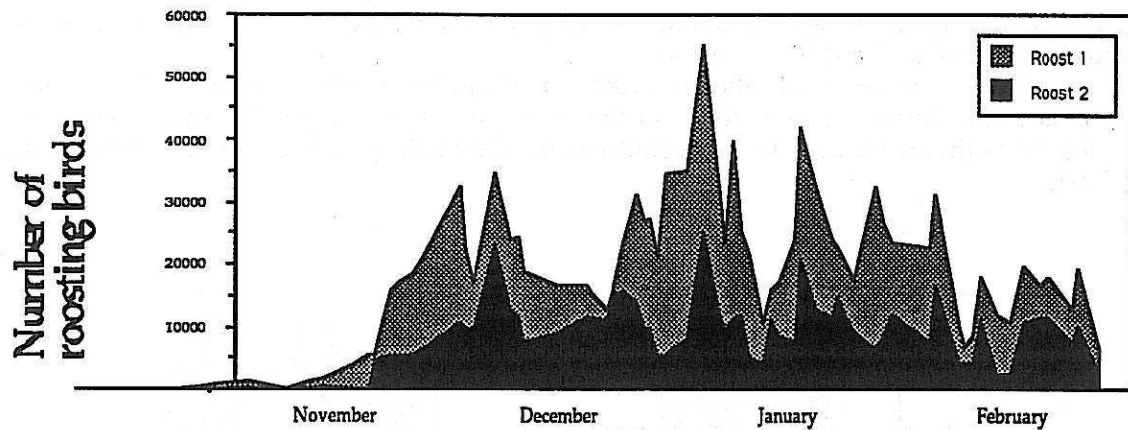
Figure 6. Evolution of the number of black-headed gulls roosting on two roosts. Example of the winter 1991-92.

These two roosts are very close to each other, directly linked in the roost network and share parts of their feeding areas. We have therefore addressed the distribution between the two roosts of the total amount of birds present on both (expressed in percent of the total). In contrast to the preceding results, this value is higly predictable from day to day (P<0.01). And even, present a rather complex pattern of evolution wich is constant from year to year over the four consecutive years (figure 7).
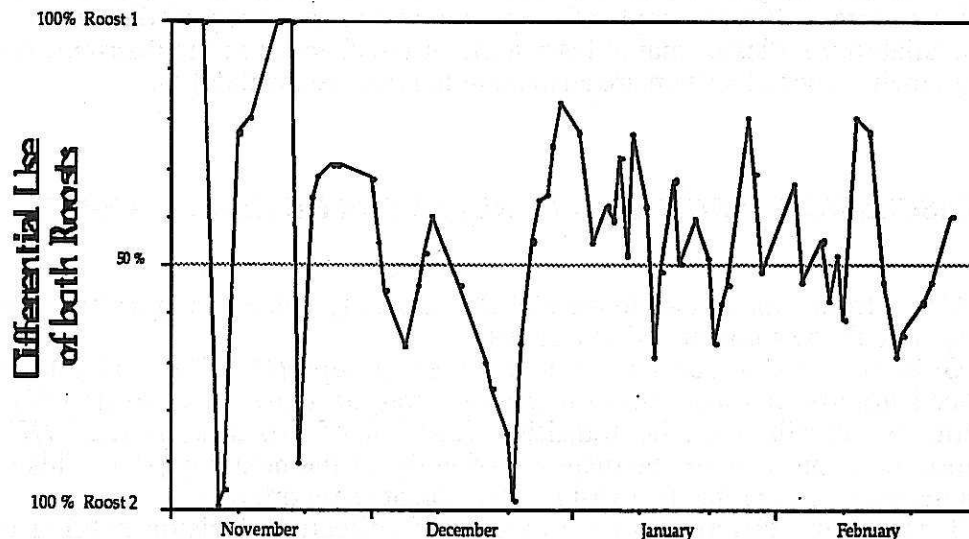

Figure 7. Distribution between both roosts of the number of birds to be distributed.

So, the proportion of birds distributed between the two roosts evolves in a complex but very predictable way, whereas the number of birds to be distributed is unpredictable from day to day. This means that the distributing process take into account the total number of birds to be distributed in order to settle the number distributed on each site. This is a regulation of the distribution of the birds in function of the amount of birds to be distributed!

Week-ends closure : adaptation to ressource availability

In Belgium dumps close on Saterdays and Sundays. For gulls, a closed dump is of bad interest.

Counts of the number of birds reaching the dump site of Mont-Saint-Guibert were performed daily during one complete winter (n=113). They were significatively less

numerous during the week-ends than during the rest of the week (p< 0,001; mean=885 n=20; mean=1969 n=93) (figure 8).

Counts on the dump, its surroudings and the fly routes indicate that birds do not forsake the dump, in fact, they do not reach it. This adaptation to the week-ends closure is therefore take into account before the feeding-site, by the dispersal system itself.
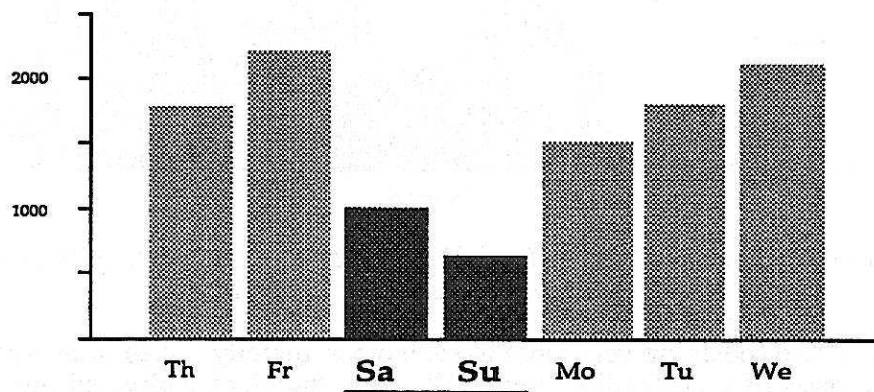

Figure 8. Mean number of black-headed gulls present at the dump of Mont-Saint-Guibert for each day of the week (winter 1986-87).

Black-headed gulls could thus adapt their dispersal to the week-end closure of their food sources. This example of adaptation to a drastic but periodic evolution of the food avaliability indicates that at least some of the changes in the distribution of birds through their dispersal system are adaptative to resource availability.

V. DISCUSSION : FROM SIMPLE RULES TO THE GLOBAL COMPLEXITY

Going from simple rules to the global complexity, the model developped all along this paper could be summarised as follows.

Gulls use simple rules to structure their groups (I). These simple rules are enhanced nightly at roost, permitting auto-catalytic mass movements (III). These movements contribue to the transition function of "roost-automata" (III). This transition function regulate the dispersal of gulls for the next day (IV). This dispersal uses a network comparable to a vast roost-automata network (II).

This scheme differs from the models of collective decision making in social insects in the way that two different complex systems are involved. The first is the autocatalytic mass movements system. It is supposed to insure transition functions inside the second one : the dispersal network.

Untill now, we do not think that these two sytems are two aspects, observed at different scales, of one unique complex system of movements. The gap between them could be that, on morning departures, the final decision is taken individually by each bird. The bird brain, another complex system, could be able to transform informations acquired during the night mass movements in diurnal dispersal choices.

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