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► To cite this version:

Aina Astudillo Fernandez, Jean Louis Deneubourg. On following behaviour as a mechanism for collective movement. *Journal of Theoretical Biology*, 2011, 284 (1), pp.7. 10.1016/j.jtbi.2011.06.001 . hal-00720865

HAL Id: hal-00720865

<https://hal.science/hal-00720865>

Submitted on 26 Jul 2012

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Author's Accepted Manuscript

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PII: S0022-5193(11)00299-2
DOI: doi:10.1016/j.jtbi.2011.06.001
Reference: YJTBI6502

To appear in: *Journal of Theoretical Biology*

Received date: 7 December 2010
Revised date: 11 May 2011
Accepted date: 1 June 2011

Cite this article as: Aina Astudillo Fernandez and Jean Louis Deneubourg, On following behaviour as a mechanism for collective movement, *Journal of Theoretical Biology*, doi:[10.1016/j.jtbi.2011.06.001](https://doi.org/10.1016/j.jtbi.2011.06.001)

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On following behaviour as a mechanism for collective movement

Aina Astudillo Fernandez ^{1a,b}, Jean Louis Deneubourg^a

^a*Université libre de Bruxelles. CP 231. Bvd. du triomphe, 1050 Brussels, Belgium*

^b*Université catholique de Louvain. Pl. croix du Sud, 5, 1348, Louvain-la-Neuve, Belgium*

Abstract

During collective movement, animals display a wide variety of mechanisms to maintain cohesion. In some species, individuals rely mainly on following their direct predecessor, thereby forming spectacular processions of individuals in single file. Despite being the simplest case of following behaviour, it is largely absent from the theoretical literature on collective migrations. The objective of this study is to quantify the efficiency of following the predecessor, in terms of ensuring cohesion. The situation we consider is a sequence of individuals facing a bifurcation. The choice between left and right is influenced by the choice of the predecessor. First, we model this situation with a two-state Markov chain with a symmetric transition matrix. Cohesion is quantified as the expected number of individuals on either side, and the expected number of consecutive followers. Although cohesion increases with the probability of following, it remains surprisingly low unless the probability is almost equal to one. Furthermore, cohesion decreases with group size regardless of the probability of following. Then, we generalise our model to situations in which individuals have a preference for one of the two choices (asymmetric transition matrix). For some parameter sets, the tendency to

¹Corresponding author: Astudillo Fernández, A. (aastudil@ulb.ac.be - Tel: +3226505119
Preprint J. Theor. Biol. 2011, 270, 1-10
Fax: +3226505987) *Journal of Theoretical Biology* May 16, 2011

24 follow each other leads a large fraction of the individuals to the non pre-
 25 ferred side. Moreover, this fraction increases with the total population size.
 26 Finally, we include the possibility to follow N individuals. This provides the
 27 link between our model and other collective migration models. If enough in-
 28 dividuals are perceived, the results shift from symmetrical (low cohesion) to
 29 asymmetrical (high cohesion) distribution of the individuals. All in all, our
 30 results suggest that following the direct predecessor must be complemented
 31 with other cohesive behaviours (involving the perception of more individuals
 32 or a navigation system) to guarantee its efficiency. We discuss our findings
 33 in the context of the different following behaviours covered in the literature.

34 *Keywords:*

35 migration, collective decision making, group cohesion, aggregation, Markov
 36 chains

37 1. Introduction

38 Social decision making is common among a wide range of species. In
 39 those species, when an individual has to make a choice between a set of
 40 options, its decision is influenced by the decision of conspecifics. When imi-
 41 tation¹ in the broad sense is involved, it can lead to complex group behaviour
 42 (Deneubourg and Goss, 1989). This often results in some level of cohesion
 43 and/or synchronisation (Sumpter, 2006). The range of perception of each

¹By imitation we mean that an individual's probability of choosing one option is in-
 creased if other individuals already chose that option. Depending on the specific context
 it can be referred to as allelomimesis, social facilitation, public information... but here we
 use it in a very broad sense.

individual determines in the number of individuals by whom it will be influenced. This factor can therefore be of key importance in the resulting group cohesion.

Many types of decisions can be socially influenced. An example is temporal decisions (when to do something). For instance, pedestrians are influenced by other pedestrians as they decide when to cross the road (Faria et al., 2010). Sometimes, the imitation of others in temporal decisions can lead to synchronisation. There are countless examples ranging from flashing in fireflies (Buck, 1988, Ramirez Ávila et al., 2003) to synchronised alternation between feeding and vigilance bouts in sheep (Michelena et al., 2006, Gautrais et al., 2007) or to synchronized clapping in human audiences (Neda et al., 2000a, 2000b). Social influence has also been widely studied in the context of spatial decisions, such as where to forage, where to settle or where to breed (Danchin et al., 2004). Finally, there are directional decisions (which direction to take). Sometimes, directional decisions and temporal decisions are not dissociated. Sheep for example, tend to move when an other sheep moves, in the same direction as the initiator (Pillot et al., 2010). In this paper, however, we focus only on directional decisions, with no particular regard for the context of the displacement (where are they going to or why). More precisely, our interest lies in the mechanisms involved in the decision at the individual level, and their consequences at the collective level.

This ambition to link individual behaviour with collective movement patterns lies at the heart of a number of mathematical modelling studies. The behaviour at stake is, on the whole, following the other individuals. Understandably, the different biological realities require different types of models

69 (for a review see Giardina, 2008). In flocks of birds or schools of fish, each
 70 individual repeatedly updates its position according to the position of others
 71 (Couzin and Krause, 2003). The majority of models of schooling or flock-
 72 ing have been individual based, self-propelled particle (SPP) models (Okubo
 73 1986, Viscek et al., 1995, Czirok et al., 1997, Couzin et al. 2002, Grégoire
 74 and Chaté, 2004).

75 Another important section of the literature on collective movement con-
 76 cerns situations in which the directional decisions are taken sequentially by
 77 each individual, rather than simultaneously. This is typically the case of
 78 species that tend to move in single file such as social caterpillars, ants or army
 79 worms. Some fish have also been observed moving heads-to-tails (Gudger,
 80 1944). Finally, single files occur in any species constrained to move in a se-
 81 quence due to the geometry of the environment, such as sheep in mountain
 82 paths or cows in cattle-handling facilities (Grandin, 1980). The question of
 83 social influence on directional choices is typically studied with binary choice
 84 set-ups in which a bifurcation presents two identical options. The outcome
 85 of such experiments is either a binomial bell-shaped distribution (no social
 86 influence) or a U-shaped distribution, with most experiments resulting in the
 87 collective selection of one of the two options (social influence). This simple
 88 experiment has put forward collective movement in species as diverse as ants
 89 (Deneubourg et al., 1990), fish (Ward et al., 2008), dust mites (Mailleux
 90 et al., 2011), sheep (Michelena et al., 2010), caterpillars (Dussutour et al.,
 91 2008), spiders (Jeanson et al., 2004, Saffre et al., 1999) and earth worms
 92 (Zirbes et al., 2010).

93 The mathematical models used to describe such collective choices are

94 often individual-based simulations coding for the particular mechanism in-
 95 volved, for example dragline attachment in the case of spiderlings (Jeanson
 96 et al., 2004). General models covering a wide range of situations have seldom
 97 been formulated. One of these general models, hereafter referred to as the
 98 trail model (Deneubourg et al., 1990) expresses the probability of choosing
 99 one option as an increasing (potentially non-linear) function of the number
 100 of individuals who previously chose that option (see section 4 for more details
 101 on this probability function). The major prediction of this model is that in-
 102 dividuals will distribute themselves asymmetrically between the two options,
 103 if the response function is non-linear. Another, perhaps more abstract model
 104 is Polya's urn model, which makes similar predictions to the trail model (for
 105 given parameter sets). One of the assumptions of these models is that indi-
 106 viduals are able to perceive the choice of every preceding individual. This
 107 assumption is justified in the case of many species, which use modification
 108 of the environment (e.g., laying a physical or chemical trail) as means of
 109 communication. As long as the modification is permanent at the time-scale
 110 considered (no or little evaporation of the trail), then the assumption holds.
 111 However, with means of communication such as sight or hearing (e.g. in
 112 birds or mammals), the assumption ceases to be valid as soon as the total
 113 number of preceding individuals exceeds the range of perception.

114 The extreme case is when perception is limited to one individual, for ex-
 115 ample when animals in a sequence perceive others through tactile cues (con-
 116 tact). This is the case of processionary caterpillars (Fitzgerald, 2003), earth-
 117 worms (Zirbes et al., 2010), spiny lobsters (Herrnkind, 1969, Berill 1975),
 118 or some self-assembling robots (Levi and Kernbach, 2010). In these species

each animal follows its direct predecessor. Despite being the simplest case possible of following behaviour, it has never been studied from a theoretical point of view. Some car traffic models, called “Follow the leader” (Gazis et al., 1960), consider the influence of the direct predecessor in decisions about speed and acceleration, but not about direction.

The question we address here, is therefore how does the number of individuals perceived affect the cohesion of the moving group? We begin by developing a model for the simplest case: following a single preceding individual. We then extend the model to cover situations in which individuals follow an environmental cue as well as the preceding individual. Finally, the link between our model and the trail model is provided by a general model allowing the perception of N preceding individuals. Our results are discussed in terms of the efficiency of the different following behaviours covered in the literature.

2. Following the previous individual

The theoretical set-up is a path leading to a bifurcation. n individuals have to take the path and choose between left and right, one after the other. Each individual’s information is limited to its direct predecessor’s choice. It has a probability p of following its predecessor, and a probability $1 - p$ of taking a different path from its predecessor ($p > 0.5$ by definition).

The process is memoryless, in the sense that every choice depends exclusively on the choice of the predecessor. The choices of everyone else that passed before that previous individual do not have any influence on the focal

individual's choice. Therefore, this system can be assimilated to a two-state Markov chain, where the two states are the possible choices of the individuals (left or right). Since the probability of following the predecessor whether he took left or right is the same, the transition matrix is symmetric:

$$\mathbf{T} = \begin{pmatrix} p & 1-p \\ 1-p & p \end{pmatrix} \quad (1)$$

The entry $T(i, j)$ in the transition matrix represents the probability of transition from state i to state j . In other words, it is the probability of choosing side j , given that the previous individual took side i .

The question we address here is whether this mechanism is efficient in terms of ensuring cohesion. We suggest two ways of answering this question. Firstly, we calculate the proportion of individuals expected to end up on the side with the most individuals (hereafter referred to as the “winning side”). A very cohesive species would have an expected fraction of individuals on the winning side that is relatively high, whereas a poorly cohesive species would have an expected fraction approaching 0.5. Secondly, we calculate the number of individuals that are expected to take the same side successively, thereby forming a chain of followers. The expected length of those chains represents an accurate estimate of cohesion because all of those successive followers will end up in the same place.

Expected fraction of individuals on the winning side

Let n be the total number of individuals that face the binary choice. First, we need to calculate the expected absolute number of individuals on

the winning side. This can be done by using the definition of the expected value in probability theory $E(X) = \sum_{k=n/2}^n k \cdot P(X = k)$, where k can be any possible number of individuals on the winning side and ranges from $n/2$ to n . $P(X = k)$ is the probability of having k individuals on the winning side.

This probability is difficult to calculate, because all of the possible sequences leading to k individuals on a given side do not necessarily have the same probability (see an example in Fig. 1). Therefore, we calculate this probability $P(X = k)$ by grouping all of those sequences in groups with the same number of switches (an individual taking the opposite side to his predecessor). The reason for grouping the sequences in such a way is simple: the probability of any given sequence depends only on the number of switches a and on the total number of individuals n . Therefore all of the sequences in each group have the same probability, that is $P(X = k) = 0.5 \cdot p^{a-1-s}(1-p)^a$. The sum of the probabilities of all those possible sequences gives us the probability of having k individuals on the winning side:

$$P(X = k) = \sum_{a=0}^{2(n-k)} 0.5 \cdot p^{n-1-a}(1-p)^a f(n, k, a) \quad (2)$$

The function $f(n, k, a)$ gives the number of sequences leading to k out of n individuals on the winning side in which a switches took place. We propose a way to calculate this function $f(n, k, a)$. The sequences can have two possible configurations depending on the side chosen by the first individual (Fig. 2). In the first configuration (a), the number of individuals who chose the left are divided into three subgroups, and in configuration (b) into two subgroups. For the individuals who took the right, it is the opposite.

Fig. 3 shows the exhaustive enumeration of all the sequences in a concrete example involving 4 switches. In that example, the number of sequences of type (a) is simply the number of different ways there are to make 3 subgroups with 3 black elements multiplied by the number of ways there are to make 2 subgroups out of 4 white elements (same reasoning for type (b)).

If we define $G(x, y)$ as the number of ways to make x subgroups out of y elements, then the total number of sequences $f(n, k, a)$ can be calculated with the expression in Eq. 3. We give some details about this $G(x, y)$ function in appendix A. This expression was verified with simulations (appendix C).

$$f(n, k, a) = \overbrace{2 G\left(\left\lceil \frac{a+1}{2} \right\rceil, n-k\right) \cdot G\left(\left\lfloor \frac{a+1}{2} \right\rfloor, k\right)}^{\text{sequences of type (a)}} + \overbrace{2 G\left(\left\lfloor \frac{a+1}{2} \right\rfloor, n-k\right) \cdot G\left(\left\lceil \frac{a+1}{2} \right\rceil, k\right)}^{\text{sequences of type (b)}} \quad (3)$$

With this formula, we calculated the expected fraction of individuals on the winning side, and how it varies with the total number of individuals passing through the binary choice set-up. This was done for different values of the probability of following. As is shown in Fig. 4, the system tends towards a symmetric distribution of the individuals between the two sides, for probabilities of following that are different from 1. In other words, even though individuals follow one another, the fraction of individuals on either side tends towards 0.5. In Markovian terms, this is easily verified by calculating the stationary distribution of the system, that is, when the probabilities of finding the system in any given state do not change over time. At the stationary distribution the probability of finding the system in state i is called $\pi(i)$ and

is given by the formula $\pi(i) = T(j, i)/(T(j, i) + T(i, j))$, where $T(i, j)$ is the entry of the transition matrix (Eq. 1) containing the probability of taking side j , given that the previous individual took side i , ($i \neq j$). In our case, $\pi(\text{left}) = \pi(\text{right}) = 0.5$.

Expected number of consecutive followers

The individuals that follow each other uninterruptedly form a “chain” of individuals that all end up on the same side. The mean length of those chains gives us an estimate of the cohesiveness of the species: the larger the mean chain length, the greater the cohesion. Note that this is true in general, even for choices that are not binary, which are more representative of the actual nature of most species’ environment. The expected size $E(C)$ (or mean size) of these chains of followers is:

$$E(C) = \sum_{c=1}^{n-1} cp^{c-1}(1-p) + np^{n-1} \quad (4)$$

As is shown in Fig. 5A, this expected chain length increases with the total number of individuals up to a certain point. From there onwards it is independent of the total number of individuals. For an infinite number of individuals, it depends exclusively on the probability of following, according to the function $E(C) = 1/(1-p)$ (Fig. 5B). It is noteworthy that the expected chain length is hardly affected by following the predecessor, except for probabilities of following superior to 0.85. For example, in a group of individuals that follow each other with a probability of 0.85, the expected number of followers would be of 6.7, whereas in a group moving independently the expected number would be 2. Chains of more than 20 individuals are only

obtained with probabilities of following superior to 0.95.

231

232 3. Following the previous individual and an environmental cue

233 So far, we have considered the probability of following to be indepen-
 234 dent of the direction taken by the preceding individual. However, in a more
 235 general case, we can include a bias or an environmental cue that causes the
 236 individuals to prefer one side over the other. The preferred side will hereafter
 237 be referred to as *the biased side*. For the first individual, let the probab-
 238 ility of taking the biased side be b . From then onwards, we can consider a
 239 two-state Markov process in which the Markovian transition matrix becomes
 240 asymmetric:

$$\mathbf{T} = \begin{pmatrix} p_B & 1 - p_B \\ 1 - p_{NB} & p_{NB} \end{pmatrix} \quad (5)$$

241 In this transition matrix, p_B and p_{NB} are the probabilities of following the
 242 preceding individual towards the biased and the non-biased side respectively.
 243 For the system to be consistent with the scenario we propose, the parame-
 244 ters require some constraints: (1) the probability of following an individual
 245 towards the biased side p_B is the highest of all probabilities (including b);
 246 (2) the probability of taking the non-biased side, even though the previous
 247 individual took the biased side p_{NB} is the lowest of all probabilities (3) if the
 248 probability of following towards the non-biased side is higher than 0.5, the
 249 attraction to others is higher than the attraction to the environmental cue
 250 causing the bias (and vice-versa).

251 In this situation, the expected number of individuals on the biased side
252 is:

$$E(X) = \sum_{k=0}^n k \cdot P(K = k) \quad (6)$$

253 The probability of having k individuals on the biased side $P(K = k)$ is
254 explained in appendix B.

255 We calculated the expected proportion of individuals on the biased side
256 for different values of the three parameters p_B , p_{NB} and b . Unsurprisingly,
257 the majority of individuals always ends up on the biased side. The expected
258 proportion tends towards a steady value as the total number of individu-
259 als increases (Fig. 6). This steady value depends on p_B , p_{NB} (Fig. 7) and
260 equals the probability of finding the system in state B , once the stationary
261 distribution is reached, that is $\pi(B)$:

$$\pi(B) = (1 - p_{NB}) / (2 - p_B - p_{NB}) \quad (7)$$

262 This value can be greater than the bias (amplification of the bias) or lower
263 than the bias (alleviation of the bias), depending on the values of p_B and p_{NB}
264 (Fig.6). This means that for certain parameter sets (satisfying $\pi(B) < b$),
265 the tendency to follow each other can lead a large fraction of the popula-
266 tion to the non-preferred side. At least, this fraction is larger than it would
267 have been if the individuals were not influenced by one another. In these
268 situations, the fraction on the non-preferred side increases with the total
269 population. Another interesting feature is that for certain values of p_B and
270 p_{NB} , satisfying $p_{NB} = (2b - bp_B - 1)/(b - 1)$, the expected fraction of in-
271 dividuals on the biased side is b . This result is identical to what it would

be, had they chosen independently from one another in a biased set-up. In other words, they can be very strongly influenced by each other, and to the observer who looks only at the end result, rather than at the dynamics, it may seem as if they had just followed a bias.

4. Following the N previous individuals

So far, we have assumed that the range of perception of individuals was limited to their direct predecessor. In order to allow for larger perception ranges, we generalise our model by defining N , the number of predecessors perceived by the focal individual. The situation we have discussed so far is in fact an extreme case where $N = 1$, the other extreme being the ability to perceive all of the preceding individuals ($N = n$), which is the case of the trail model when the trail does not evaporate.

Let us go back to a non-biased environment. Each individual perceives N preceding individuals, and chooses preferentially the side where most of them went. The choice is made according to the choice function of the trail model (Deneubourg et al., 1990):

$$p_L = \frac{(\kappa + N_L)^\epsilon}{(\kappa + N_L)^\epsilon + (\kappa + N_R)^\epsilon} \quad \text{and} \quad p_R = \frac{(\kappa + N_R)^\epsilon}{(\kappa + N_L)^\epsilon + (\kappa + N_R)^\epsilon} \quad (8)$$

In this choice function, p_L and p_R are the probabilities of choosing the left and the right, respectively. N_L and N_R are the number of perceived individuals that went to the left and to the right, respectively. Parameter κ represents the inherent attractiveness of each side. For high values of κ , the

branches are so attractive that the attractiveness added by the social term
 (N_L or N_R) does not greatly influence the probability. Therefore, when κ
 tends towards infinity, both probabilities tend towards 0.5, and the resulting
 probability distribution is the binomial distribution. The exponent ϵ gives
 an estimate of the system's amplification potential. If $\epsilon = 0$, the probability
 distribution is also binomial. This choice function was previously used to
 model trail following in ants (Deneubourg et al., 1990) and in dust mites
 (Mailleux et al. 2011). Actually, in the latter study the function used is a
 slightly modified version, but it shares the same properties, namely the gener-
 ation of great asymmetries in the distribution of individuals when $\epsilon > 1$. For
 this trail model, it is possible to calculate the exact probability distribution,
 that is the probability of all possible outcomes, expressed as the probability
 $p(l, r)$ of having l individuals to the left and r individuals to the right. The
 initial probabilities are $p(0, 1) = p(1, 0) = 0.5$. The probabilities of having a
 negative number of individuals on either side ($p(x, y)$ with $x < 0$ or $y < 0$)
 are naturally equal to zero. From there onwards the probability distribution
 is given by:

$$p(l, r) = p(l - 1, r)p_L + p(l, r - 1)p_R \quad (9)$$

For numbers of perceived individuals lower than the total number of in-
 dividuals, we used Monte Carlo simulations to generate the probability dis-
 tributions. This was done for various values of the parameters N , κ , and ϵ .
 Fig. 8 shows a sample of the the parameter sets we used. As expected, the
 lower the inherent attractiveness of the branches κ , the higher the asymme-
 try. Also, when $\epsilon = 1$, the average number of individuals on the winning

side is relatively low, even when many preceding individuals are perceived (high values of N). Very low values of κ ($\kappa \leq 1$) might make the expected number on the winning side higher, but this is due to a high probability of every individual taking the same side. In fact, for amplification to appear, the exponent ϵ has to be higher than one. As Fig. 9 shows, the asymmetries increase with the number of perceived individuals (N).

5. Discussion

In this paper we study the efficiency (in terms of group cohesion) of following the preceding individual. This question is largely absent from the theoretical literature on collective movements and socially influenced decisions. As we show in this paper, the question is far less trivial to answer than to ask. Our main results may seem somewhat counter-intuitive: cohesive behaviour at the individual level (following the preceding individual) does not lead to cohesion at the collective level. Eventually, it leads to a homogeneous dispersal of the group. Some other results are more intuitive, such as the positive relationship between cohesiveness and the probability of following, or the cohesion obtained from increasing the number of perceived individuals, but they remain worth quantifying. By providing a quantitative description of the relationship between parameters and variables, our model offers a set of predictions that experimenters can compare their results with.

This study concerns binary-choice experiments made on groups, which are extremely popular in ethology and psychology. The set-up of these experiments (reviewed in Jeanson and Deneubourg, 2009) can either present two identical options (as in Mailleux et al. 2011, or Zirbes et al., 2010) or

340 two different options (as in Canonge et al., 2009 or Ward et al. 2008). The
 341 former is an elegant way of putting forward social influence on the choice
 342 of individuals. The latter can be used to study the interplay between social
 343 interaction and individual preference. Our predictions cover both situations,
 344 and can provide insight into the interpretation of such experimental results.
 345 For example, a homogeneous distribution of individuals between two identi-
 346 cal options is typically interpreted as an absence of social interaction. Here,
 347 we show that a homogeneous distribution can happen, even in the presence
 348 of strong social influence, provided that the perception range is limited (by
 349 the nature of the communication used, or by the experimental set-up) to
 350 a relatively small number of predecessors. Therefore, questions on percep-
 351 tion mechanisms and population density in the set-up must be taken into
 352 account. Furthermore, the models we propose can be used to validate (or
 353 invalidate) hypotheses on the mechanisms by which animals influence one
 354 another. Take for example the hypothesis that individuals follow each other
 355 by contact. It can be tested by calculating the probability of following the
 356 direct predecessor, based on the behaviour of the second individual. From
 357 that probability and our model it is possible to predict the behaviour of the
 358 subsequent individuals (Fig. 4). The comparison between this prediction
 359 and the experimental results could confirm (or invalidate) the hypothesis.
 360 Another conclusion that can be drawn from our results is that it is useful
 361 to calculate the mean length of chains of consecutive followers. Indeed, this
 362 variable can be crucial to distinguish between a situation in which there is
 363 no social interaction and one in which each individual follows its the direct
 364 predecessor. It can also be used to make the difference between following the

365 predecessor and following a trail.

366 The model we study in this paper is general enough to cover a wide range
 367 of situations. Animals that use tactile cues to perceive and follow their pre-
 368 decessor, such as processionary caterpillars (Fitzgerald, 2003), spiny lobsters
 369 (Herrnkind, 1969) or earthworms (Zirbes et al., 2010) are the obvious exam-
 370 ples. But our predictions can extend to self-assembling robots designed to
 371 form chains, or even to humans in situations where information is limited to
 372 one's direct predecessor, such as some situations in car traffic. In fact, the
 373 model can apply to socially influenced decisions that are not directional deci-
 374 sions. For example, it is well known that conformism can make humans very
 375 influenced by other people's decisions (Asch, 1951). Therefore, situations
 376 in which humans have to make decisions sequentially and can perceive the
 377 decisions of others (typically consumer behaviour) can be studied through
 378 the theoretical perspective we propose.

379 More generally, the mathematical questions raised in this study are rele-
 380 vant to any situation that can be assimilated to a two-state Markov chain.
 381 These situations can be found even outside the context of decisions. For ex-
 382 ample, a classical model to predict precipitation is a two-state Markov chain
 383 (Todorovic et al., 1975). Other studies have tackled some of the mathemat-
 384 ical questions raised here in completely different contexts. The question of
 385 the exact expression for the probability distribution discussed in the first
 386 section (Eqs. 2 and 3) is explored from a purely mathematical point of view
 387 in the context of a correlated random walk through the integers (Renshaw
 388 and Henderson 1981). The more general case of the asymmetric environment
 389 was studied from a purely abstract perspective by Gabriel (1959). The exact

expressions derived in these two studies are in essence very similar to ours. However, our objective here is to use these mathematical explorations to infer properties to a biological system, that is to a group of animals in motion.

One interesting feature of our results is the fragility of the cohesion of groups of followers. Indeed, we show that for probabilities of following $p < 0.85$, the expected chains are not drastically longer than they would be if individuals acted independently of one another (6.7 versus 2). Furthermore, what we define as the probability of following p , contains in fact the probability of perceiving multiplied by the probability of following the preceding individual. In our theoretical set-up, we have implicitly considered the probability of perceiving the preceding individual to be equal to one. In natural situations, where the linear density of individuals can be low, this assumption does not necessarily hold. This potentially decreases the cohesion of groups. In addition to this, even for high probabilities of perceiving and of following (different from one), large groups will end up homogeneously distributed across the options. Cohesion actually decreases with the size of the group.

Not only does cohesion decrease with group size, but in some cases accuracy also decreases with group size. Indeed we show that in situations in which individuals have a preference for one of the options, a large fraction can end up choosing the non-preferred option, if the probability of following is large enough. More importantly, we show that this fraction increases with group size. This is directly opposed to the outcome of other types of collective decision making models, such as the trail model (Deneubourg 1990) or quorum responses (Sumpter and Pratt, 2009). In the latter, cohesiveness and

most often accuracy increase with group size. The key difference is that in these models, there are non-linearities that arise from positive feedbacks. In our memoryless situation, it is impossible for amplification to happen, hence the importance of perceiving more than one individual, and of non-linear response functions to maintain cohesion. Indeed, as we show in section 4, stable asymmetries in the distribution happen only when the number of perceived individuals increases and when the exponent of the probability function is higher than one.

Nevertheless, the theoretical results we present must be put into perspective with the biological reality that they represent. First of all, the cohesive species that we have talked about display behaviours that potentially increase the probability of following, or more precisely the probability of perceiving the predecessor. For example, they can synchronise departures, which increases the potential linear density. It is true that the larger the group, the lower the cohesion. Nevertheless, the groups in some cases are small enough to ensure sufficient cohesion. The smallest group size are groups of two, which is the case of ant recruitment tandems. This type of recruitment requires constant antennal contact between the following ant and the leading ant's abdomen (Franks and Richardson, 2006, Möglich et al 1974). It is very efficient, and most of the time both ants end up in the same food source. Caterpillars move in larger groups: Edwards (1910) reports processions of up to 300 individuals. Spiny lobsters also seem to migrate in large groups: every autumn, in the Bahamas, thousands of Spiny lobsters (Herrnkind, 1969) migrate to the South-West in parallel chains of 3 to 30 individuals (Herrnkind and Cummings, 1964). It is necessary for them to rely on complementary

mechanisms to ensure cohesion. caterpillars use silk and chemical cues as a trail (Fitzgerald, 2003), and spiny lobsters are capable of true navigation in a magnetic field (Boles and Lohmann, 2003). However it has been shown in both cases that tactile cues are the most important cues for maintaining cohesion (Fitzgerald 2003, Herrnkind, 1969).

In this paper we formulate a model that provides answers to questions concerning the efficiency of following behaviour. By studying the simplest case possible of following behaviour, we put forward three important factors in ensuring cohesion: the number of perceived individuals, the potential for amplification, and group size.

Aknowledgements

A.A. is supported by a grant from the FRIA (Fonds pour la Formation à la Recherche dans Industrie et l'Agriculture). J.L.D. is research associate from the Belgian National Funds for Scientific Research. We also wish to thank O.Astudillo Fernandez and D.Lalor for their helpful comments and suggestions.

Appendix A. The number of combinations resulting in A switches

Although intuitive, the $G(x, y)$ function requires a few definitions in order to be calculated correctly:

- There is one way to make 0 subgroups with 0 elements
- There is no way to make x subgroups with y elements if $x > y$
- There is no way to make 0 subgroups with y elements if $y \neq 0$

- 462 - If x and/or y are negative, $G(x, y) = 0$
- 463 - Otherwise, $G(x, y) = C_{x-1}^{y-1} = \frac{(y-1)!}{(y-x)!(x-1)!}$

464 Appendix B. Generalisation to any two-state Markov chain

465 Let $P_{(a)}(K = k)$ be the probability of having k individuals on the biased
 466 side given that the first one chose the biased side and $P_{(b)}(K = k)$ the
 467 probability, given that the first one chose the non-biased side. The probability
 468 $P(K = k)$ of having k individuals on the biased side after n individuals have
 469 passed is the sum of those two probabilities.

$$\begin{aligned}
 P(K = k) &= P_{(a)}(K = k) + P_{(b)}(K = k) \\
 P_{(a)} &= b \sum_{a=0}^{2(n-k)} p_B^{k - \lceil \frac{a+1}{2} \rceil} p_{NB}^{n-k - \lfloor \frac{a+1}{2} \rfloor} (1 - p_B)^{\lceil \frac{a}{2} \rceil} (1 - p_{NB})^{\lfloor \frac{a}{2} \rfloor} \\
 &\quad G\left(\left\lceil \frac{a+1}{2} \right\rceil, k\right) \cdot G\left(\left\lfloor \frac{a+1}{2} \right\rfloor, n-k\right) \\
 P_{(b)} &= (1-b) \sum_{a=0}^{2(n-k)} p_B^{k - \lfloor \frac{a+1}{2} \rfloor} p_{NB}^{n-k - \lceil \frac{a+1}{2} \rceil} (1 - p_B)^{\lfloor \frac{a}{2} \rfloor} (1 - p_{NB})^{\lceil \frac{a}{2} \rceil} \\
 &\quad G\left(\left\lfloor \frac{a+1}{2} \right\rfloor, k\right) \cdot G\left(\left\lceil \frac{a+1}{2} \right\rceil, n-k\right)
 \end{aligned}$$

470 The validity of this expression was verified (appendix C).

471 Appendix C. Verification of the exact expressions for the probabil- 472 ity distributions

473 We conducted Monte-Carlo simulations in order to verify that the exact
 474 expressions for the probability distributions in sections 1 and 2 are correct. In

each simulation n virtual individuals were sequentially faced with the choice between left and right. The probability of taking left and right depended on the choice of the preceeding individual, and on the environment (homogeneous or heterogeneous) according to the transition matrices (Eqs. 1 and 5). For each individual, a random number was generated. If the random number was lower than the probability of taking left, the individual's choice would be left, otherwise it would be right. Repeating this simulation a million times gave a good approximation of the frequency distribution of each possible outcome (analogous to a probability distribution). Fig. 10 shows that the exact expression and the simulations converge to the same distribution.

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Figure 1: Sequences of 5 individuals leading to 3 individuals on the right. The sequences of individuals are represented by a sequence of squares, where each square is the choice of one individual: black means it chose the left, white means it chose the right. The different sequences can have different probabilities (P), depending on the order of the squares. More precisely, the probability depends on the number of individuals that took a different path than their predecessor (number of switches a). the function $f(n, k, a)$ gives the number of sequences in each subgroup.

Figure 2: If there are four switches, it means that the first one(s) go to the left, then some go to the right, then some more to the left again ending with some on the right, or the opposite starting with the right

Figure 3: All the sequences satisfying $n = 7$, $k = 4$, and $a = 4$, in which the winning side is the right. It has to be multiplied by two, in order to obtain the total number of sequences $f(n, k, a)$

Figure 4: Expected fraction of individuals on the winning side according to the total number of individuals. As the total number of individuals increases, the system tends towards symmetry (with the number on the winning side approaching 50%)

Figure 5: Mean length of the chains according to (A.) the total number of individuals and (B.) the probability of following the preceding individual. For every probability of following different from 1, after the total number of choosers exceeds a certain size, the mean length of the chain does no longer depend on the number of choosers. This dependency is strong with probabilities higher than 0.9.

Figure 6: Example of the evolution of the system as individuals pass. For a given value of the bias ($b = 0.6$) and a given value of the tendency to follow the previous individual towards the biased side ($p_B = 0.7$), the bias can be amplified (if $\pi(B) > b$, so $p_{NB} < 0.55$) or weakened ($p_{NB} > 0.55$)

Figure 7: Proportion of individuals on the biased side for an infinite total number of passing individuals, for various values of p_B and p_{NB} and an environmental bias of $b = 0.6$.

Figure 8: The expected percentage of individuals on the winning side after 2000 individuals have passed. Different sets of parameters were used in the Monte Carlo simulations. For each parameter set, we ran 2500 simulations and what appears in the figure is the average of the 2500 simulations.

Figure 9: The distribution of the simulation results for a total number of individuals $n = 200$, and for a fixed attractivity of each branch ($\kappa = 8$). The distributions change as we move from one extreme ($N = 1$) to the other ($N = n = 200$). For $\epsilon = 1$, the distribution remains bell shaped, but spreads around the most likely result (half of the individuals on each side). For $\epsilon = 2$, however, the distribution changes from bell-shaped to U-shaped. The most likely results become the asymmetric results (most individuals on one of the two sides).

Figure 10: Probability distributions calculated with exact expressions (solid line) and with simulations (histogram). The parameters taken were $n = 40$, $p = 0.75$, $b = 0.6$, $p_B = 0.8$ and $p_{NB} = 0.7$.

Figure 4

Figure 9

Figure 10

(a) homogeneous environment

(b) heterogeneous environment

Highlights

- The potential for collective movement is evaluated in groups of individuals that tend to follow their direct predecessor.
- This behaviour is quantified with a two-state Markov chain model.
- The results show that the cohesion resulting from following the direct predecessor is weak.
- A generalized model shows that the perception of more predecessors is needed to ensure cohesion.

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