Journal of Theoretical Biology 270 (2011) 112–126

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Understanding soaring bird migration through interactions and decisions at the individual level

E.E. van Loon*, J. Shamoun-Baranes, W. Bouten, S.L. Davis

University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, Science Park 904, 1098 XH Amsterdam, The Netherlands

ARTICLE INFO

Article history:
Received 15 December 2009
Received in revised form
20 September 2010
Accepted 29 October 2010
Available online 12 November 2010

Keywords:
Individual-based model
Thermal convection
Emergent patterns
Social interactions
Flocking

ABSTRACT

Many soaring bird species migrate southwards in autumn from their breeding grounds in Europe and Central Asia towards their wintering grounds. Our knowledge about interactions between migrating birds, thermal selection during migration and mechanisms that lead to flocking or convergent travel networks is still very limited. To start investigating these aspects we developed an individual-based simulation model that describes the local interactions between birds and their environment during their migratory flight, leading to emergent patterns at larger scales. The aim of our model is to identify likely decision rules with respect to thermal selection and navigation. After explaining the model, it is applied to analyse the migration of white storks (*Ciconia ciconia*) over part of its migration domain. A model base-run is accompanied by a sensitivity analysis. It appears that social interactions lead to the use of fewer thermals and slight increases in distance travelled. Possibilities for different model extensions and further model application are discussed.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Hundreds of thousands of flocking soaring birds that breed in the northern ranges of North America, Europe and central Asia migrate southwards in autumn to their wintering grounds. Some species belonging to this group are white storks (*Ciconia ciconia*), white pelicans (*Pelecanus onocrotalus*), and several species of raptors (*Order Accipiteriformes*). These birds use thermal convection for soaring flight and generally avoid crossing large bodies of water. This leads to migratory bottlenecks where birds from distant breeding or wintering areas converge in space and time. Two main areas of convergence for western Palearctic soaring migrants are on the western and eastern borders of the Mediterranean sea at Gibraltar and Israel, respectively (Bildstein and Zalles, 2005; Leshem and Yom-Tov, 1996a). Convergence may also occur due to natural leading lines such as mountain ranges and coastlines (e.g. Fuller et al., 1998; Kerlinger, 1989; Leshem and Yom-Tov, 1998), although some species such as the white stork migrate along very narrow pathways without the direct effect of a leading line (Berthold, 2001). The connection between large scale migration patterns and fine scale patterns or movements has not been made. Fine scale patterns are often related to flocking behaviour, and several disconnected qualitative observations found in the ornithological literature indicate that flocking may facilitate migration. Using satellite telemetry data Chernetsov et al. (2004) show that displaced and delayed juvenile white storks showed a much wider spread in migratory directions than adults that migrate on time and from natal areas (most likely in flocks). Non-flocking soaring migrants seem to migrate along a broader front than flocking migrants (Leshem and Yom-Tov, 1998). Large flocks show higher glide ratios, faster climb rates and stronger compensation for lateral drift than single birds and small flocks (Liechti et al., 1996). Due to the limited possibilities to collect sufficient observations under comparable circumstances it is however still unclear whether flocking is indeed the result of the interactions between birds (which can through these interactions migrate more efficiently), or just the result of the prevailing environmental conditions. Considering the entire system of soaring bird migration, including aspects like thermal detection and selection strategies, choice of flight speed and direction, selection of resting sites, our current knowledge is very fragmentary. The information available is often from isolated studies, focusing on a single species or a specific region and evaluating a single aspect of migratory behaviour (see e.g. Mandel et al., 2008; Pennycuick, 1998; Shamoun-Baranes et al., 2003a; Shannon et al., 2002a; Thorup et al., 2003). An overall integrative picture of the various physical and biological processes and behavioural patterns that operate at the fine scale and explain patterns emerging at a coarser scale is lacking. To fill this gap we built an individual-based model of soaring bird migration that can explain patterns at the population level (like overall migration speed and the variability therein over a long distance, number of travel paths, average effects of social or non-social behaviour) for a species or a heterogeneous group of migrating birds from a small set of deterministic behavioural rules

---

* Corresponding author. Tel.: +31 20 5257448; fax: +31 20 5257832.
E-mail address: vanloon@uva.nl (E.E. van Loon).

0022-5193/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2010.10.038

that operate at the individual level. The model is meant to identify the most likely behavioural rules in soaring bird migration, and thereby generate hypotheses that can be tested in field research. The most likely rules can in our view be identified best by matching model variables (or summary variables derived from these) to similar variables observed in the field. As a demonstration and also to prepare for future field research we use the model to evaluate migration efficiency of white storks using different thermal selection strategies and modes of social behaviour (a so-called base run). A sensitivity analysis on uncertain parameters relating to bird sight and moment of departure is used to identify whether the patterns found in the base run are stable. Although we do not compare model results to field observations in this study, we define model statistics such that these can be compared with relative ease to future field observations.

2. White stork migration

This paper uses the white stork as a model species. We therefore provide some general information on white stork migration. The European white stork breeding population was recently estimated at 180,000–220,000 breeding pairs (Burfield and Bommel, 2004). The majority of these birds migrate to spend the winter in the Sahel and East and South Africa (Berthold et al., 2004, 2002) migrating on average 250 km/d (Berthold et al., 2000; Shamoun-Baranes et al., 2003b). White storks are diurnal flocking migrants relying on thermal convection and thus most birds migrate either east or west of the Mediterranean to avoid crossing long stretches of the Mediterranean Sea, converging in Israel and Gibraltar, respectively. For juvenile birds, social interactions seem to play an important role in shaping migratory routes (Chernetsov et al., 2004). The mean annual migratory population that passes through northern Israel in autumn exceeds 180,000 individuals (Alon et al., 2004; Leshem and Yom-Tov, 1996a), with 90% of the population passing in approximately 3 weeks along the Jordan Valley over a narrow front approximately 20 km wide (Leshem and Yom-Tov, 1998). An illustration of this migration pattern is shown via an interpreted radar image in Fig. 1. At the fine scale storks alter their flight altitudes in relation to environmental conditions including topographic elevation, thermal intensity (lift rate) and thermal depth (Shamoun-Baranes et al., 2003a) and do not seem to adapt their flight behaviour to optimize cross country speed (Liechti et al., 1996).

3. Model description

Simsoar is an individual-based model (IBM) (Grimm and Railsback, 2005). In individual- (or agent-) based models each individual operates according to a set of rules which describe how the individual interacts with other individuals and its biotic and abiotic environment. The rules can be identical for all individuals but can also differ for sub-sets of individuals. Due to

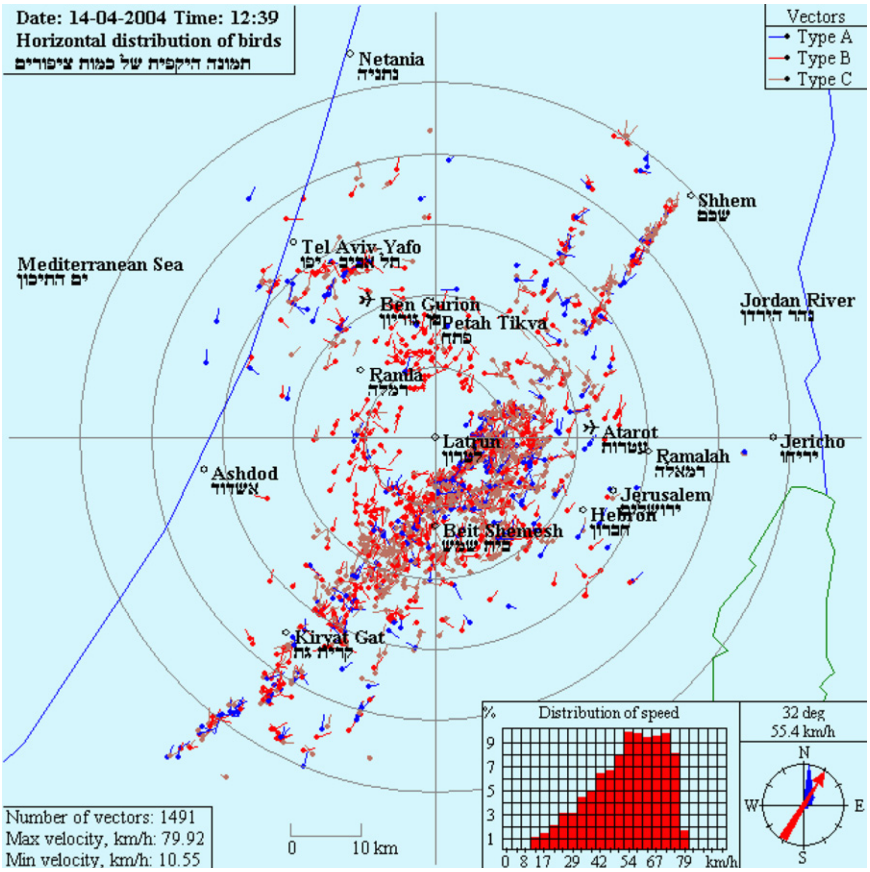

Fig. 1. A radar image showing white storks migrating over Israel at 14 April 2004, 12:39 PM. The average azimuth of the flocks is 32° (i.e. flying NE) and the average flight speed is 55.4 km h^{-1}. Three types of movement are distinguished in the image: (1) blue (type A), vectors of birds in constant direction and velocity; (2) red (type B), vectors with constant velocity and non-constant direction; and (3) brown (type C), vectors with non-constant direction and velocity. At the lower right corner the red arrow gives the mean direction of all vectors, and the bar chart gives the distribution of flight speeds. The storks are flying predominantly parallel to the Mediterranean coast along the Judian and Sumerian mountains. Each vector may represent one individual or a small flock of several birds. The image shows a continuous stream (> 100 km long) of thousands of migrants in a narrow band creating a concentrated flyway network of migrants, a "mega-flock". (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the interactions between the individuals and their environment, patterns emerge. A large body of literature exists on the design of individual based models (Grimm, 1999; Grimm and Railsback, 2005, and references therein). In the following sections we describe Simsoar according to the ODD template (Overview, Design concepts, Details) suggested by Grimm et al. (2006). Some terms in the sub-sections Overview, Design concepts and Details are in italics because they refer to the key items of this ODD template.

3.1. Purpose

The *purpose* of Simsoar is to integrate the scattered knowledge that is available for migrating soaring birds on flight behaviour, thermal selection and interactions between individual birds. Through this integration Simsoar provides a means to test existing theories and generate new hypotheses about expected small-scale as well as large scale patterns in soaring bird migration. It also provides a means to communicate the current understanding of the system and a way to elicit critiques from (field) experts. To achieve this latter aim the model code (in Matlab), documentation and ancillary data are made available as supplementary material with this article (see Appendix A).

3.2. State variables and scales

In order to understand the *state variables* in the model it is convenient to understand the main model dynamics and constraints. This is why we briefly describe these here. Simsoar works with a three-dimensional spatial domain in which soaring birds and thermals are placed. Each bird is a point object in the domain, and each thermal is a cylindrical object. The individual birds move through the domain, while the thermals have a fixed location over the simulation length. Fig. 2 shows an example of the three dimensional space for a particular simulation, and the travel network of four birds that may arise in such a space. Birds in Simsoar can either climb in a thermal or glide between thermals (flapping flight does not exist), and birds know their final destination perfectly. Once a bird starts to glide, its default direction is towards the destination. In this glide phase it continuously senses its environment. As soon as it detects one or more thermals, the best thermal (according to a prescribed decision rule) is selected as the next (intermediate) target and the bird glides towards that thermal. If the target thermal is reached, the bird starts to climb in it until it reaches the top. At that point the bird starts to glide towards the destination again.

Each bird has nine *state variables* which keep track of (1) its current location, (2) the location of its current target, (3) the thermals that are in view, (4) the thermals that can be reached, (5) whether it is aloft, (6) whether it has reached the destination, (7) whether it is climbing in a thermal, (8) whether it is gliding towards a thermal, (9) whether it is gliding towards the destination. These nine state variables are described in Table 1. Only the state variables dealing with the bird location and the location of a target thermal have units, the other state variables are dimensionless. Thermals are characterised by four state variables: (1) location (x and y coordinates of the thermal centre), (2) diameter, (3) height and (4) thermal lift (see Table 1). Thermal lift is the average upward speed of the air rising in a thermal. It should be noted that in the current implementation of Simsoar the state variables of the thermals are fixed over the simulation length but in future implementations these state variables could also be dynamic. Fig. 3 presents the various concepts from Table 1 graphically.

The *scales* that are of interest are the distance between thermals, which is in the order of 1000–5000 m, and the size of a total simulation domain, which is in the order of 10^6–10^{11} m^2. The simulation length can lie between 1 h (corresponding to visiting a dozen thermals) and 8 h (which corresponds to migration over 1 day, Leshem and Yom-Tov, 1996b), and the simulation time step should approximately be 1 min. A time-step of 1 min, in combination with realistic model parameter values (see Table 2), prevents overshooting when a bird glides towards or climbs in a thermal.

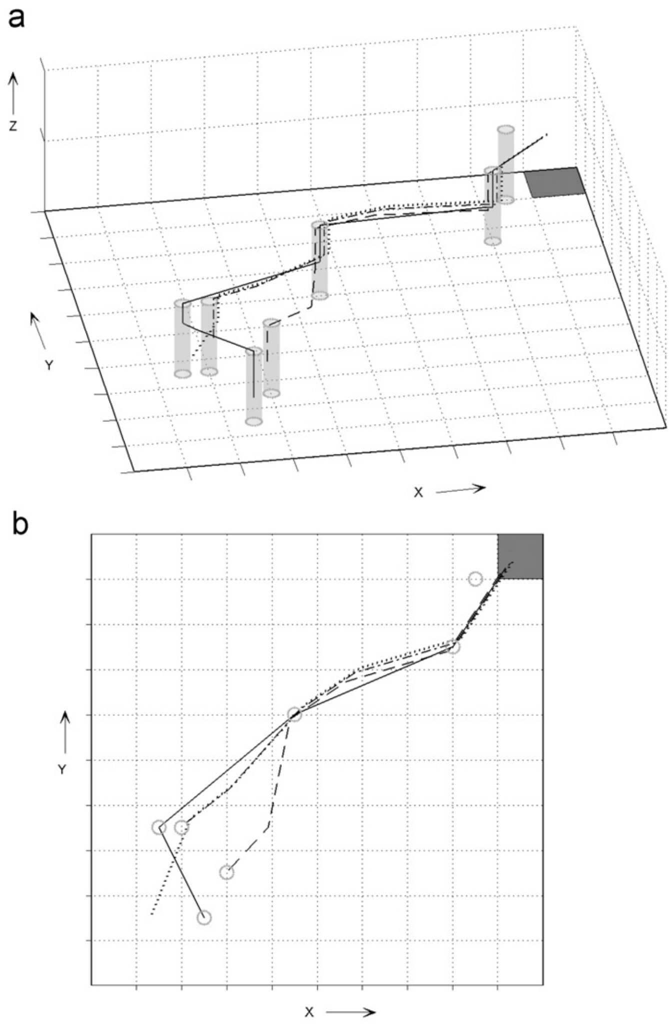

Fig. 2. (a) An example of the three-dimensional space where four birds move in and between cylindrically shaped thermals. Flight paths are shown as lines. Each bird is indicated by a different line type. The lines are shifted a little bit to better show the individual trajectories. The destination area is shown as a grey shaded square. At the start of the simulation three birds are located in thermals and one is gliding towards a thermal. (b) A top-view of the predicted travel network, same data as in illustration a.

3.3. Process overview and scheduling

Birds move towards their destination using gliding flight. In the context of this paper gliding pertains to flight between targets (thermals or the destination) on fixed wings where altitude is lost with distance in accordance with the bird's lift to drag ratio (Table 2). Birds depart from an initial location in the domain and aim to reach a fixed final destination. From the start onwards birds know their current location relative to the destination. To reach the final destination birds choose a thermal in their surrounding as a temporary target. Once this thermal is reached, birds increase their altitude by climbing in that thermal. When at the top of the thermal, they glide to another thermal or to the destination. Birds have to stay aloft until reaching the destination. If a bird cannot

Table 1
Explanation of the bird and thermal state variables in Simsoar. See also Figs. 2 and 3 for a visual explanation of some concepts in this table.

State variable	Unit	Explanation
Bird		
Current location	m	*x*, *y* and *z* coordinates of a bird (coordinates are relative to an arbitrary reference location).
Target location	m	*x* and *y* coordinates of the current target (a target is a thermal or the destination area).
In view	–	List of all the thermals that are viewed by a bird, given its current location.
In reach	–	List of all the thermals that are in view and that a bird may glide to, given its current location.
In domain[a,b]	–	Logical variable indicating whether a bird is currently in the simulation domain (i.e. aloft and not at destination).
At destination[a,b,c]	–	Logical variable indicating whether a bird did arrive at the destination.
In thermal[c]	–	Logical variable indicating whether a bird is currently climbing in a thermal.
To thermal[c]	–	Logical variable indicating whether a bird is currently gliding towards a thermal.
To destination[c]	–	Logical variable indicating whether a bird is currently flying towards the final destination.
Thermal		
Location	m	*x* and *y* coordinates of the centre of a thermal.
Diameter	m	Diameter of a thermal
Height	m	Height of a thermal
Thermal lift	$\mathrm{m\,s^{-1}}$	The speed with which the air in a thermal rises.

[a] Only one of these variables can be true (the other is then by definition false).
[b] If both in domain and at destination are false, it implies that a bird hit the ground.
[c] Only one of these variables can be true (the others are then by definition false).

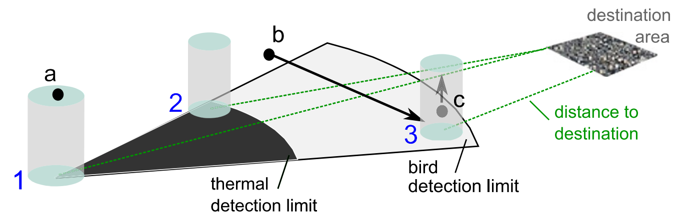

Fig. 3. Illustration of some important model parameters and concepts. The figure shows three thermals (cylinders: 1, 2 and 3) and three birds (dots: a, b, c). From each thermal there is a dotted line indicating the shortest distance to the destination. The perspective in this figure is from Bird a. It just reached the top of thermal 1, and orients around the shortest distance to destination in a pie-shaped region. If Bird a is using a non-social decision rule it can detect only Thermal 2 (which is in the dark area: within the thermal detection limit); if Bird a is using a social decision rule it can detect both Thermal 2 and 3 (which are within the dark and light-shaded areas: within the bird detection limit). However, Thermal 2 will not be selected by bird a since there are no birds in it while Thermal 3 contains a bird. Bird b is gliding from Thermal 2 towards Thermal 3, and in its glide phase not of interest to Bird a.

reach the nearest thermal or the destination by gliding it hits the ground and is removed from the simulation.

Behavioural decision rules describe the criteria according to which individual birds select a thermal as a current target to glide to. Ten decision rules are evaluated in this study. These rules are described in Table 3. One set of rules applies to birds that do not consider other birds when selecting a thermal, whereas a second set of rules applies to birds that consider other birds soaring in thermals when selecting a thermal. For brevity we call birds that follow the first strategy ‘non-social birds’ and the latter group ‘social birds’. An important reason to distinguish between non-social and social birds is the dependence of thermal detection on the presence of birds in that thermal. Thermals without birds climbing in it can only be detected when nearby, but as soon as birds are climbing in a thermal it can be detected by other birds over much longer distances. The 5 decision rules within the classes ‘social’ and ‘non-social’ are chosen to evaluate the extremes of birds’ behaviour with regard to three aspects: (1) the use of navigation skills, (2) local or global maximization of the speed with which a bird gets closer to its migration destination, (3) risk aversion or risk taking. At one end we place decision rules whereby birds use destination location to select a thermal (decision rules 3, 4, 8 and 9) whereas at the other end we have decision rules whereby birds rely on other sources of information (decision rules 1, 2, 6 and 7). For the decision rules that rely on destination location we distinguish decision rules that maximize the distance covered to the destination only for the local domain that can be sensed by a bird (decision rules 3 and 8) from the decision rules that maximize the distance covered to the destination over the entire migratory journey (decision rules 4 and 9). For the decision rules that only use other information than destination location, an optimality principle with regard to migration speed does not make sense, but we consider a principle relating to risk relevant in this case. We distinguish between rules which avoid taking the risk of not reaching a thermal (decision rules 1 and 6 select the nearest thermal as temporary target) and rules which take this risk (decision rules 2 and 7 select the furthest thermal). Finally, we consider decision rules that can act as a null-model. These decision rules (5 and 10) use orientation towards the destination and are further based on complete randomness.

3.4. *Design concepts*

Emergence: The emerging processes in Simsoar are the flight paths and properties derived from these, like convergence of paths or the number of thermals visited.

Fitness: We use the number of thermals a bird visits and distance that a bird travels over one typical migration-day as proxies for fitness (in Section 4 the choice to use the number of visited thermals and relative distance travelled is further explained). The birds in Simsoar select the best thermal according to their individual decision rule for thermal selection, and by doing so they aim at reaching their destination. The birds do not directly maximize or minimize the number of thermals visited or distance travelled on their migratory journey. However, by comparing the number of thermals visited and distance travelled for different decision rules, fitness is considered when evaluating model results.

Interactions: A bird’s decision is influenced by other birds only if it is using a social strategy. Moreover, only those birds that are within detection distance and that are climbing in a thermal can have an impact. This mechanism is supported by evidence from field observations on soaring bird migration (Leshem and Yom-Tov, 1996a; Pennycuick, 1972, 1998) as well as foraging scavengers, which follow other birds when searching for food within a similar detection distance as the birds in Simsoar (Jackson et al., 2008).

Sensing: In order to make decisions a bird has to sense its own location relative to the destination and nearby thermals. A bird knows at any moment its location relative to its destination and the

Table 2
Overview and explanation of input parameters and initial values used in Simsoar. See also Fig. 3 for a visual explanation of some concepts in this table. The column at the right contains parameter values used in the simulation experiment for white storks. The value for lift to drag ratio is calculated as proposed by Pennycuick (1989) using biometric measurements (Leshem and Yom-Tov, 1996b); v_a is based on field measurements in Israel and Africa (Leshem and Yom-Tov, 1996b; Liechti et al., 1996; Pennycuick, 1972). Thermal parameters are representative for soaring conditions during the migration season in Israel (e.g. Shamoun-Baranes et al., 2003a).

Parameter	Unit	Explanation	Values
Related to thermals			
Thermal density	nb km^{-2}	The density of thermals in the simulation domain (used to generate the thermal locations).	0.1[a]
Thermal location	m	The *x* and *y* coordinates of a thermal.	Random[b]
Thermal height	m	Height of a thermal.	1000
Thermal diameter	m	Diameter of a thermal.	400
Thermal lift (*tl*)	m s^{-1}	The speed with which the air in a thermal rises.	3
Related to birds			
Bird density	nb km^{-2}	The density of birds in the simulation domain (used to generate the initial positions of birds).	0.01[a]
Bird location	m	The *x*, *y* and *z* coordinates of a bird.	Random[c]
Bird air speed (v_a)	m s^{-1}	The airspeed of a bird due to gliding. Note that v_a is normally not measured directly but rather derived from observed wind speed, wind direction and ground speed, and track heading (Shamoun-Baranes et al., 2007).	12
Lift to drag ratio (*ldr*)	–	The ratio of the forward motion by a bird to its descent (Pennycuick, 1989).	15
Climbing efficiency (*ce*)	–	The relative efficiency by which a bird can utilize the thermal lift.	0.8
View angle	deg.	The angular range that a bird considers to find thermals in view. This sets a view range which is a pie-shaped domain, centred around the direction of the shortest path towards the destination.	120
Thermal detection limit	m	The distance within which a bird can detect a thermal without any birds.	4000
Bird detection limit	m	The distance within which a bird can still detect another bird that is climbing in a thermal.	10,000
Related to simulation domain and timing			
Simulation domain	km^2	A rectangular domain within which thermals are placed and birds can move.	200 × 100
Departure area	km^2	A rectangular domain within the simulation domain from where the birds are departing.	1 × 80
Destination area	km^2	A rectangular domain within the simulation domain that birds attempt to reach.	1 × 80
Total simulation time	s	Total period over which model calculations take place.	8 × 60 × 60
Simulation time step	s	Period over which the model states are re-calculated.	60
Departure period	s	Period at the start of a simulation, within which the entire population starts to fly	60

[a] With a simulation domain of 20,000 km^2 this leads to 2000 thermals and 200 birds.

[b] Based on the thermal density and the size of the simulation domain, the *x* and *y* coordinates of the thermal locations are selected from uniform random distributions such that the thermals fall within the simulation domain and do not touch or intersect each other.

[c] Based on the bird density and the size of the simulation domain, the *x* and *y* coordinates of the initial bird locations are selected from uniform random distributions such that these fall within the departure area. The initial height (*z* coordinate) for each bird is 1000 m.

Table 3
Overview of the ten decision rules (in this study) for selecting a thermal. If no thermal is in view or in reach none of these decision rules is applicable and birds fly towards the destination.

Non-social behaviour—next thermal is in view, in reach, and
  (1) nearest to the bird
  (2) furthest from the bird
  (3) nearest to destination
  (4) nearest to destination direction
  (5) randomly selected

Social behaviour—next thermal is in view, in reach, holds birds[a], and is
  (6) nearest to the bird (1)
  (7) furthest from the bird (2)
  (8) nearest to destination (3)
  (9) nearest to destination direction (4)
  (10) randomly selected (5)

[a] If no thermal with birds is in view or in reach, thermals without birds are considered as a fall-back option according to the rule in parentheses.

shortest path towards its destination. In addition, a bird can also sense distances to thermals within its thermal view radius, and thermals with birds within its bird view radius. When climbing in a thermal a bird can sense when it reaches the top of that thermal. And finally, a bird can sense its own height and by using that information estimate whether a thermal or the destination can be reached by gliding. All sensing by birds is assumed to be perfect.

Stochasticity: For most decision rules (except for decision rules 5 and 10, see Table 3) there is no stochasticity in the simulation process. In decision rules 5 and 10 stochasticity is introduced by the random selection of a target thermal out of the thermals that are in reach and in view. All thermals have an equal probability of being selected. The initial locations of the birds and the locations of thermals in a simulation are determined randomly. In both cases the placement is according to a uniform distribution, under the constraint that thermals may not intersect. For birds the domain of initial random placement is within a small departure area at one end of the simulation domain, from which they leave within a given departure period. For thermals random placement is within the entire simulation domain. The flight trajectories and outputs (number of thermals visited and relative distance travelled) are sensitive to small changes in the initial locations of birds and thermals. Since the effects of changes in initial locations of birds and changes in thermal placement are the same, only one of these needs to be considered while the other can remain fixed. We remove the stochastic effects by initial bird location and thermal location through a Monte Carlo technique where several simulations (in this study 200) are conducted with exactly the same settings for all parameters except the location of the thermals (the initial locations of the 200 birds are the same for each simulation).

After the simulation, the statistics of interest can be averaged per bird trajectory, over all trajectories for a single thermal field, but also over all trajectories and all thermal fields. In this study we consider the disaggregated values.

Prediction: Due to the randomness of the thermal field, birds cannot predict anything beyond the thermals that are visible. So the best they can do is to select the best thermal locally and, in case no thermal is visible, to glide towards the destination. With a random thermal field, encountering a thermal is as likely along this path as anywhere else. The individuals in Simsoar do know their location with respect to the destination perfectly, do not have a memory and do not learn.

Observation: Spatially explicit dynamic simulation models potentially generate a lot of output. This gives flexibility in selecting or defining variables to evaluate simulation results. In this respect Simsoar is no exception. A great number of output variables can be chosen or defined, e.g. average flight speed, number of thermals visited, distance travelled, the ratio climbing time/gliding time. In this study two model outputs are used: number of thermals visited (*tv*) and relative distance travelled (*rdt*). Table 4 defines these outputs as well as other important variables which can be derived from simulation results. The reason for choosing *tv* and *rdt* in this study is explained in Section 4.

3.5. Initialization

Simsoar is *initialized* by specifying a simulation length, simulation time step and a three dimensional spatial domain. A departure area as well as a destination area is specified as closed polygons on the ground surface inside the domain. Birds are placed at initial locations in this domain inside the departure area and thermals are placed in the entire domain. The values used for the simulations in this paper are shown in Table 2. It should be noted that Simsoar is spatially explicit but does not involve grid-based calculations. A discretisation of the spatial domain is not required because the simulation takes place in continuous Cartesian space where exact locations of individual birds are calculated at each simulation time step.

3.6. External input

We treat the thermal field as an integral part of Simsoar. In the current study the thermal field is static; hence there are no external inputs. However, the structure of the model is such that the thermal field can be time-varying and also be influenced by wind as well as temperature and radiation fields in combination with land cover and terrain shape. In the time-varying case, the fields of wind, temperature, radiation, land cover and terrain would be external inputs.

3.7. Submodels

The model-components SENSE, THINK and ACT jointly form Simsoar, and operate as follows.

In SENSE a bird first evaluates whether the migration destination is in reach, and if so the bird starts to THINK (the list of selected thermals by SENSE is empty). Otherwise the bird inventorizes all the thermals that are in view and in reach. Little is known about distances at which birds can sense thermals yet we expect thermals with birds in them to be detectable at farther distances than thermals without birds. Field observations show that storks regularly fly to thermals that are several kilometres away and occasionally use visual cues to reach thermals that are even tens of kilometres away (Leshem and Yom-Tov, 1996b). A study on foraging seabirds showed that the mean recruitment distance to ephemeral foraging flocks was 4.5 km but could reach 20 km (Haney et al., 1992). For a social bird, the distance over which it can detect thermals will be further than for a non-social bird, see the thermal and bird detection limits in Table 2. The bird selects those thermals that are located in the area determined by the view angle and sufficiently high (so that a bird can actually gain height when arriving at a thermal). After collecting this information about its surroundings a bird proceeds to THINK.

In THINK a bird chooses its target (a point in the horizontal plane, specified by x and y coordinates) to fly to. If the list of thermals selected during SENSE is empty, the bird selects the nearest point in the destination polygon as its target. Otherwise a bird selects the best thermals according to the decision rule among the thermals identified in SENSE. If different thermals are as good, they are considered equally likely and one of them is selected randomly. After choosing its target, a bird proceeds to ACT.

In ACT the bird glides towards its current target or climbs in its current thermal. Climbing in a thermal is described by a constant climb rate and gliding is described by a constant glide rate. If a bird is inside a thermal, its movement is described by the following set of equations:

$$\begin{aligned} dx/dt &= 0 \\ dy/dt &= 0 \\ dz/dt &= ce\, tl \end{aligned} \tag{1}$$

where dx/dt, dy/dt and dz/dt are the changes in location coordinates of an individual over a small time step dt, tl is the thermal lift in $\mathrm{m\,s^{-1}}$, and ce is the climbing efficiency (no unit) (for both parameters see also Table 2). Climbing efficiency accounts for the difference between thermal lift and the actual climb rate of the bird; climb rate is influenced by its specific morphology and the characteristics of the thermal. In our simulations ce is set to 0.8 to account for time lost during circling (Leshem and Yom-Tov, 1996b).

Table 4
Explanation of several important concepts and output variables to describe Simsoar results. All concepts/output variables, except pathway and trajectory, are in this study calculated between departure point and destination polygon per individual and thermal field.

Concept/output variable	Abbreviation	Unit	Explanation
Distance to destination	*dtd*	m	Shortest distance in the x–y plane from an individual bird to the polygon denoted as its destination area.
Number of thermals visited	*tv*	nb	The total number of thermals in which a bird did climb during a given time interval.
Relative distance travelled	*rdt*	–	The total distance travelled (*tdt*), divided by the distance to destination (*dtd*) at the start of the time interval over which *tdt* is calculated. The closer this value is to 1, the straighter a travel path and the more efficiently a bird has moved through a thermal field.
Pathway	–	–	Consecutive (x,y)-locations where several trajectories coincide.
Total distance travelled	*tdt*	m	The distance in the x–y plane travelled by an individual bird during a given time interval.
Total time travelled	*ttt*	s	The time it takes to move between two locations. It includes both time spent gliding between thermals and time spent climbing in thermals.
Trajectory	–	–	The set of consecutive (x,y)-locations visited by a single bird.

When entering a thermal, a bird is (for simplicity but without loss of generality) placed in the centre of the thermal and climbs in a straight vertical line. Birds climb in a thermal until they reach the top, when they enter the glide phase.

The equations describing the movement of a bird when gliding are

$$\begin{aligned} dx/dt &= v_g \sin\gamma \\ dy/dt &= v_g \cos\gamma \\ dz/dt &= -v_g/ldr \end{aligned} \tag{2}$$

where γ is the track heading in degrees (0° is in the direction of positive y and 90° is in the direction of positive x), v_g is the ground speed in m s^{-1}, and ldr is the lift to drag ratio (no unit). In this study, winds are not present, hence $v_g = v_a$. When including a wind field, Eq. (2) will remain unchanged. v_g and γ will become functions of v_a, bird heading, wind speed and wind direction (see Shamoun-Baranes et al., 2007).

Track heading is calculated as the inverse tangent of the ratio of the distances between target and current location in the x and y directions, respectively (see Eq. (3)):

$$\begin{aligned} \gamma &= \tan^{-1}((x_{target}-x)/(y_{target}-y)) && \text{if } x \geq 0 \text{ and } y \geq 0 \\ \gamma &= 360+\tan^{-1}((x_{target}-x)/(y_{target}-y)) && \text{if } x < 0 \text{ and } y \geq 0 \\ \gamma &= 180+\tan^{-1}((x_{target}-x)/(y_{target}-y)) && \text{if } y < 0 \end{aligned} \tag{3}$$

where x_{target} and y_{target} are the x- and y-coordinates of the target (a target is the centre of a thermal or the nearest point of the destination area), and $\tan^{-1}$ is the inverse tangent, operating in degrees.

Birds reorient themselves when choosing a new target after reaching the top of a thermal or when detecting a thermal when flying towards the destination, hence the track heading (γ) changes only at these times. Birds never change direction if they are flying towards a thermal or if they can reach the destination. The ‘in view’ window is always oriented symmetrically around the track heading (see Fig. 3). If the destination is a polygon (like in this study) and not a point, the bird always orients towards the nearest point in the polygon, meaning that the x and/or y coordinates used as a reference for the destination by each bird is likely to change.

4. Model application: white stork migration efficiency

As explained in the introduction, we want to apply Simsoar to investigate if and under which circumstances social behaviour by white storks enhances migration efficiency. We use the number of thermals visited (*tv*) and relative distance travelled (*rdt*) to quantify migration efficiency. We consider the use of fewer thermals as more efficient because it implies that the system is less dependent on thermal density and we consider a shorter relative distance travelled as more efficient because it implies less travel time and consequently more time to select a feeding or resting site. The reason why we do not use total time travelled (*ttt*) for evaluating the model is based on the fact that the distance can be related better to data that is available from the literature (e.g. Leshem and Yom-Tov, 1996b).

Our prior expectation for *tv* and *rdt* is that social decision rules will lead to lower values because the *bird detection limit* is larger than the *thermal detection limit* and consequently social birds have much more thermals (and potentially better ones) to choose from. However, due to the discrete character of the system, several thresholds and non-linearities (viz. Eqs. (1)–(3)) in combination with the system heterogeneity (random placement of birds and thermals), we can test our expectations only by evaluating simulation results. An example of a non-linear relation for which the overall effect is hard to evaluate is the change in number of thermals that can be selected due to a change in view angle. An example of a threshold is the fact that the detection limit of a social bird may suddenly decrease when all other birds in its surrounding leave their thermals. So to investigate our expectations with respect to *tv* and *rdt* under different decision rules for white stork migration we conduct an experiment with Simsoar. Parameters and initial conditions that are representative for the white stork are specified a priori on the basis of our knowledge from the literature and personal experience from field observations (Table 2). All individuals in the simulation have the same parameter values (note that the state variables as listed in Table 1 are different for each bird). No parameter optimization is employed to tune the model, so that particular results are achieved. The simulation length is 8 h, a typical duration of one day of flight for white storks (Leshem and Yom-Tov, 1996b), the domain is 100 km in width and 200 km in the migration direction, with a departure area of 1 km × 80 km at one side of the spatial domain and a destination area of 1 km × 80 km at the opposite side of the spatial domain. The dimensions of this domain are such that all birds can travel the distance from departure to destination site within the given simulation length. The birds leave the departure area within a given departure period (typically within 30 min). The simulation is repeated 200 times. In each simulation, the locations of thermals differ (uniform random distribution over the simulation domain), but the starting locations of the birds remain the same. We consider the decision rules listed in Table 3 (5 non-social, and 5 corresponding social decision rules). We analyse the results by comparing number of thermals visited and relative distance travelled for an 8 h simulation length. Although the model is applied to 200 thermal fields and there is considerable variability in the results between different thermal fields, we do not average the model results over the 200 thermal fields. In Appendix B the differences between averaging over thermal fields or birds are explained further.

After conducting a base run (using the parameters in Table 2), a sensitivity analysis is employed in two steps. The first step is explorative in nature and meant to identify a limited number of parameters or initial conditions (for simplicity we refer to these with the term ‘parameters’) which are most influential on the model output. These most influential parameters are then used for a more thorough sensitivity analysis. The explorative sensitivity analysis involves a relatively large number of parameters (7): thermal density, bird density, thermal detection limit, bird detection limit, view angle, lift to drag ratio and departure period. These seven parameters are selected because they are expected to influence *tv* and *rdt* (the remaining parameters in Simsoar are expected to be non-influential). The last parameter (departure period) may need some explanation, as it was not mentioned before. In the base run all birds depart at the same moment. The absence of a departure period means that most birds are flying at the same distance from the destination at any time due to the narrow departure area and it makes it less likely for any structure to emerge, such as a structure with a few leading birds and a number of followers. Perhaps this initial condition does not reflect reality very well, where there may be some variation in departure period by birds. So in the sensitivity analysis the effect of heterogeneity in departure period on *tv* and *rdt* is investigated.

Each of the seven parameters is varied over four levels (see Table 5, second column) and evaluated for only a limited number of combinations (28 for each of the ten decision rules, over all birds and thermal fields in a simulation) through a latin hypercube scheme (Iman and Helton, 1988). The sensitivity of *tv* and *rdt* to each parameter is calculated for each of the ten decision rules by the following equation:

$$S_{O,P,D} = \frac{CV_{O,D}}{CV_{P,D}} \tag{4}$$

where $CV_{O,D}$ is the coefficient of variation of model output O (*tv* and *rdt* in this case) and decision rule D, $CV_{P,D}$ is the coefficient of variation for the different values of model parameter P and decision rule D, and $S_{O,P,D}$ is the sensitivity measure describing the relative

Table 5
The sensitivity of the number of thermals visited (*tv*) and the relative distance travelled (*rdt*) for changes in seven parameters and initial conditions (column at the left). The levels for the parameters are shown in the second column. The sensitivities are calculated according to Eq. (4) (a higher value means that the model output is more sensitive to changes in the particular parameter). The effect of the parameters on *tv* and *rdt* is averaged over the 5 social and non-social decision rules and over all 10 decision rules as well. In the last column the sensitivities for *tv* and *rdt* are averaged. The shaded rows denote the three parameters to which *tv* and *rdt* are jointly most sensitive, i.e. for the three highest values in the column at the right.

parameter[a]	**levels**	**sensitivity to parameter change, averaged over**						
		social decision rules		non-social decision rules		all decision rules		
		tv	***rdt***	***tv***	***rdt***	***tv***	***rdt***	***average***
thermal density (nb km^{-2})	0.07, 0.09, 0.11, 0.13	0.14	0.13	0.12	0.11	0.13	0.12	0.13
bird density (nb km^{-2})	0.004, 0.008, 0.012, 0.014	0.16	0.11	0.03[b]	0.02[b]	0.16	0.11	0.14
departure period (min)	0, 10, 20, 30	0.39	0.32	0.02[b]	0.03[b]	0.39	0.32	0.36
thermal detection limit (km)	2.5, 3.5, 4.5, 5.5	0.21	0.18	0.27	0.21	0.24	0.20	0.22
bird detection limit (km)	7, 9, 11, 13	0.49	0.45	0.00[b]	0.01[b]	0.49	0.45	0.47
view angle (deg.)	90, 110,130, 150	0.51	0.35	0.57	0.31	0.54	0.33	0.44
lift to drag ratio (-)	12, 14, 16, 18	0.08	0.06	0.12	0.07	0.10	0.07	0.08

[a] Strictly speaking, the items that are varied in the sensitivity analysis are initial conditions (above the dashed line) as well as model parameters (below the dashed line).
[b] These values should be zero in theory as these parameters are not affecting bird behaviour in Simsoar under non-social decision rules. The values shown here are however calculated rather than set to zero a priori. Due to the latin hypercube sampling scheme small sensitivity values may appear instead of zeros. For the calculation of the average sensitivity values over all decision rules (last three columns of the table), these sensitivity values are treated as missing values.

contribution of parameter *P* to the total variation of model output *O* under decision rule *D*. The larger $S_{O,P,D}$, the more influential parameter *P* for output *O* under decision rule *D*. This sensitivity measure is described in Saltelli et al. (2000).

$S_{O,P,D}$ appears to vary most for different parameters and much less for different decision rules. In addition there appear to be only small differences between social and non-social decision rules. On the basis of this we choose to average the sensitivities over the ten decision rules (resulting in seven sensitivity values for *tv* and seven for *rdt*) as well as over *tv* and *rdt* (resulting in a total of seven sensitivity values), see Table 5. On the basis of this averaged sensitivity value per parameter, the three most influential parameters are chosen for a more elaborate evaluation. As Table 5 shows, the model results appear to be especially sensitive to three parameters (view angle, bird detection limit and departure period) whereas for the other variables the (averaged) sensitivity is considerably lower. This second part of the sensitivity analysis uses for view angle the values 90°, 110°, 130° and 150°, for the bird detection limit the values 7, 9, 11 and 13 km, and for the departure period the value of 0 min (all birds start to fly at the first model time step), 10 min (at each model time step, 10% of the birds start to fly) and 20 min (at each second model time step 10% of the birds start to fly). The departure period is reduced by one level in comparison to the exploratory sensitivity analysis as it appears to have no effect above a value of 20 min. These levels are combined in a full factorial design (i.e. all combinations of the different parameter values are evaluated), resulting in 48 runs for each of the 10 decision rules. It should be noted that each run in the sensitivity analysis is, similar to the base-run, in fact a composite Monte Carlo run with 200 individuals over 200 thermal fields.

The results from the base run are analysed by comparing the differences between the 10 decision rules with regard to the number of thermals visited and relative distance travelled with a one-way ANOVA followed by a multi-comparison test using the Tukey–Kramer method. The differences between decision rules are analysed by calculating the minimum required sample size at a maximum level of significance and minimum power using a *T*-distribution (a technique also known as power analysis). This sample size calculation follows the method outlined in Sokal and Rohlf (1995).

The results from the sensitivity analysis are analysed by multiple least squares linear regression, with the three variables from the sensitivity analysis (and a constant) as the only explanatory variables. Before applying the regression procedures, the three variables are *z*-transformed, so that the parameter values obtained through regression can be interpreted at the same scale. A model selection procedure is applied (evaluating all combinations of the three variables, including the interaction terms). In the model selection procedure only those models are retained that (i) are highly significant ($p < 0.0001$), (ii) contain only significant parameters ($p < 0.01$) and (iii) where a Jarque–Bera test on the residuals (Jarque and Bera, 1987) does not detect deviations from normality and a visual inspection of the residuals does not suggest heteroscedasticity or deviations from linearity (Draper and Smith, 1998). All statistical analyses are conducted in Matlab and made use of some functions in the Matlab Statistical toolbox (all the Matlab scripts used for the analysis in this study are contained in Appendix A).

5. Results

5.1. General patterns in simulated white stork migration

The 200 individual birds, departing from an 80 km-wide area, quickly converge into 3 to 10 pathways, for all social decision rules except rule 10 (Fig. 4). The number of pathways for non-social decision rules is approximately twice the number of pathways for the corresponding social ones. Furthermore, the non-social decision rule 5 leads to no convergence, in contrast to the equivalent social decision rule 10. The variation between different thermal fields with respect to the location of travel paths chosen is considerable (based on visual comparison). In spite of this variation, however, nearly all of the trajectories are successful in the sense that nearly all birds (more then 99.5%) arrive at the destination within the 8 h simulation time. This success rate is almost the same for the different decision rules. In 0.3% of the cases birds are still aloft but do not reach the target, in 0.2% of the cases birds hit the ground. Aggregating the simulations over all decision rules, the average time it takes for a bird to travel over the 200 km from departure to destination is 6 h and 39 min with a standard deviation (std) of 16 min. The total distance travelled (per bird) is on average 229 km (std 6.6 km). On average 58 (std 9) thermals are visited. From the 2000 thermals in every simulation, 874 (std 295) different thermals are used by the birds. The reported standard deviations are those for the raw data, for each bird and each thermal field separately (40,000 values).

By using the 200 replicate birds and thermal fields, two important sensitivities can be calculated from the base run: sensitivity of birds

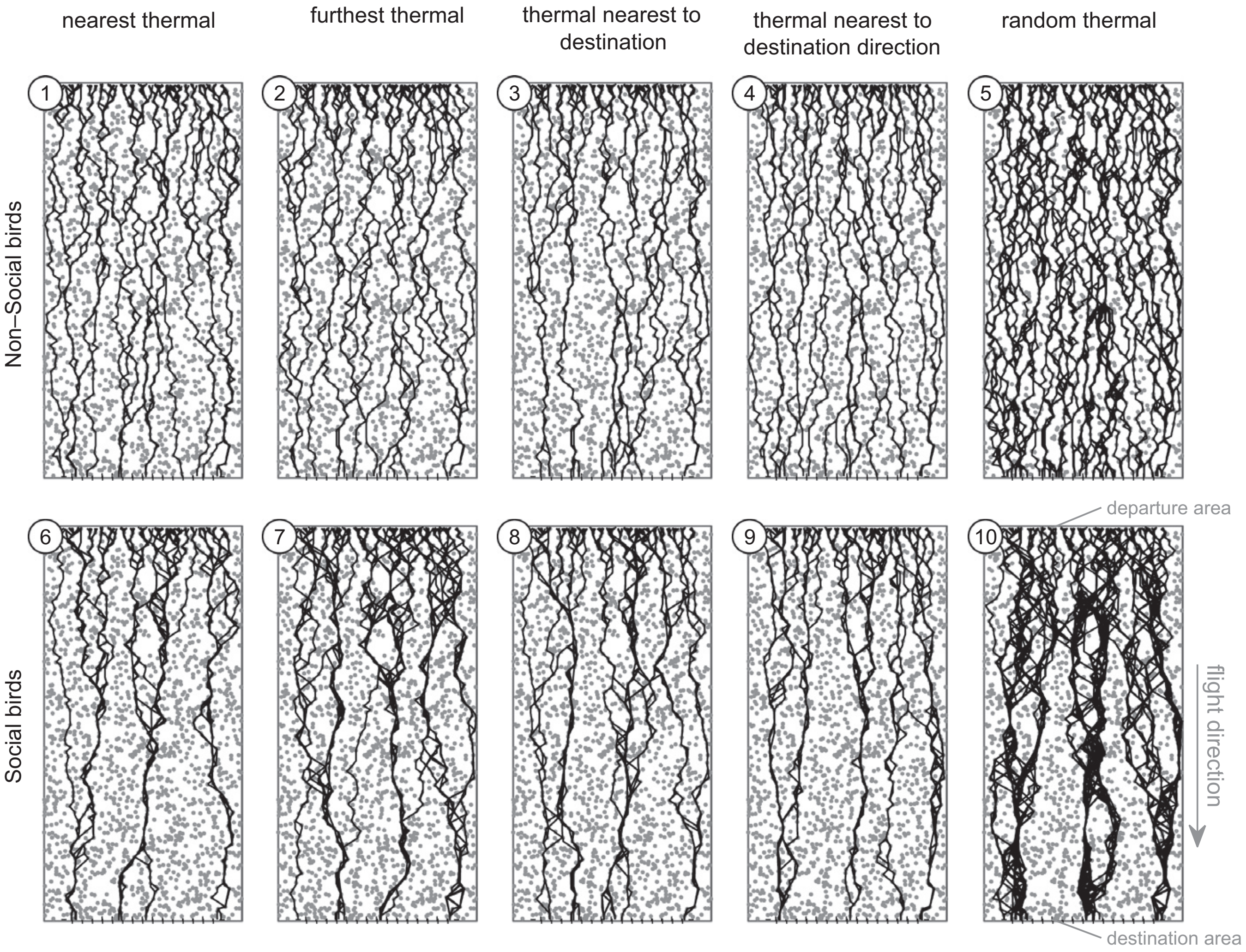

Fig. 4. Typical model results when simulating white stork migration. The top row shows a travel network when using decision rules 1–5, and the bottom row shows the travel networks when using decision rules 6–10. All simulations are for 200 birds (the solid lines) and 2000 thermals (the grey dots) and the simulation domain is 200 km × 100 km. For all simulations the parameters as listed in Table 2 are used. The thermal field as well as initial bird locations are identical for the 10 decision rules.

to different starting positions and sensitivity of birds to different thermal configurations. The variability between birds within a thermal field represents the sensitivity of birds to different starting positions whereas the variability of a bird over different thermal fields represents a sensitivity of birds to different thermal configurations. It turns out that both sensitivities are comparable (we use the standard deviation to express the variability and measure sensitivity). The standard deviation of the number of thermals visited is 5.1 when considering different starting positions and 5.2 when considering different thermal configurations. For the total distance travelled these values are 4.1 and 4.4 km, respectively (see Table B1 in Appendix B for the values per decision rule). We conclude that the sensitivity to different thermal configurations is slightly higher than the sensitivity to different starting positions.

5.2. *Effects of decision rules on number of thermals visited and relative distance travelled*

Fig. 5 shows the distribution for the number of thermals visited (*tv*, Fig. 5a) and the relative distance travelled (*rdt*, Fig. 5b) when applying the different decision rules. The most striking aspect of these results is the fact that, for a given thermal selection strategy, *tv* discriminates relatively well between all social and non-social decision rules. In contrast, *rdt* discriminates only between decision rules 3,4, 8 and 9 versus the other decision rules and between decision rules 9 and 10. The observed differences between social and non-social decision rules with respect to *tv* are according to prior expectations, but for *rdt* they are opposite.

Analysis of variance, comparing the effect of decision rules on *tv* as well as *rdt* leads to significant effects ($p < 0.01$), and a multi-comparison test leads to significant pairwise differences for most combinations. However, when using simulation data where the number of individual birds can be set to any value (200 in this study), significance is not informative. We rather use a sample size analysis to estimate required number of birds in future field research (e.g. via GPS-tagged individuals) to discriminate between any pair of decision rules. Required sample sizes to detect differences between decision rules are shown in Table 6. It appears that for *tv* especially decision rules 1, 5 and 7–10 can be discriminated from all other decision rules but that decision rules 2–4 and 6 cannot be discriminated when considering (for fieldwork) reasonable sample sizes. For *rdt* there are fewer pairs of decision rules that can be discriminated. However, by using *rdt*, decision rules 2 and 6 can be discriminated from 3 and 4. Hence *rdt* is a useful complement to *tv* when evaluating decision rules.

The average distance between selected thermals is shown per decision rule in Table 7. This distance is around 4 km and social

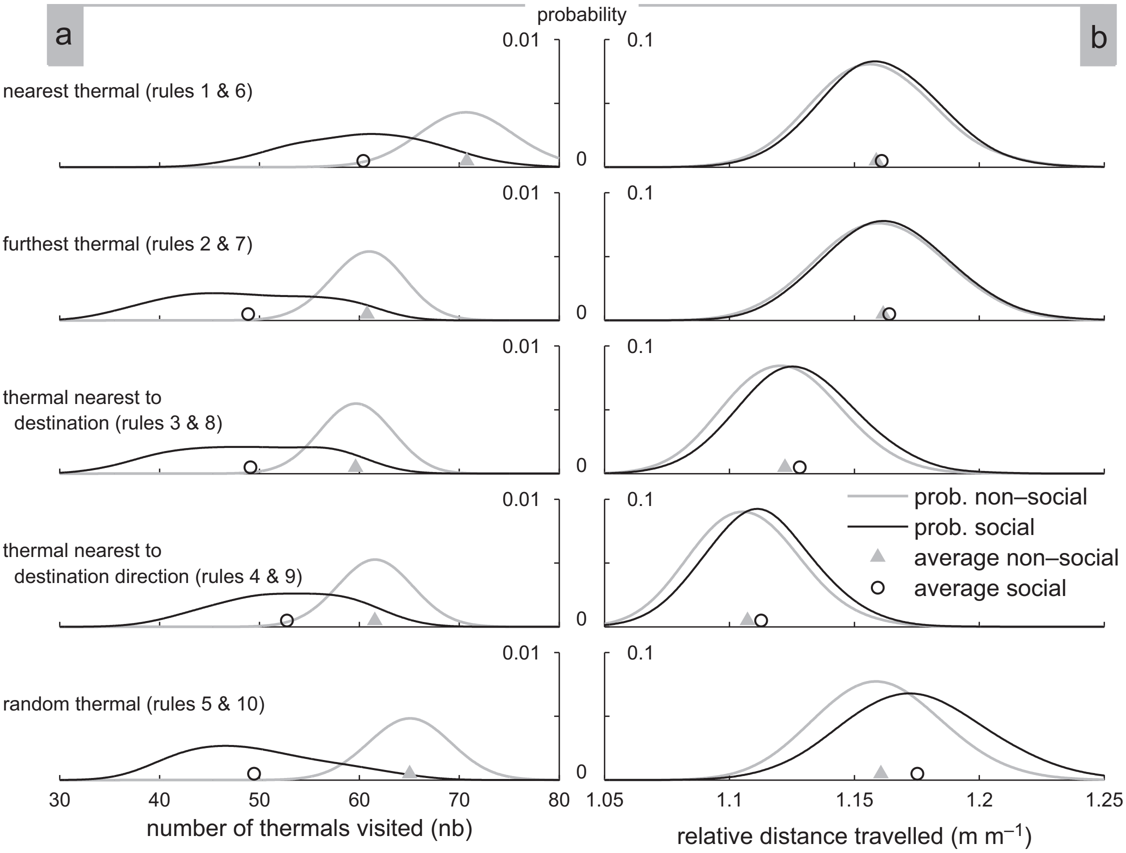

Fig. 5. The probability distributions and average values for number of thermals visited (a) and relative distance travelled, (b) per decision rule (each row). Simulation results are used for 200 birds over 200 thermal fields (40,000 values in total) for each probability distribution. The probability distributions are estimated by a kernel smoother, using a Gaussian shaped kernel with an optimal bandwidth as described in Bouwman and Azzalini (1997).

birds hardly exploit their potentially larger detection range (*bird detection range* of 10 km) in comparison with that of non-social birds (*thermal detection range* of 4 km). This is clearly shown by the fraction of the potential (thermal or bird) detection limit that is effectively used. When close to one it means that the birds are selecting thermals at a distance close to their detection limit. The non-social decision rules lead to values relatively close to 1. The result that the detection limit is not completely exploited by the social birds (especially relevant for decision rules 7–9) is explained by the fact that when selecting a new thermal, there are often no birds in view. This is partially due to the short departure period and narrow departure area, which leads to a situation where relatively few birds can take advantage of the birds further ahead (in comparison to a longer departure period), but the phenomenon is also influenced by the number of birds in the domain in combination with the thermal density. The effect of the short departure period is investigated in the sensitivity analysis (see next sub-section), but the effect of bird density and thermal density is not further investigated here as it was shown to be not very influential in the exploratory phase of the sensitivity analysis.

5.3. Sensitivity analysis with respect to view angle, bird detection limit and departure period

The values for *tv* and *rdt* have been calculated for different combinations of the parameters: bird detection limit (7, 9, 11 and 13 km), view angle (90°, 110°, 130° and 150°) and departure period (0, 10 and 20 min) while all other parameters (see Table 2) in the model run remained unchanged. On the basis of these results the sensitivity of *tv* and *rdt* for these three parameters is analysed through multiple least squares linear regression. The resulting parameter estimates (only those significantly different from zero) are shown in Table 8. For most models only the view angle appears to be significant, and only for the social decision rules in the '*tv*-models' all three parameters appear to be significant. Interaction-terms are never significant. The interpretation of the parameters in Table 8 is straightforward. Take e.g. the parameter value of view angle for *tv*, decision rules 1 through 10. The fact that it is positive implies that a positive change of the view angle would result in a considerable increase in number of thermals visited (in this case a change of one *z*-transformed unit equals a change in view angle of 25°). Comparing this parameter value with the other parameter values in the same column shows that decision rule 1 is most sensitive for a change in this parameter. So while decision rule 1 is already characterised by the largest values for *tv* (see Fig. 5a), this characteristic will only become more pronounced with an increase in view angle.

The main result from the sensitivity analysis is that changes in the three parameters (bird detection limit, view angle and departure period) will most likely not influence *rdt* much, but will impact *tv*. The number of thermals visited will mostly increase for the non-social rules and decrease for the social rules, which makes the difference between a social and corresponding non-social rule even larger in comparison to the base run. The only parameter which has a significant impact on the two variables under study is the view angle. For *tv* and decision rules 7 to 10, the (reverse) effects of the bird detection limit as well as the departure period are more important than the effect by view angle. The direction of all effects is consistent with what was expected a priori.

Table 6
The sample size required to discriminate between any pair of decision rules at significance level of 0.05 and power of 0.8, when observing individual birds in individual thermal fields. Translating this to the field research: the sample size in a cell refers to the number of migration days of individual birds (not necessarily the same migration day for each bird, and not necessarily the same bird over different days) that should at least be investigated to enable the discrimination of a pair of decision rules (at 0.05 level of significance). The lower triangle gives the required sample sizes when considering number of thermals visited, the upper triangle when considering relative distance travelled. The white cells are those pairs of decision rules that can be discriminated with sample sizes up to 10 individuals (feasible in terms of field work effort that would be required). The light-shaded cells identify pairs of decision rules, for which sample sizes of 11–50 individuals are required (difficult to achieve). The dark shaded cells are those pairs of decision rules, for which more than 50 individuals are required (infeasible).

Decision rule:	1	2	3	4	5	6	7	8	9	10
1		***537***	6	4	***1220***	***884***	***156***	7	5	**18**
2	4		6	4	***5045***	***11,702***	***772***	7	5	**26**
3	4	***61***		**18**	5	5	5	***103***	**41**	4
4	5	***132***	**22**		4	4	4	10	***107***	3
5	7	7	5	9		***43,119***	***404***	7	5	**23**
6	4	***549***	***122***	***66***	7		***422***	6	4	**21**
7	3	3	3	3	3	6		6	4	**38**
8	3	3	3	3	3	6	***9424***		**19**	5
9	3	4	4	4	3	9	**33**	**35**		4
10	3	3	3	3	3	6	***1372***	***3371***	**32**	

Table 7
The average distance between selected thermals under the different decision rules. The distance between thermals is calculated by *tdt*/*tv* for each bird passing a thermal field and then averaged per decision rule. The second column shows the average and standard deviation of the distance between thermals. The fourth column expresses the average distance as a fraction of the maximum range at which thermals can be detected under the given decision rule (detection limit, third column).

Decision rule	Distance between thermals selected by birds		
	Avg/std (km)	Detection limit (km)	Relative (–)
1	*3.29/0.18*	*4*	*0.82*
2	*3.77/0.17*	*4*	*0.94*
3	*3.83/0.17*	*4*	*0.96*
4	*3.64/0.17*	*4*	*0.90*
5	*3.58/0.17*	*4*	*0.89*
6	*3.90/0.49*	*10*	*0.39*
7	*4.71/0.79*	*10*	*0.47*
8	*4.89/0.84*	*10*	*0.49*
9	*4.27/0.57*	*10*	*0.43*
10	*4.85/0.74*	*10*	*0.49*

6. Discussion and conclusions

6.1. Integrating knowledge about soaring bird migration

Simsoar was intentionally designed as a very simple representation of soaring migration. This simplicity has contributed to its success in making an operational model to evaluate a realistic scenario of white stork migration. Not only can complexity in an IBM lead easily to programming errors, it would have also been difficult to provide realistic values for initial conditions and parameters in our first simulations. We experienced that while it is relatively easy to specify behavioural rules in a model and set up a model for a single example-run, it is much more difficult to design an experiment with different initial conditions, repetitions, and output variables for answering a specific question with that model. It is even more challenging to properly analyse the output of such an experiment and draw ecological conclusions (Grimm et al., 2005). This study not only presents the structure and logic of Simsoar itself clearly, making it possible to extend and change it in further studies, but also provides a template for further experimentation and scenario testing. To our knowledge, only two other models describing soaring bird migration have been published, a dynamic continuum-based model developed by Brandes and Ombalski (2004) and a dynamic data-driven model developed by Mandel et al. (2008) (for model definitions see Shamoun-Baranes et al., 2010). Both studies consider the thermal field (atmospheric boundary layer) as a continuum, in contrast with the individual thermals in Simsoar. As a result of this, these models can be calibrated with observations using a gradient based method rather than a Monte Carlo technique. There are considerable conceptual differences between the models by Brandes and Ombalski (2004) and Mandel et al. (2008). The first adopts a flow-line calculation, analogous to what is common in hydrologic modelling, and applies it to situations where the updrafts resulting from horizontal surface winds deflecting off sloping terrain are the dominant source of lift. The second is in fact not a single model but a set of four autoregressive linear mixed-effect models which relate bird movement to wind speed, turbulent kinetic energy in the atmosphere, cloud height and terrain features. The models by Brandes and Ombalski (2004) and Mandel et al. (2008) demonstrate that specific route choices are determined to a large extent by wind, topography and availability of turbulent uplift. Neither of the models offers the opportunity to consider interactions between individuals or the evaluation of a heterogeneous set of decision rules, and differ especially in this respect from Simsoar. We think it would be worthwhile to investigate whether the three models for soaring bird migration could be interfaced, and whether they could complement one another in answering some research questions on soaring bird migration.

In the remainder of this section we first discuss the results from the experiment that we conducted with Simsoar to analyse white stork migration. Next, we discuss these results in the light of several model assumptions and at the end some possibilities for future use and extensions are discussed.

6.2. Model results for white stork migration

The results from our model base-run and a sensitivity analysis suggest that, for a range of decision rules and under the environmental conditions tested, where thermal depth, diameter and lift rate are homogenous, being social mostly influences *tv* but not *rdt*. Under these conditions social birds are more efficient with respect to the number of thermals they visit but not directly through straighter travel paths (i.e. a lower relative distance travelled). The reason why the non-social decision rules lead to slightly lower *rdt* than the social decision rules appears to be the fact that the sample of thermals with birds is relatively small compared to the sample of thermals without birds (due to the high thermal density and low bird density). So social birds will choose thermals further away, but these are often less well placed. This effect appears to be especially large for decision rules 5 and 10. In the case of *tv* (Fig. 5a) the standard deviation is much higher for the social than the non-social

Table 8
Sensitivity analysis of the number of thermals visited and relative distance travelled for changes in bird detection limit (7, 9, 11 and 13 km), view angle (90, 110, 130 and 150°) and departure period (0, 10 and 20 min) by multiple linear regression. The response variables are the expected number of thermals visited and the relative distance travelled for an individual bird over one thermal field. All three independent variables are z-transformed, so that the parameter values in the table can be interpreted at the same scale. The z-transformed levels for bird detection limit and view angle are -1.16, -0.39, 0.39 and 1.16; and for departure period the levels are -1, 0 and 1. The table shows the parameter values and associated standard errors. Results are shown for models that result from a model selection procedure. In all cases the model is highly significant ($p<0.0001$), parameters are significant ($p<0.01$) and residual tests do not detect non-normality, heteroscedasticity or deviations from linearity. The italic cells (models for the non-social birds) are cases where parameters were expected to be not included in the model a priori because the variation of the bird detection limit and departure period cannot influence the behaviour of non-social birds in Simsoar. The abbreviation n.i. stands for 'not included' and indicates that a variable was not included in the significant model for the corresponding decision rule.

Decision rule		Parameter		
	Constant	***Bird det. limit***	***View angle***	***Departure period***
nb of thermals visited (*tv*)				
1	71 (0.012)	*n.i.*	10 (0.012)	*n.i.*
2	59 (0.059)	*n.i.*	5 (0.059)	*n.i.*
3	61 (0.015)	*n.i.*	6 (0.015)	*n.i.*
4	61 (0.056)	*n.i.*	5 (0.056)	*n.i.*
5	65 (0.014)	*n.i.*	8 (0.014)	*n.i.*
6	60 (0.25)	-2 (0.25)	5 (0.25)	-1 (0.25)
7	46 (0.28)	-4 (0.28)	1 (0.28)	-3 (0.28)
8	46 (0.33)	-5 (0.34)	2 (0.34)	-3 (0.34)
9	51 (0.22)	-2 (0.22)	1 (0.22)	-2 (0.22)
10	49 (0.31)	-4 (0.31)	1 (0.31)	-2 (0.31)
Relative distance travelled (*rdt*)				
1	1.18 (0.94×10^{-3})	*n.i.*	0.07 (0.95×10^{-3})	*n.i.*
2	1.14 (0.30×10^{-3})	*n.i.*	0.04 (0.30×10^{-3})	*n.i.*
3	1.19 (1.2×10^{-3})	*n.i.*	0.08 (1.2×10^{-3})	*n.i.*
4	1.12 (0.26×10^{-3})	*n.i.*	0.04 (0.26×10^{-3})	*n.i.*
5	1.19 (1.1×10^{-3})	*n.i.*	0.08 (1.1×10^{-3})	*n.i.*
6	1.18 (1.0×10^{-3})	n.i.	0.07 (1.0×10^{-3})	n.i.
7	1.14 (0.86×10^{-3})	n.i.	0.04 (0.87×10^{-3})	n.i.
8	1.19 (1.3×10^{-3})	n.i.	0.07 (1.3×10^{-3})	n.i.
9	1.12 (0.95×10^{-3})	n.i.	0.04 (0.96×10^{-3})	n.i.
10	1.20 (1.2×10^{-3})	n.i.	0.08 (1.2×10^{-3})	n.i.

birds. The explanation for this is that social birds sometimes behave like non-social birds (if there are no other birds in view), with the accompanying lower view range and selection of closer thermals.

The apparent (nearly) similar migration efficiency for social and non-social birds is not in line with the findings of Liechti et al. (1996) who presented evidence that birds soaring in flocks are more efficient than single birds, not only due to higher climb rates but also higher cross country speeds and less directional scatter. Our explanation for this discrepancy is that Liechti studied birds in a heterogeneous environment while the environment in our simulations was homogenous (all thermals had equal properties). We might in fact get results similar to those observed by Liechti et al. (1996) when extending the study to heterogenous conditions where birds select thermals according to thermal lift (which varies in space and time). In addition Simsoar is lacking some key processes (e.g. those leading to directional scatter), which makes it difficult to compare model results to the aforementioned detailed field observations. We would like to apply appropriate model extensions and collect field observations in the future to resolve this issue.

The values for *rdt* in this simulation can be compared with the values from observations on white stork migration with a motorized glider by (Leshem and Yom-Tov, 1996b, in their Table 4). Leshem and Yom-Tov observe 12.5% extension of the migration route by flying from thermal to thermal, which corresponds to an *rdt* value of 1.125. This value is in the same order of magnitude as the results from Simsoar (Fig. 5b). Following along these lines, it would lead to selection of decision rules 4 and 9 (with mean values of 1.12 and 1.13 for *rdt*) as those rules that match best with the observations currently available. It is striking that the decision rule to select the thermal in the direction closest to the destination direction (4 and 9) is in fact the most efficient decision rule thinkable with respect to minimization of relative distance travelled (or travel duration). Similar values were also found for lesser spotted eagles. However, white pelicans and honey buzzards showed considerably larger route extensions in the field. In the same study, Leshem and Yom-Tov also found that the mean number of thermals visited per hour was 5.6, corresponding to 44.8 thermals in 8 h, which is quite close to the range of values resulting from social decision rule simulations. So we conclude that for white storks the social decision rule to select the thermal in the direction closest to the destination direction matches the field observations best. It implies that these birds are probably selecting thermals with other birds in it and navigate almost perfectly at a fine scale. Unfortunately, we did not find other information in the literature on thermal use by soaring birds that can be compared to our model results for *tv*. In addition, the possible relevance of *tv* for migration efficiency has never been discussed to our knowledge. We expect *tv* to be relevant for migration efficiency in two ways. In the first place it may be relatively costly for a bird to find and enter a thermal. If that is the case then selecting the minimum number of thermals would be energetically efficient. On the other hand, selecting thermals which are far increases the risk that these cannot be reached by gliding if conditions (like wind direction) turn out to be adverse. If a thermal cannot be reached a bird would be forced to cover some distance with flapping flight, which is energetically much more costly than gliding flight (Pennycuick, 1989). This is an argument against selecting thermals far away rather than being social, albeit that with the current decision rules in Simsoar social behaviour does lead to selecting thermals further away. Both effects, the energetic costs of finding and entering a thermal and the risk of not reaching a thermal, are currently not included in Simsoar and this discussion therefore only refers to the interpretation of *tv* in field situations and not the interpretation of the model simulation results. Overlooking these two effects for *tv*, we consider the energetic costs involved in finding and entering a thermal to be more important and would associate a lower *tv* with a higher fitness.

It was stated in the introduction that fine scale movement patterns in bird migration are often related to flocking. We consider flocking as a phenomenon where individuals concentrate in space and time, corresponding to the definition by Reynolds (1987). An expression of this phenomenon is the merging of many different flow paths into a few common flow paths as migration proceeds (which we will call convergence). In this study, convergence is not measured quantitatively, like *rdt* and *tv*, but rather considered qualitatively. Our qualitative assessment showed that social decision rules led to stronger convergence (fewer pathways) than non-social decision rules, suggesting that large scale convergence is the result of fine scale decision rules. In future studies it would be helpful to have measures for convergence. However, defining such a measure is not trivial. On the basis of results from Simsoar convergence could be measured elegantly by counting the number of thermals actually used by birds divided by the number of thermals available at a given distance range from the destination. The disadvantage of this method to quantify convergence is the difficulty to measure an equivalent entity in field research. Alternative ways to quantify convergence in a travel network of migrating birds do not yet exist and can perhaps be derived from concepts in other disciplines like the width function for flow networks in hydrology (Moussa, 2008).

6.3. Model assumptions and implications for our results

A major assumption underlying the current version of Simsoar is that individuals are able to establish their location relative to their destination without error or, equivalently, individuals are aware of their exact drift from the main migration direction and correct for that drift. Furthermore, once selecting a thermal, birds will not re-evaluate their selection until that thermal is reached. If a thermal is not in view or in reach birds will glide towards the destination. However, if during this trajectory a thermal becomes visible and reachable birds will alter their heading and fly towards the thermal. If the destination is actually in view and in reach, birds will fly towards the destination and not re-evaluate their selection. Other (less strong) assumptions are that birds can detect thermals over a fixed distance and that birds can be characterised by a parameter set (parameters like lift to drag ratio and a climbing efficiency) which is fixed over time. With respect to the thermal field the major assumptions and simplifications are that thermals have static cylindrical shapes with fixed locations and possess constant properties (a constant lift, diameter and height). We think that generalizing with respect to these properties would not change the conclusions with regard to the difference between social and non-social behaviour.

The argument could be made that the birds in Simsoar are unrealistically perfect with respect to both long-range navigation skills and thermal selection. However, white storks return to the same nest and the same wintering sites year after year. So it can be argued that, at the large scale, white storks navigate perfectly (Berthold et al., 2004). At the small scale, birds may in fact make even better decisions than currently possible in Simsoar because they adjust their selection of thermals more dynamically, for example while already climbing in a thermal or while gliding towards a target (Leshem and Yom-Tov, 1996b; Liechti et al., 1996). Also with respect to this point we do not see a direct consequence for the difference between social and non-social behaviour.

In nature, the properties of thermals vary over space and time. Variability in convective conditions and the influence of wind and topography make travel via straight paths and the establishment of optimal flight strategies more difficult. In the case of static bird properties and flight mechanics, variability in convective conditions and wind would lead to less optimal results with regard to relative distance travelled. However, in nature birds have the ability to vary their flight behaviour to compensate for environmental heterogeneity. For example, some soaring species may try to optimize their cross country speed by adjusting their inter-thermal glide speed (Pennycuick, 1998; Spaar and Bruderer, 1997), although a field study did not show evidence of this behaviour in white storks (Liechti et al., 1996). Soaring birds can change their gliding performance by altering their wing span and shape (Tucker, 1987) or the spread of their outer primaries (Tucker, 1995) or tail feathers. This kind of heterogeneity and birds' response to it would not influence the difference between social or non-social behaviour. However, if variability in thermal convection is considerable and birds can evaluate thermal lift in a distant thermal by considering other individuals, a clear advantage of social over non-social decision rules may appear: thermals with on average a higher lift (hence a faster travel speed) may be selected via social decision rules. In this last case there would probably not be an effect on the number of thermals visited and relative distance travelled, but rather total time travelled would be influenced. When including heterogeneous thermal lift indices in Simsoar, total time travelled would not be related directly to relative distance travelled anymore.

6.4. Possibilities for model extension

Most of the model assumptions can be relaxed through relatively simple model extensions. However, we do not suggest to simply implement all these extensions because, with the present state of knowledge, many of these would not be based on observational evidence but rather comprise empirical relations with very uncertain parameter values. Under these circumstances adding extra model details would lead to confusion rather than enlightenment. We would rather promote a thoughtful gathering of additional observations on part of the system, followed by model extensions. We will describe some of the most promising extensions and the required observations for them.

The inclusion of wind is an extension that will have to be introduced in Simsoar to relate the model results to field observations. Although the physical impact of wind on flight speed and direction does not require any new research or observations since this constitutes pure geometry, the extent to which soaring birds will adjust their behaviour to wind is predominantly unknown (but see Alpert et al., 2000; Shamoun-Baranes et al., 2003b; Thorup et al., 2003). The introduction of wind will impact thermal convection (Stull, 1988). When including wind in Simsoar, it would be logical to add (partial) compensation and to make the inter-thermal glide speed (v_g in Eq. (2)) variable. A third item that would be worth considering in relation to the inclusion of wind is the possibility that soaring birds occasionally use flapping flight. Both the relations to describe the inter-thermal glide speed as well as the choice between flapping and gliding flight could be based on flight energetics theory (Hedenstrom, 1993; Pennycuick, 1998; Shamoun-Baranes and van Loon, 2006) and further supported by field observations of variability in glide performance and flight strategy through high-frequency GPS-tags with built-in accelerometer.

With respect to bird behaviour there are several ways by which the model could be extended and be made more realistic. As explained in the previous sub-section, birds could select thermals based on observing thermal lift that other birds experience in a nearby thermal and evaluate whether it is advantageous to glide to that thermal. The behaviour with respect to leaving thermals could be extended with options to leave a thermal as soon as an opportunity arises to reach another thermal. This could potentially lead to increased migration speeds in comparison to those predicted by Simsoar in its current form. This extension seems especially worth implementing, because for some species observations are available about the actual heights where soaring birds leave thermals in combination with actual thermal depth (e.g. Shamoun-Baranes et al., 2003a; Shannon et al., 2002a).

Another set of decision rules could be introduced to deal with re-evaluation of flight-direction continuously during a gliding phase (instead of evaluating flight direction only when leaving a thermal). Also in this case observations on the actual change of direction during the gliding phase of birds would be required before implementing these extensions. Furthermore, birds do perhaps initially not glide towards other thermals when leaving a thermal but may choose a direction in relation to the directions chosen by other individuals. For example, field observations of white pelicans show very structured formation gliding between thermals

(Pennycuick, 1972; Weimerskirch et al., 2001), which could further facilitate the locating of thermals.

In this study, thermals have constant properties throughout a simulation and regular cylindrical shapes with an internally constant lift index. However, in nature the properties of thermals are dynamic and heterogeneous. An individual thermal may exist for a limited time span and properties such as the lift index are not constant along the vertical and horizontal axis of a thermal (Stull, 1988). The convective boundary layer (which can be considered as a population of thermals) has dynamic properties that can be described at a temporal resolution of hours. Therefore, an obvious extension of Simsoar would be to provide the properties of thermal convection such as thermal depth and strength during the course of a day by incorporating a convection boundary layer model (Allen, 2006; Shamoun-Baranes et al., 2003a; Shannon et al., 2002b). To be effective, such a model would have to be tuned to the atmospheric conditions and landscape properties of the region of interest and checked independently from the other processes in Simsoar. For that purpose, observations would be required on the longevity, strength and shape of thermals in the field or, indirectly, by monitoring the (variability in) thermal and sensible heat fluxes.

In conclusion we would like to emphasize that in its current form Simsoar is a tool to study soaring bird migration for various species, and as such it is instrumental for some of the aims and research questions that require a more integrative research approach (Bauer et al., 2009; Bowlin et al., 2010). However, it can with relative ease be adapted to study a wider variety of bird movements, ranging from the searching behaviour of soaring scavengers (Deygout et al., 2009; Jackson et al., 2008) to goal oriented movement in general where thermals are replaced by suitable stopover habitat (Klaassen et al., 2006). The model may also have several applications for conservation. For example, the model can be used to assess the potential risk that wind turbine parks (Barrios and Rodriguez, 2004) and power lines (Janss, 2000) may pose for birds under varying atmospheric conditions. Furthermore, if social behavioural increases migration efficiency then population size (and isolation from other populations) may indirectly influence migration success and survival. This can be particularly relevant for the long term success of reintroduction projects of social birds (e.g. Berthold et al., 2000; Gouar et al., 2008; Schaub et al., 2004) and these interactions can be studied and scenarios tested with an IBM like Simsoar (Seddon et al., 2007). For anyone interested, the model code is available as supplement to this paper (see Appendix A).

Acknowledgements

This study was facilitated by the BiG Grid Infrastructure for eScience. The authors wish to thank Volker Grimm for an early review and helpful suggestions to implement the ODD template. Gil Bohrer is kindly acknowledged for checking the properties of the thermal fields used in our study. Yossi Leshem helped the authors by providing Fig. 1. Four anonymous reviewers provided very detailed and constructive comments to the original manuscript, leading to many improvements.

Appendix A

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2010.10.038.

References

Allen, M.J., 2006. Updraft model for development of autonomous soaring uninhabited air vehicles. In: Proceedings of the 44th AIAA Aerospace Sciences Meeting and Exhibit, American Institute of Aeronautics and Astronautics, Reno, Nevada.

Alon, D., Granit, B., Shamoun-Baranes, J., Leshem, Y., Kirwan, G.M., Shirihai, H., 2004. Soaring-bird migration over northern Israel in Autumn. British Birds 97, 160–182.

Alpert, P., Tannhauser, D.S., Leshem, Y., Kravitz, A., Rabinovitch-Hadar, M., 2000. Migrating soaring birds align along sea-breeze fronts; First evidence from Israel. Bulletin of the American Meteorological Society 81, 1599–1601.

Barrios, L., Rodriguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. Journal of Applied Ecology 41, 72–81.

Bauer, S., Barta, Z., Ens, B.J., Hays, G.C., McNamara, J.M., Klaassen, M., 2009. Animal migration: linking models and data beyond taxonomic limits. Biology Letters 5, 433–435.

Berthold, P., 2001. Bird Migration: A General Survey. Oxford University Press, Oxford.

Berthold, P., Fiedler, W., Querner, U., 2000. White stork (*Ciconia ciconia*) migration studies: basic research devoted to conservation measures. Global Environmental Research 4, 133–141.

Berthold, P., Kaatz, M., Querner, U., 2004. Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. Journal of Ornithology 145, 356–359.

Berthold, P., van den Bossche, W., Jakubiec, Z., Kaatz, C., Kaatz, M., Querner, U., 2002. Long-term satellite tracking sheds light upon variable migration strategies of White Storks (Ciconia ciconia). Journal Fur Ornithologie 143, 489–493.

Bildstein, K.L., Zalles, J.I., 2005. Old world versus new world long-distance migration in accipiters, buteos, and falcons. The interplay of migration ability and global biogeography. In: Greenberg, R., Marra, P.P. (Eds.), Birds of Two Worlds: The Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, pp. 154–167.

Bouwman, A.W., Azzalini, A., 1997. Applied Smoothing Techniques for Data Analysis: The Kernel Approach with S-Plus Illustrations. Oxford University Press, Oxford.

Bowlin, M.S., Bisson, I.-A., Shamoun-Baranes, J., Reichard, J.D., Sapir, N., Marra, P.P., Kunz, T.H., Wilcove, D.S., Hedenström, A., Guglielmo, C.G., Åkesson, S., Ramenofsky, M., Wikelski, M., 2010. Grand Challenges in Migration Biology. Integrative and Comparative Biology 50, 261–279.

Brandes, D., Ombalski, D.W., 2004. Modeling raptor migration pathways using a fluid-flow analogy. Journal of Raptor Research 38, 195–207.

Burfield, I., Bommel, F.v. (Eds.), 2004. Birds in Europe: Population Estimates, Trends and Conservation Status. BirdLife International, Cambridge.

Chernetsov, N., Berthold, P., Querner, U., 2004. Migratory orientation of first-year white storks (Ciconia ciconia): inherited information and social interactions. Journal of Experimental Biology 207, 937–943.

Deygout, C., Gault, A., Sarrazin, F., Bessa-Gomes, C., 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. Ecological Modelling 220, 1826–1835.

Draper, N.R., Smith, H., 1998. Applied Regression Analysis. John Wiley & Sons, New York.

Fuller, M.R., Seegar, W.S., Schueck, L.S., 1998. Routes and travel rates of migrating Peregrine Falcons Falco peregrinus and Swainson's Hawks *Buteo swainsoni* in the western hemisphere. Journal of Avian Biology 29, 433.

Gouar, P.L., Robert, A., Choisy, J.-P., Henriquet, S., Lecuyer, P., Tessier, C., Sarrazin, F., 2008. Roles of survival and dispersal in reintroduction success of griffon vulture (*Gyps fulvus*). Ecological Applications 18, 859–872.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling 115, 129–148.

Grimm, V., Railsback, S.F., 2005. Individual-based Modeling and Ecology. Princeton University Press, Princeton.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Muller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198, 115–126.

Haney, J.C., Fristrup, K.M., Lee, D.S., 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. Ornis Scandinavica 23, 49–62.

Hedenstrom, A., 1993. Migration by soaring or flapping flight in birds—the relative importance of energy-cost and speed. Philosophical Transactions of the Royal Society of London Series B—Biological Sciences 342, 353–361.

Iman, R.L., Helton, J.C., 1988. An investigation of uncertainty and sensitivity analysis techniques for computer models. Risk Analysis 8, 71–90.

Jackson, A.L., Ruxton, G.D., Houston, D.C., 2008. The effect of social facilitation on foraging success in vultures: a modelling study. Biology Letters 4, 311–313.

Janss, G.F.E., 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biological Conservation 95, 353–359.

Jarque, C.M., Bera, A.K., 1987. A test for normality of observations and regression residuals. International Statistical Review/Revue Internationale de Statistique 55, 163–172.

Kerlinger, P., 1989. Flight Strategies of Migrating Hawks. The University of Chicago Press, Chicago.

Klaassen, R.H.G., Nolet, B.A., van Gils, J.A., Bauer, S., 2006. Optimal movement between patches under incomplete information about the spatial distribution of food items. Theoretical Population Biology 70, 452–463.

Leshem, Y., Yom-Tov, Y., 1996a. The magnitude and timing of migration by soaring raptors, pelicans and storks over Israel. Ibis 138, 188–203.

Leshem, Y., Yom-Tov, Y., 1996b. The use of thermals by soaring migrants. Ibis 138, 667–674.

Leshem, Y., Yom-Tov, Y., 1998. Routes of migrating soaring birds. Ibis 140, 41–52.

Liechti, F., Ehrich, D., Bruderer, B., 1996. Flight behaviour of white storks *Ciconia ciconia* on their migration over southern Israel. Ardea 84, 3–13.

Mandel, J.T., Bildstein, K.L., Bohrer, G., Winkler, D.W., 2008. Movement ecology of migration in turkey vultures. Proceedings of the National Academy of Sciences 105, 19102–19107.

Moussa, R., 2008. What controls the width function shape, and can it be used for channel network comparison and regionalization? Water Resources Research 44, W08456.

Pennycuick, C.J., 1972. Soaring behaviour and performance of some east African birds, observed from a motor-glider. Ibis 114, 178–218.

Pennycuick, C.J., 1989. Bird Flight Performance: A Practical Calculation Manual. Oxford University Press, Oxford.

Pennycuick, C.J., 1998. Field observations of thermals and thermal streets, and the theory of cross-country soaring flight. Journal of Avian Biology 29, 33–43.

Reynolds, C.W., 1987. Flocks, herds and schools: a distributed behavioral model. ACM SIGGRAPH Computer Graphics 21, 25–34.

Saltelli, A., Chan, K., Scott, E.M., 2000. Sensitivity Analysis. Wiley Series in Probability and Statistics. John Wiley & Sons, Chichester, England.

Seddon, P.J., Armstrong, D.P., Maloney, R.F., 2007. Developing the science of reintroduction biology. Conserv. Biol. 21, 303–312.

Schaub, M., Pradel, R., Lebreton, J.-D., 2004. Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? Biological Conservation 119, 105–114.

Shamoun-Baranes, J., van Loon, E., 2006. Energetic influence on gull flight strategy selection. Journal of Experimental Biology 209, 3489–3498.

Shamoun-Baranes, J., Bouten, W., vanLoon, E., 2010. Integrating meteorology into research on migration. Integrative and Comparitive Biology 50, 280–292.

Shamoun-Baranes, J., Leshem, Y., Yom-Tov, Y., Liechti, O., 2003a. Differential use of thermal convection by soaring birds over central Israel. Condor 105, 208–218.

Shamoun-Baranes, J., van Loon, E., Liechti, F., Bouten, W., 2007. Analyzing the effect of wind on flight: pitfalls and solutions. Journal of Experimental Biology 210, 82–90.

Shamoun-Baranes, J., Baharad, A., Alpert, P., Berthold, P., Yom-Tov, Y., Dvir, Y., Leshem, Y., 2003b. The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. Journal of Avian Biology 34, 97–104.

Shannon, H.D., Young, G.S., Yates, M.A., Fuller, M.R., Seegar, W.S., 2002a. American White Pelican soaring flight times and altitudes relative to changes in thermal depth and intensity. Condor 104, 679–683.

Shannon, H.D., Young, G.S., Yates, M.A., Fuller, M.R., Seegar, W.S., 2002b. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. Boundary-Layer Meteorology 104, 167–199.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. W.H. Freeman and Co., New York.

Spaar, R., Bruderer, B., 1997. Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. Behavioral Ecology 8, 288–297.

Stull, R.B., 1988. An Introduction to Boundary Layer Meteorology. Kluwer Academic Publishers, Dordrecht.

Thorup, K., Alerstam, T., Hake, M., Kjellén, N., 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. The Royal Society Biology Letters 270, 8–11.

Tucker, V.A., 1987. Gliding birds: the effect of variable wing span. Journal of Experimental Biology 133, 33–58.

Tucker, V.A., 1995. drag reduction by wing tip slots in a gliding harris hawk, Parabuteo-Unicinctus. Journal of Experimental Biology 198, 775–781.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., Jiraskova, S., 2001. Energy saving in flight formation—Pelicans flying in a ‘V’ can glide for extended periods using the other birds’ air streams. Nature 413, 697–698.