Stigmergy as a mechanism to produce collective vortex behaviours: a study case in shoveler ducks

ZOOLOGY 2014

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Taking in sufficient quantities of nutrients is vital for all living beings. In doing so, individuals typically reduce local nutrient availability and thereby affect the local resource environment. Some collective behaviours are suspected to improve ability or efficiency for individuals to exploit nutrient resources. Interestingly, feeding animal groups can also impact the resource landscape beyond simply depleting it, and can do so even just by their displacement.

Northern shoveller duck (*Anas clypeata*, Anatidae) is a species of dabbling duck which is highly specialized for filter-feeding on zooplankton. Shovellers display a range of behaviours whilst filter-feeding (Fig.1). In shallow water, they adopt swirling and vortex behaviours, helping to raise prey items to the surface and therefore within the birds' reach. We briefly introduce a model of interactions between feeding individuals and the resource landscape inspired by these duck behaviours, and focus on the emergent movement dynamics resulting from these interactions.

The model

The key assumption and novelty of our model is that, as well as nutrient consumption, individuals can cause the release of additional nutrients. In this way, individuals leave a trace in the environment that affects the actions of other individuals, thereby leading to indirect interactions via the resource landscape. This presents a mechanism of indirect coordination between individuals, a concept called 'stigmergy'. The boxes below define the model rules.

Box 1: Individual behaviour:

$x_i(t+\Delta t) = x_i(t) + v_i(t+\Delta t)\,\Delta t$ => Individual position

$v_i(t+\Delta t) = v_i(t) + F_{i(all)}(t)\,\Delta t$ => Individual velocity

$F_{i(all)}(t) = Fi_{(drag)}(t) + Fi_{(avoid)}(t) + F_{i(food)}(t) + F_{i(stoch)}(t)$ => Force acting on individual

with

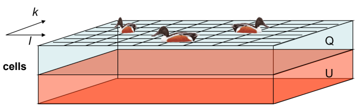
$F_{i(drag)}(t) = -\gamma\, v_i(t)$ => Friction force

$F_{i(avoid)}(t) = \Sigma j{\neq}i\ \theta(r - dij)\ (xi(t)-xj(t))\ /\ |(xi(t)-xj(t))|$ => Short range interactions with others

$F_{i(stoch)}(t)$ => Stochastic force

$F_{i(food)}(t)$ => Attraction to the highest nutrient gradient within sensory range *R*

Box 2: Environment dynamics:



Two nutrient fields:

$Q_{k,l}$ is directly available to foraging individuals

$U_{k,l}$ encapsulates the underlying distribution of nutrients not directly available

$$
\begin{aligned}
Q_{k,l}(t+\Delta t) = \ & Q_{k,l}(t) \\
& + \delta_{infuse}\,\Delta t\, U_{k,l}(t) && \text{Diffusion } U \to Q \\
& - \delta_{decay}\,\Delta t\, Q_{k,l}(t) && \text{Decantation } Q \to U \\
& + \delta_{diffuse}\,\Delta t\,[(Q_{k+1,l}(t) + Q_{k-1,l}(t) + Q_{k,l+1}(t) + Q_{k,l-1}(t)) - 4\,Q_{k,l}(t)] && \text{Diffusion in } Q \\
& + \delta_{disturb}\,\Delta t\,\Sigma j\ \psi(k,l,j)\,|v_j(t)|\,Uk,l(t) && U \to Q \text{ due to duck activity} \\
& - \delta_{deplete}\,\Delta t\,\Sigma j\ \psi(k,l,j)\,Q_{k,l}(t) && \text{Removal from } Q \text{ due to food intake}
\end{aligned}
$$

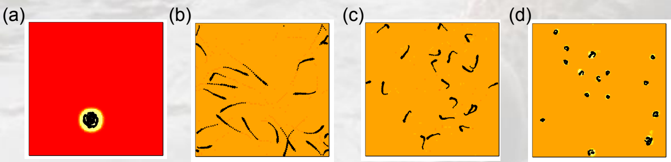
$$
U_{k,l}(t+\Delta t) = \underbrace{\delta_{decay}\,\Delta t\, Qk,l(t)}_{\text{Decantation } Q \to U} - \underbrace{\delta_{infuse}\,\Delta t\, U_{k,l}(t)}_{\text{Diffusion } U \to Q} - \underbrace{\delta_{disturb}\,\Delta t\,\Sigma j\ \psi(k,l,j)\,|v_j(t)|\,U_{k,l}(t)}_{U \to Q \text{ due to duck activity}}
$$

Box 3: Brief description and values explored for all model parameters

Parameter	Values explored	Description
N	*20–500*	Number of individuals in the population.
L	*10 units*	Side-length of simulated space.
Δt	*0.1 s*	Length of time-step between model updates.
γ	$1.2\ s^{-1}$	Friction coefficient.
ξ	*1.0 units*	Maximum length for stochastic component of individual behaviour.
r	*0.3 units*	Interaction radius for short range repulsion between individuals.
R	*0.5 units*	Sensory range over which individuals detect nutrient field gradients.
δ_{infuse}	$0.001\ s^{-1}$	Controls the rate at which nutrients become available from *U* into *Q*.
δ_{decay}	$0.1\ s^{-1}$	Controls the rate at which nutrient decay from *Q* into *U*.
$\delta_{deplete}$	$0–1\ s^{-1}$	Controls the rate at which individuals deplete local nutrients (removed from system)
$\delta_{diffuse}$	$0.001\ s^{-1}$	Controls the rate at which nutrients diffuse in *Q*.
$\delta_{disturb}$	$0–1\ s^{-1}$	Strength of the impact individual movement has on making nutrients available from *U* into *Q*.

Results:

1. Different group dynamics



(a) 'Vortex' — $\delta_{deplete} = 1$, $\delta_{disturb} = 0.01$

(b) Linear trajectory — $\delta_{deplete} = 1$, $\delta_{disturb} = 0$

(c) Tortuous trajectory — $\delta_{deplete} = 1$, $\delta_{disturb} = 0.01$

(d) Swirling — $\delta_{deplete} = 1$, $\delta_{disturb} = 0.1$

Fig.2: Illustration of different group dynamics obtained from simulation of 20 individuals. *We show the distribution of available nutrient Q at the end of a 20 sec simulation. Individual trajectories over the last 1.5 sec are shown in black. Lighter background colours, consistent across a-d, correspond to higher nutrient concentrations in Q. (a) 'vortex' around an area of high underlying nutrient concentration. Nutrient in U are initially concentrated in one patch. (b)-(d)have initially homogeneous underlying nutrient field U.*

→ Spatial food distribution affects directly behaviours.

→ More tortuous individual paths and higher levels of aggregation can be seen in populations in homogeneous environments where individual movement makes nutrients available.

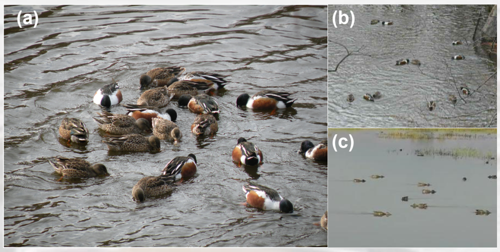


Fig.1: Illustration of three types of feeding behaviour observed in Northern shovellers (Anas clypeata). *(a) A large group of Shovellers swim head to tail in a compact vortex formation. The pictures show that most individuals have their beak in the water and are actively filtering the water, illustrating that nutrients are available close to the water surface. (b) Individual birds and small groups of birds swim in tight circles. (c) The individual trajectories are approximately linear and individuals are relatively distant from each other.*

2. Depleting the nutrient field

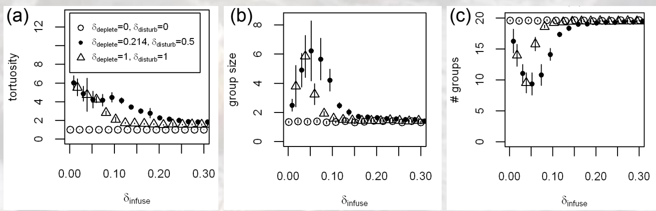


Fig.3: The effect of depleting the nutrient field: *(a) on the tortuosity of individual movement, (b) the size of the largest group, and (c) the number of groups in the population. N =20 individuals, initial homogeneous underlying nutrient field U, and δ_{infuse} varies from 0 to 0.3. We show averages over the last 50 seconds of simulation time (on 300 sec) and report the mean over 10 replicate simulations. We explore three different parameter combinations of $\delta_{deplete}$ and $\delta_{disturb}$. error bars: +/−1 s.d.*

→ The rate at which nutrients become available from U to Q have a direct effect on behaviours.

→ Combination of high values of δdeplete and δinfuse lead to a faster local depletion of nutrients; the behaviours rapidly become the same as when individuals do not interact with the nutrient field.

→ Local depletion of nutrients induces aggregations because of, in a finite environment, the reduction of the space individual prefer to occupy.

3. Population density

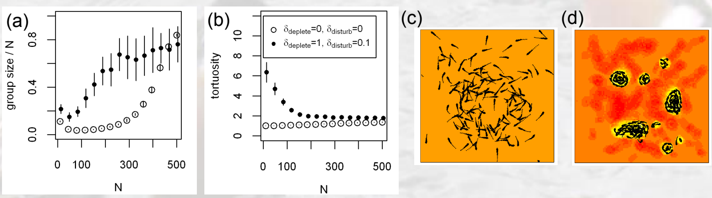


Fig.4: The effect of increasing the population density. *In (a-b) we show mean values over 15 simulations (error bars:+/−1 s.d.). We explore two different parameter combinations: ($\delta_{deplete}$, $\delta_{disturb}$) = (0, 0) as a base-line (individuals do not interact with nutrient field) and (δdeplete, δdisturb) = (1, 0.1). (a) the size of the largest group in the population normalised by the population size N. Panel (b) shows the tortuosity of individual movement. (c,d) Movement dynamics and available nutrient field Q for N = 150 at the end of a 300 second simulation, showing the last second of each individual trajectory. In (c) we show the case when ($\delta_{deplete}$, $\delta_{disturb}$) = (0, 0) and in (d) we show log values of the available nutrient field Q for the case ($\delta_{deplete}$, $\delta_{disturb}$) = (1, 0.1). Lighter background colours indicate higher levels of available nutrients in Q. The darker regions in (d) show that the separate groups move slowly through the environment and 'graze' the available nutrients. All simulations start from a homogeneous underlying nutrient field U.*

→ Interactions of individuals with the nutrients fields promote aggregation.

→ The largest group size (normalised by the population size *N*) increases faster than in the base-line case, but seems to saturate for large *N*.

→ High density of interacting individuals induce vortex behaviours.

Discussion & Conclusions

→ Restricted social interactions to collision avoidance and indirect interactions via the nutrient field can result in varied movement dynamics.

→ We demonstrate that stigmergy is a potential mechanism to induce collective vortex behaviours.

→ Movement dynamics change when local nutrient sources are depleted or when the population density increases.

More information: further details, results and discussion are available on this open-access publication: **Bode NWF, Delcourt J (2013)** Individual-to-Resource Landscape Interaction Strength Can Explain Different Collective Feeding Behaviours. ***PLoS ONE*** **8(10): e75879. doi:10.1371/journal.pone.0075879**

Acknowledgements*:* NWFB is supported by an AXA research fellowship and JD is supported by the F.R.S.-FNRS (Fonds de la Recherche Scientifique, Belgium, FRFC grant 2.4.617.08F). The funders had no role in study design, data collection and analysis, decision to publish. Pictures in Fig.1 (a,b) by Johann Delcourt, location: Central Park, New-York City, USA, winter 2012. Picture in Fig.1(c) by Larry Jordan, location: Sacramento National Wildlife Refuge, California, USA, late summer 2011.