

# A phenomenological model for the collective landing of bird flocks

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A three-dimensional phenomenological model was developed to describe the collective landing of bird flocks. The employed individual based model included the landscape (as an external field) and a continuous internal variable  $G$ , to characterize the landing intent of the birds. The birds' interaction with the landscape was coupled adaptively to their landing intent. During the flight, a sharp crossover is observed in the dynamics of the landing intent, i.e. from the initial, non-landing state (small  $G$ ) to the landing state (large  $G$ ) that was terminated by the landing of the flock. In the model, the landing process appears to be a highly concerted, collective motion of the birds, in agreement with the field observations.

**Keywords:** flocking; collective behaviour; self-organization; nonlinear systems

## 1. INTRODUCTION

Collective behaviour in living systems is a rather profound and rich phenomenon and it has always posed intriguing questions for scientific modelling. The prolific manifestations include synchronization (Mirollo & Strogatz 1990; Strogatz & Stewart 1993), collective motion of bacteria aggregates (Shapiro & Dworkin 1997), insect swarms (Seeley 1995; Buhl *et al.* 2006; Grünbaum 2006), fish schools (Partridge *et al.* 1983; Krause *et al.* 2000), mammal herds (Gueron & Levin 1993), and bird flocks (Davis 1980; Feare 1984).

Animal grouping provides evolutionary benefits to the members by offering improved circumstances for foraging and reproduction. Grouping also leads to better, collective means of defence against predation and it can decrease the energy expenditure of the individuals (Parrish & Hamner 1997). For example, it is known that some migratory birds (e.g. the common crane (*Grus grus*) and the greylag goose (*Anser anser*)) fly in a well ordered V-shaped pattern that might significantly reduce their energy consumption. In such formations, there is a dominant bird leading the flock.

There are some shorebird species that form flocks without an apparent leader (e.g. dunlin (*Calidris alpina*) and common redshank (*Tringa totanus*) and perform acrobatic flights including highly coherent, visually impressive sharp turns (Davis 1980).

Similarly, the flight of starling flocks (*Sturnus vulgaris*) appears to be a highly concerted phenomenon taking place without the presence of a leader. In order to obtain a first-hand insight on the collective behaviour of starling flocks, I carried out numerous field observations both in Hungary (Karcag, Etyek) and in Italy (Rome: Termini, EUR). Besides its aerial beauty, the flock's well coordinated, almost instantaneous turns, their advanced, collective

manoeuvres to avoid predators, their rather extensive, fascinating aerial displays, as well as their collective landings (figure 1) raise challenging problems both for fundamental and phenomenological modelling (Parrish & Edelstein-Keshet 1999).

Individual based minimal-models, including only the position of the birds and a local, direction averaging interaction with neighbours were able to account for the ordering of bird flocks (e.g. Vicsek *et al.* 1995; Grégoire *et al.* 2003). In the framework of a Boltzmann approach, hydrodynamic equations for the velocity and density fields were derived for a two-dimensional self-propelled particle system (Bertin *et al.* 2006). Models with distance dependent interaction, i.e. with adhesion among birds/fishes were also developed. Such models assume repulsion between birds/fishes at small distances (to avoid collision) and attraction at large distances that promotes flocking (e.g. Inada & Kawachi 2002; Couzin & Krause 2003). Such models could also describe the ordering within flocks, as well as the flock shape. Besides models aimed to describe the formation and ordering within flocks, there are further models to study the predator–prey interaction. In these approaches, the predator represents an object to be avoided, i.e. a source of repulsion. In a three-dimensional approach (Couzin & Krause 2003), the local propagation of information about the presence of the predator was sufficient to capture some aspects of the escape mechanisms of birds. Another, two-dimensional approach used an exponentially decaying predator–prey interaction potential to describe the anti-predatory response of the flock (Lee *et al.* 2006).

The existing models for collective motion and flocking describe the ordering and collective motion in bird flocks or manoeuvring in the presence of a predator. However, none of these approaches takes into account the presence of a surrounding landscape. Such an object should inevitably be incorporated into a model that attempts to describe the collective landing of bird flock.

At Karcag (Hungary) I have observed numerous landings of starlings where there were no predators around

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.1444> or via <http://journals.royalsociety.org>.

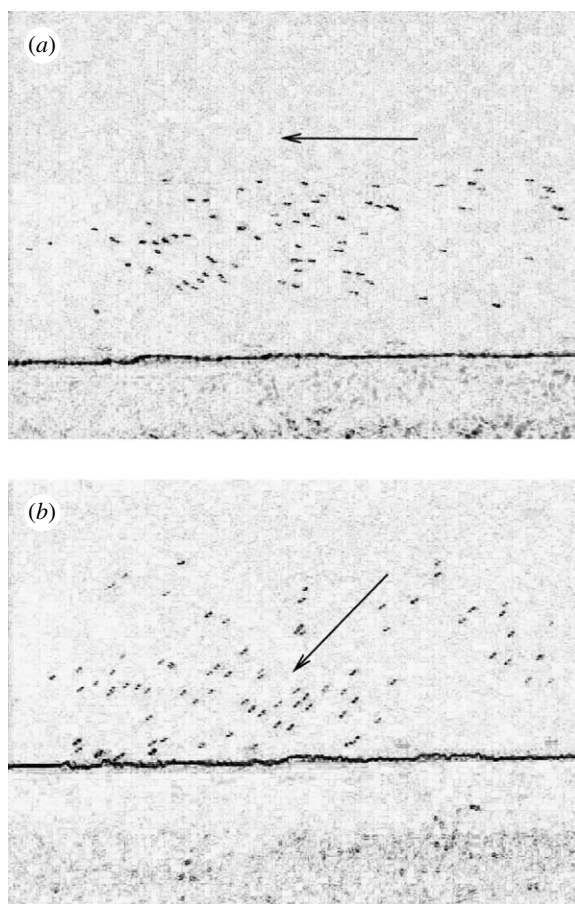


Figure 1. The landing of a sparse starling flock above a food rich area. To obtain a better contrast, the Laplacian of the original image was taken. (a) Horizontal flight. (b) Landing. The arrows indicate the average flying direction of the flock. The elapsed time between the two frames is a few seconds. (Karcag, Hungary, August 2006.)

and the flock was performing a foraging flight. The landing of such flocks was a relatively smooth phenomenon. Nevertheless, a rapid crossover between the horizontal flight and the landing phase of an order of a few seconds in duration could be clearly observed. The landing model presented in this paper attempts to describe such situations.

## 2. MODEL FORMULATION

In the minimal self-propelled particle models of flocking (e.g. Vicsek *et al.* 1995; Grégoire *et al.* 2003) one describes birds as point-like particles with a time-dependent velocity vector. These simple models are successful in describing the formation of ordered flocks and can even account for some aspects of the dynamics of the anti-predatory response (e.g. Couzin & Krause 2003; Lee *et al.* 2006). However, they fail to reproduce the *rapid collective changes* taking place during the flock's turning and landing. These latter processes inevitably include enhanced neuroendocrinal activity within the birds. Because of the interaction of the birds, these intra-bird processes are coupled among the members of the flock. Thus, in order to model such phenomena, presumably one needs to include at least one *internal variable* that characterizes the internal state of the bird with respect to the pertaining process. For example, one can consider the directly non-observable vigilance level of the foraging birds when formulating a detailed model of the individual responses to predation risk (Sirot 2006), or in

case of the flock's landing process, the birds' *landing intent* could be considered as an appropriate internal variable. The goal of this paper is to formulate and discuss the model we have developed to describe the collective landing of bird flocks under simple circumstances.

We considered a three-dimensional, individual based self-propelled particle model. Birds were taken into account as point-like particles and characterized by their position, velocity and by the adhesive 'social' forces acting among them.

The evolution of animal groups lead to an effective physical interaction between the members that enabled them to achieve an evolutionary stable individual and group regulation. The members of a bird flock gather information and interact with their physical environment as well as with their companions. They react to their neighbours' position, flying direction (velocity vector) and attitude. Just as the Newtonian forces acting between simple, lifeless particles, the interactions between the birds can be taken into account as effective social forces or interaction potentials (Vicsek *et al.* 1995; Parrish & Hamner 1997; Grégoire *et al.* 2003).

Probably, the most prominent characteristic of flocking is that birds fly in an ordered pattern, i.e. with aligned velocity vectors. During the flight, this can be achieved if the given bird adjusts its velocity vector towards the average flying direction of its neighbourhood. We take this effect into account by the velocity averaging force ( $f^{\text{aver}}$ ). The neighbourhood of a bird comprises those birds that stay within the interaction radius  $R$ .

In a steady flight pattern, birds tend to keep a more or less constant distance from each other. If they come closer to each other than this value, a repulsive social force is set into action. If they get farther apart, they get effectively attracted to each other. This is taken into account by a relative distance-dependent interaction force. If there are more birds within the interaction radius ( $R$ ), the total adhesive force ( $f^{\text{adh}}$ ) will be the sum of the individual pair interaction forces.

Furthermore, birds have an optimal cruising velocity. Departures from this value induce a velocity regulating force ( $f^{\text{reg}}$ ) to restore the preferred velocity.

The detailed description of these social forces acting among the birds can be found in appendix A.

The landscape was incorporated into the landing model as follows. It is reasonable to assume that in a steady flight, birds experience the landscape as a steady external field. During a foraging flight, the birds neither want to fly too high, nor do they want to get too close to the ground. Flying too high would reduce their chances of recognizing the food rich spots and/or their energy expenditure would be too high for changing the altitude. Flying too low would restrict their field of vision regarding the landscape. Furthermore, flying close to the ground might also increase the energy expenditure of birds as they have to manoeuvre round landscape objects (trees, bushes, etc.). These effects can be taken into account by a flying altitude dependent landscape force ( $f^{\text{land}}$ ) that stabilizes the horizontal flight of the individuals within the flock. If a bird flies higher than the optimal altitude, it experiences a downward force. If a bird gets closer to the ground, an upward force is set into action. Finally, a damping term ( $f^{\text{dam}}$ ) in the vertical ( $z$ ) direction was introduced in order to avoid the artificial oscillations triggered by  $f^{\text{land}}$ .

Table 1. Model parameters and their typical values used for the runs. Their physical units are composed of the unit distance  $r_0$ , the unit velocity  $v_0$  and the unit time  $t_0$ .

parameter	function	typical value [physical unit]
$v_{cr}$	cruising velocity	1 [ $v_0$ ]
$v_{max}$	maximal velocity	2 [ $v_0$ ]
$\alpha$	velocity regulation coefficient	1 [ $1/(v_0 t_0)$ ]
$\gamma$	vertical damping coefficient	1 [ $1/t_0$ ]
$R$	interaction radius	10 [ $r_0$ ]
$r_{rep}$	radius of repulsion	0.5 [ $r_0$ ]
$r_{attr}$	radius of attraction	2 [ $r_0$ ]
$f_{rep}$	strength of repulsion	200 [ $v_0/t_0$ ]
$f_{attr}$	strength of attraction	-2 [ $v_0/t_0$ ]
$A^{down}$	vertical restoring coefficient: down	90 [ $v_0/(t_0 r_0)$ ]
$A^{up}$	vertical restoring coefficient: up	10 [ $v_0/(t_0 r_0)$ ]
$G_t$	first threshold landing intent	0.1 [dimensionless]
$G_l$	second threshold landing intent	0.9 [dimensionless]
$B$	coefficient of the landing intent	0.25 [ $1/t_0$ ]
$A$	amplitude of noise	0.2 [dimensionless]
$p$	noise probability parameter	0.053 [ $1/t_0$ ]
$L$	linear size of the simulation box	100 [ $r_0$ ]
$z_0$	optimal cruising altitude	50 [ $r_0$ ]
$N$	flock size	200 [dimensionless]

The quantitative nature of the employed landscape force is explained in detail in appendix B.

The introduced landscape force could account for the steady flight of birds. What might change in the birds or in the flock that makes them land? The simplest thing to presume is that they sense how long and how much they wish to stay in the air or whether they would wish to land. In order to model this effect, we introduced a continuous internal variable  $G$  (such that  $0 < G < 1$ ) that characterizes the individual bird's intent to land. For  $G=0$ , the bird does not want to land at all, while for  $G=1$ , the bird definitely wants to land.

The dynamics of the landing intent of the birds is governed by the complex and nonlinear interplay between external and internal stimuli and circumstances. In this model, we consider two sources of the landing intent.

First, an external stimulus (e.g. the visual sensation of a food-rich field), can *stochastically* increase the landing intent. For each bird, this stochastic increment was generated with probability  $p$  per unit time. In order to render the individually perceived stochastic increments  $\xi_i^{land}$ , we used a time-wise delta-correlated sampling from an even distribution on the interval  $[0, A]$ , where  $0 \leq A \leq 1$ .

Second, as a social reinforcement effect, the landing intent can be induced (or damped) by the neighbouring birds' average landing intent. If the average landing intent in a given bird's range of interaction  $R$ ,  $\langle G_i \rangle_R$  is smaller than a threshold value  $G_t$ , then the given bird's landing intent ( $G_i$ ) will decrease (no sufficient motivation from the neighbourhood). However, if the average landing intent of the neighbouring birds  $\langle G_i \rangle_R$  exceeds the threshold value  $G_l$ , it motivates the given bird to increase its landing intent. These threshold dynamics are described by the *deterministic* term

$$\frac{\partial G_i}{\partial t} = B(\langle G_i \rangle_R - G_i), \quad (2.1)$$

where  $B$  is a positive coefficient and  $\langle G_i \rangle_R$  is the landing intent averaged over the neighbours of the given bird. Considering the above two contributions, we get the

following equation for the dynamics of the landing intent

$$\frac{\partial G_i}{\partial t} = B(\langle G_i \rangle_R - G_i) + \xi_i^{land}, \quad (2.2)$$

where  $\xi_i^{land}$  denotes the stochastically generated landing intent described above.

Finally, the landing intent  $G_i$  is coupled to the motion of the birds as follows. When birds perform a steady flight at the optimal cruising altitude  $z_0$ , they presumably experience the ground as a repulsive object and consequently they do not land. However, when their intent to land increases and reaches a second threshold value  $G_l$ , their relation to the landscape changes in character and they experience an effective attraction to the ground (or to other landscape objects). Thus, the presence of the landing intent influences the coefficient of the landscape force

$$A_i^{down}(G_i) = A^{down}(1 - G_i/G_l), \quad (2.3)$$

where  $G_i$  is the landing intent of bird  $i$ . For small landing intents,  $A_i^{down}$  is positive and thus amounts to be a repulsive force, while for high values of the landing intent ( $G_i > G_l$ ),  $A_i^{down}$  becomes negative, and the pertaining attractive potential expedites the landing of the given bird. Note, that the presence of the landing intent does not modify the coefficient  $A^{up}$ .

Summarizing the above social force terms (velocity regulation, velocity averaging, adhesion, landscape forces, and vertical damping), one can get the equation of motion for the individual birds comprising the flock in analogy with the Newtonian dynamics

$$\frac{d\mathbf{v}_i}{dt} = \mathbf{f}_i^{reg} + \mathbf{f}_i^{aver} + \mathbf{f}_i^{adh} + \mathbf{f}_i^{land} + \mathbf{f}_i^{dam}, \quad (2.4)$$

where  $\mathbf{v}_i$  is the velocity of the bird  $i$ . Furthermore, the dynamics of the landing intent is governed by equation (2.2). The parameters of the model are summarized in table 1.



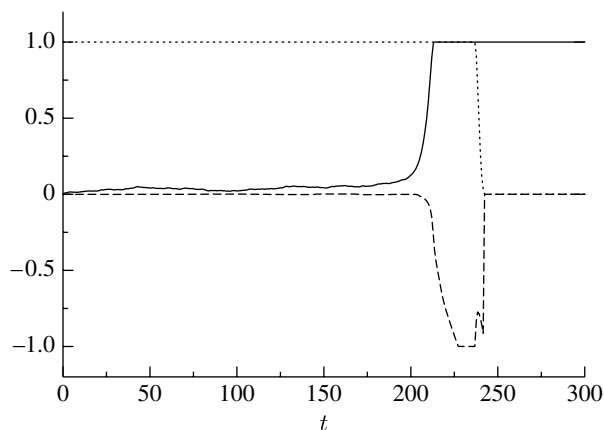


Figure 2. Time evolution of the average landing intent ( $\langle G \rangle$ ) (solid line). One can distinguish two phases. For  $t < 210$ , there is a *no landing phase* characterized by small and stochastically fluctuating landing intents. At  $t \approx 210$ , there is a sharp crossover to the *landing phase* characterized by large landing intents  $G \approx 1$ . The rapid change in the landing intent is accompanied by the rapid landing process of the whole flock. The dashed line shows the average vertical velocity of the flock,  $\langle v_z \rangle/2$ , and the dotted line corresponds to the fraction of birds staying in the air,  $n_{\text{fly}}/N$ . The parameters used for this simulation are summarized in table 1.

### 3. RESULTS

On the basis of the above model, we investigated the flight of flocks consisting typically of 200 birds. The equations of motion and of the landing intent were solved numerically. To that purpose, first we scaled the parameters of the model. We set the unit distance as the typical nearest neighbour distance of the starlings  $r_0 = 1$  m (Ballerini *et al.* 2008), and their typical cruising velocity  $v_0 = 10 \text{ m s}^{-1}$  was chosen to be the unit of the velocity (Tobalske 1995). These two quantities determine the unit of time,  $t_0 = r_0/v_0 = 0.1$  s. For most of the runs, we used the scaled model parameters listed in table 1. Furthermore, the typical values of the parameters were chosen such as to obtain directionally ordered and stable flocks displaying a three-dimensional globular shape.

The evolution of the average landing intent of the whole flock,  $\langle G \rangle$  is displayed in figure 2 (solid line). One can see that the behaviour can be divided into two phases. The *no landing phase* is characterized by a low and stochastically changing average landing intent, while in the *landing phase*, birds have the maximal possible landing intent,  $G = 1$ . The two phases are separated by a sharp crossover. This crossover is also manifested in the change of the average vertical velocity of the flock  $\langle v_z \rangle$  (dashed line, figure 2). When the landing intent reaches the second threshold  $G_1$ , the birds are attracted by the landscape and consequently they accelerate until they reach their maximum velocity  $v_{\text{max}} = 2$ . The fraction of the number of birds that stays in the air  $n_{\text{fly}}/N$  decreases sharply during the landing process. As displayed in figure 3a, in the no landing phase the flock performs a steady and horizontal flight, while in the landing phase they move towards the ground highly coherently, (figure 3b). The duration of this rather fast crossover behaviour is of the order of  $\Delta t = 10$  time units, that physically corresponds to  $t_0 \Delta t = 1$  s. This value is consistent with my field observations (e.g. figure 1).

To characterize the influence of some model parameters on the dynamics of the landing intent, the mean

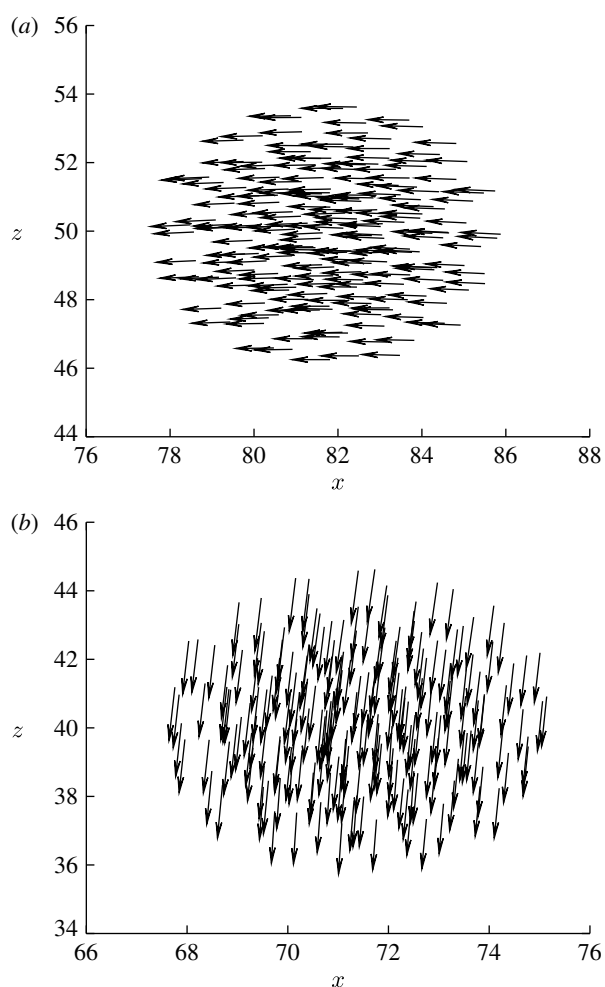


Figure 3. Two  $xz$  projected snapshots of a flock comprising 200 birds, taken at times (a)  $t = 100$  and (b)  $t = 220$ . While (a) demonstrates the horizontal flight of the flock, (b) shows the highly correlated landing process. The parameters used for this simulation are summarized in table 1.

time needed for the flock to reach an average landing intent  $G = 0.5$  was determined by averaging over 100 independent runs. This mean time, denoted  $t_{0.5}$ , gives a good estimate of the crossover and landing times.

First, the dependence of the mean crossover times  $t_{0.5}$  on the interaction radius  $R$  was investigated (figure 4a). The radius of repulsion  $r_0 = 0.5$  and the radius of attraction  $r_1 = 2$  were fixed, together with all the other model parameters. For  $R$  between 2 and 10 there is a moderate change in the crossover times. For  $R < r_1 = 2$ , there is effectively no attraction between the birds. Consequently, the flock falls apart and no landing occurs. Owing to the presence of the landscape force, the birds behave as a two-dimensional gas localized at the altitude of  $z_0$ . This change of behaviour underlines the collective nature of the landing process in the framework of this model.

There is only a moderate decay of the mean crossover times with the increase of the number of birds in the flock ( $N$ ), (figure 4b). The plateau-like behaviour for larger flock sizes can be described as a saturation effect: the number of birds in the interaction radius of a selected individual will not increase significantly after a certain flock size  $N = 400$  is reached.

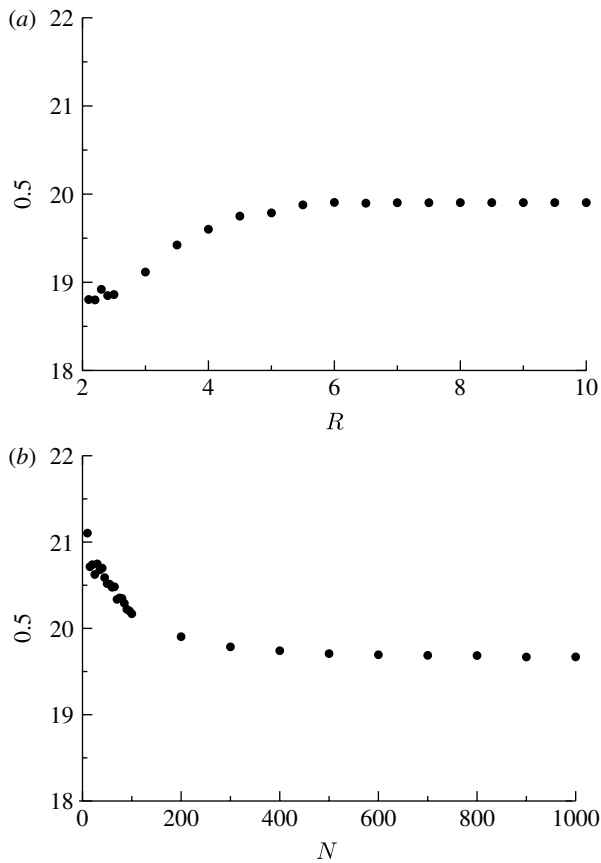


Figure 4. (a) The interaction range ( $R$ ) dependence of the mean crossover time  $t_{0.5}$  (that is defined as the time at which the landing intent reaches the value  $G=0.5$  and is averaged over 100 independent runs). One can observe a moderate change for  $R > 2$ . However, due to the diminished cohesion among birds there is a sharp transition in the crossover time for  $R < 2$ : the flock falls apart and the birds spread out in the two-dimensional plane at the altitude  $z_0$  selected by the landscape force. For  $R < 2$  no landing occurs in the investigated time interval  $t_{0.5} < 1000$ . (b) Flock size dependence ( $N$ ) of the mean crossover time  $t_{0.5}$ . One finds only a slight decrease with increasing flock size. The parameters used for this simulation are summarized in table 1, except for  $A=0.25$  and  $p=0.1$ .

In both cases, the actual value of the crossover times, (the time it takes for the flock to decide on landing after noticing the food rich area) is about  $t_{0.5}=20$ , that corresponds to  $t_{0.5}t_0=2$  s of physical time.

Finally, one can see in figure 5 that the mean crossover time decays rapidly with increasing both the amplitude  $A$  and the generation probability  $p$  of the noise. This is what one can expect intuitively since bigger increments of the landing intent or its more frequent generation lead to a faster landing. Furthermore, it can be seen that for a wide range of parameters  $A$  and  $p$ , the average crossover time stays below  $t_{0.5}=40$ , that physically corresponds to  $t_{0.5}t_0=4$  s.

#### 4. CONCLUSIONS

This paper presents a quantitative model and description of the collective landing of bird flocks. As far as we know this is the first such model.

The employed formulation attempts to create a bridge between the basic, conceptual physical models and the very detailed, descriptive biological frames. Even though

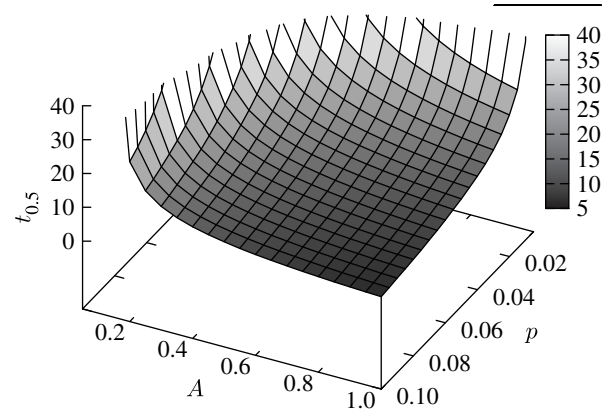


Figure 5. The noise dependence of the mean crossover time  $t_{0.5}$ . One can see that there is a rapid decay as a function of both the amplitude  $A$  and the generation probability  $p$  of the noise in the landing intent. The parameters used for this simulation are summarized in table 1.

the model contains a number of parameters, it is thought to be an effective parameterization scheme of this rather complex biological phenomenon.

The introduction of an internal variable, the landing intent of the birds and the pertaining nonlinear dynamics were motivated by our field observations that revealed rich patterns of the birds' collective flight and behaviour. The use of an internal variable offers a novel approach and as it is, it points beyond the usual self-propelled particle models that characterize the birds with the help of a few external variables only (e.g. position, velocity, etc.). Furthermore, we believe that the use of the landing intent was necessary to capture the coherent and inherently nonlinear aspects of the landing process.

This work provides a relatively simple description of the rather complex and delicate process of collective landing under simple conditions (foraging flights). In particular, the model accounts for the abrupt, yet highly concerted nature of the landing process in accordance with the field observations. The obtained behaviour is found to be quite robust against the change of the model parameters.

However, there are circumstances (e.g. landscape irregularities, presence of predator, etc.) that point beyond the applicability of the current model. Furthermore, our field observations indicate that long-term memory effects together with possible anticipation capacity (or purposefulness?) of starlings might also play a crucial role in shaping their long-scale flight patterns. These very rich and diverse flocking phenomena present a fruitful and cross-fertilizing ground for further physical modelling and biological descriptions.

The author is grateful to Tamas Vicsek for introducing him into this subject and thanks to Claudio Carere for stimulating discussions and for helping with the field observations in Rome, as well as Michel Droz and Zoltán RÁCZ for their useful comments. This work has been supported by the EU FP6 grant 'STARFLAG' and partly by the Swiss National Science Foundation.

#### APPENDIX A

In this section, we provide a detailed description of the social forces acting on the birds in the employed individual-based, self-propelled particle model.

We assume that the magnitude of the birds' velocity can vary between 0 and  $v_{\max}$  and there is also a preferred, optimal cruising velocity,  $v_{\text{cr}}$ . If the magnitude of the bird's velocity departs from  $v_{\text{cr}}$ , a velocity regulating force emerges to restore the preferred velocity

$$\mathbf{f}_i^{\text{reg}} = \alpha(v_{\text{cr}} - v_i)\mathbf{v}_i, \quad (\text{A } 1)$$

where  $v_i$  is the magnitude of the actual velocity vector  $\mathbf{v}_i$  of the bird  $i$ . Note, that this force does not change the direction of the velocity  $\mathbf{v}_i$ .

During their flight, the members of the flock compare their velocities with their neighbours within the range of interaction  $R$  and they adjust their trajectory such as to maintain flocking and to avoid collisions. Such a direction averaging interaction can be taken into account by the following, simple velocity averaging force acting on the  $i$ th bird

$$\mathbf{f}_i^{\text{aver}} = \beta \sum_{j \sim i} (\mathbf{v}_j - \mathbf{v}_i), \quad (\text{A } 2)$$

where summation extends for all birds within the range of interaction  $R$  of the  $i$ th bird. Without loss of generality, the coefficient  $\beta$  was chosen to be unity. In order to keep this landing model numerically tractable, we did not include noise in the velocity averaging interaction. However, simulations performed on an extended version of the current model including small to moderate levels of directional noise indicate that the qualitative features of the emerging behaviour remain the same.

The adhesive (interaction) force between birds ( $\mathbf{f}_{ij}^{\text{int}}$ ) was chosen to represent a short-range repulsion and a long-range attraction with a cut-off interaction range  $R$ . The form of the potential was simply chosen to be piecewise linear. For inter-bird separations smaller than  $r_{\text{rep}}$ , there is a hard-core repulsion, for intermediate separations there is a transition from repulsion to attraction, and for separations greater than  $r_{\text{attr}}$ , there is attraction

$$\mathbf{f}_{ij}^{\text{int}}(r_{ij}) = \begin{cases} f_{\text{rep}} \mathbf{e}_{ij}, & \text{if } r_{ij} \leq r_{\text{rep}} \\ \left\{ (f_{\text{attr}} - f_{\text{rep}}) \frac{r_{ij} - r_{\text{attr}}}{r_{\text{attr}} - r_{\text{rep}}} + f_{\text{attr}} \right\} \mathbf{e}_{ij}, & \text{if } r_{\text{rep}} < r_{ij} \leq r_{\text{attr}} \\ f_{\text{attr}} \mathbf{e}_{ij}, & \text{if } r_{\text{attr}} < r_{ij} \leq R \\ 0, & \text{if } R < r_{ij}, \end{cases} \quad (\text{A } 3)$$

where  $r_{ij}$  is the distance between birds  $i$  and  $j$ ,  $\mathbf{e}_{ij}$  is a unit vector pointing from  $i$  to  $j$ ,  $f_{\text{rep}} (>0)$  is the value of the maximal repulsive force, and  $f_{\text{attr}} (<0)$  is the value of the attractive force. Thus, the total adhesive force acting on bird  $i$  can be expressed as

$$\mathbf{f}_i^{\text{adh}} = \sum_{j \sim i, j \neq i} \mathbf{f}_{ij}^{\text{int}}, \quad (\text{A } 4)$$

where the summation extends to all the birds within the interaction radius  $R$ , and there is no self-interaction.

## APPENDIX B

In this section, we describe the nature of forces acting on birds in the presence of a landscape.

The landscape can be represented by an external landscape force that selects an optimal cruising altitude

$z_0$  for the birds. Departures from this elevation are penalized by the external field (force). We used a simple linear restoring force  $f^{\text{up}}(z) = -A^{\text{up}}(z - z_0)$  for  $z > z_0$  to avoid flying too high, while a linear repulsive force exerted by the ground was incorporated to avoid flying too low:  $f^{\text{down}}(z) = -A^{\text{down}}(z - z_0)$  for  $z < z_0$ . Thus, the overall force experienced by the birds due to the presence of the landscape reads

$$\mathbf{f}_i^{\text{land}}(z) = \{f^{\text{up}}(z)H(z - z_0) + f^{\text{down}}(z)H(z_0 - z)\}\mathbf{e}_z, \quad (\text{A } 5)$$

where  $H(z) = 1$ , if  $z > 0$ , and  $H(z) = 0$ , if  $z < 0$  and  $\mathbf{e}_z$  is a unit vector pointing in the  $z$  direction. Note, that for a steady, horizontal flight the coefficients  $A^{\text{up}}$  and  $A^{\text{down}}$  are both positive.

A damping term in the vertical ( $z$ ) direction was introduced in order to avoid the artificial vertical oscillations triggered by the above discussed linear restoring landscape force

$$\mathbf{f}_i^{\text{dam}} = -\gamma(\mathbf{v}_i \cdot \mathbf{e}_z)\mathbf{e}_z, \quad (\text{A } 6)$$

where  $\gamma$  is the damping coefficient,  $\mathbf{v}_i$  is the actual velocity of bird  $i$ , and  $\mathbf{e}_z$  is a unit vector pointing in the  $z$  direction. This vertical damping force is present only when the selected bird performs a horizontal flight, i.e. when its landing intent  $G$  is smaller than the second threshold landing intent  $G_1$  (defined in the main text).

## REFERENCES

- Ballerini, M. *et al.* 2008 Interaction ruling animal collective behaviour depends on topological rather than metric distance: evidence from a field study. *Proc. Natl Acad. Sci. USA* **105**, 1232–1237. (doi:10.1073/pnas.0711437105)
- Bertin, E., Droz, M. & Grégoire, G. 2006 Boltzmann and hydrodynamic description for self-propelled particles. *Phys. Rev. E* **74**, 022 101–022 104. (doi:10.1103/PhysRevE.74.022101)
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R. & Simpson, S. J. 2006 From disorder to order in marching locusts. *Science* **312**, 1402–1406. (doi:10.1126/science.1125142)
- Couzin, I. D. & Krause, J. 2003 Self-organization and collective behavior in vertebrates. *Adv. Study Behav.* **32**, 1–75.
- Davis, J. M. 1980 The coordinated aerobatics of Dunlin flocks. *Anim. Behav.* **28**, 668–673. (doi:10.1016/S0003-3472(80)80127-8)
- Feare, C. J. 1984 *The starlings*. Oxford, UK: Oxford University Press.
- Grégoire, G., Chaté, H. & Tu, Y. 2003 Moving and staying together without a leader. *Physica D* **181**, 157–170. (doi:10.1016/S0167-2789(03)00102-7)
- Grünbaum, D. 2006 Align in the sand. *Science* **312**, 1320–1322. (doi:10.1126/science.1127548)
- Gueron, S. & Levin, S. A. 1993 Self-organization of front patterns in large wildebeest herds. *J. Theor. Biol.* **165**, 541–552. (doi:10.1006/jtbi.1993.1206)
- Inada, Y. & Kawachi, K. 2002 Order and flexibility in the motion of fish schools. *J. Theor. Biol.* **214**, 371–387. (doi:10.1006/jtbi.2001.2449)
- Krause, J., Hoare, D. J., Krause, S., Hemelrijk, C. K. & Rubenstein, D. I. 2000 Leadership in fish shoals. *Fish and Fish.* **1**, 82–89.

- Lee, S.-H., Pak, H. K. & Chon, T.-S. 2006 Dynamics of prey-flock escaping behavior in response to predator's attack. *J. Theor. Biol.* **240**, 250–259. (doi:10.1016/j.jtbi.2005.09.009)
- Mirollo, R. E. & Strogatz, S. H. 1990 Synchronization of pulse-coupled biological oscillators. *SIAM J. Appl. Math.* **50**, 1645–1662. (doi:10.1137/0150098)
- Parrish, J. K. & Edelstein-Keshet, L. 1999 Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284**, 99–101. (doi:10.1126/science.284.5411.99)
- Parrish, J. K. & Hamner, W. H. (eds) 1997 *Animal groups in three dimensions*. Cambridge, MA: Cambridge University Press.
- Partridge, B. L., Johansson, J. & Kalisk, J. 1983 Structure of schools of giant bluefin tuna in Cape Cod Bay. *Environ. Biol. Fishes* **9**, 253–262. (doi:10.1007/BF00692374)
- Seeley, T. D. 1995 *The wisdom of the hive*. Cambridge, MA: Cambridge University Press.
- Shapiro, J. A. & Dworkin, M. (eds) 1997 *Bacteria as multicellular organisms*. Oxford, UK: Oxford University Press.
- Siro, E. 2006 Social information, antipredatory vigilance and flight of bird flocks. *Anim. Behav.* **72**, 373–382. (doi:10.1016/j.anbehav.2005.10.028)
- Strogatz, S. H. & Stewart, I. 1993 Coupled oscillators and biological synchronization. *Sci. Am.* **269**, 102–108.
- Tobalske, B. W. 1995 Neuromuscular control and kinematics of intermittent flight in the European starling (*Sturnus vulgaris*). *J. Exp. Biol.* **198**, 1259–1273.
- Vicsek, T., Czirók, A., Ben-Jacob, E., Cohen, I. & Shochet, O. 1995 Novel type of phase transition in a system of self-driven particles. *Phys. Rev. Lett.* **75**, 1226–1229. (doi:10.1103/PhysRevLett.75.1226)