How birds weather the weather: avian migration in the mid-latitudes

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The FLow-Assistance Trajectory model (i.e. FLAT model) comprises a set of coupled differential equations which describe displacement of an individual animal over the surface of the Earth. Here we present the solutions of the discretized form of the equations. All angles and directions are considered in radians, locations in latitude and longitude, distances in meters, and speeds in meters per second.

We start by describing the forward ($M_{F,t}$) and sideways movement ($M_{S,t}$) of an animal in relation to its preferred direction of movement ($\alpha_t$). In general, $M_{F,t}$ and $M_{S,t}$ are functions of $\alpha_t$, north/south ($v_t$) and east/west ($u_t$) flow components describing the direction into which the flow is moving (north and east being positive, respectively), and possible other variables that describe aspects of the animal’s strategy, behavior, or capabilities. Hence, $M_{F,t} = f(u_t, v_t, \alpha_t, \ldots)$ and $M_{S,t} = g(u_t, v_t, \alpha_t, \ldots)$. The specific form of the function for $M_{F,t}$ and $M_{S,t}$ depend on (known or assumed) prior assumptions about the animal’s behavior. In FLAT these assumptions are cast in various flow-assistance equations. The following equations are distinguished.

\begin{align*}
\text{EQ}^{\text{FlowSpeed}} \\
M_{S,t} &= (y_t + z_t) \cdot \sin(\theta_t) \\
M_{F,t} &= (y_t + z_t) \cdot \cos(\theta_t) \\
\text{EQ}^{\text{NegFlowSpeed}} \\
M_{S,t} &= (y_t - z_t) \cdot \sin(\theta_t)
\end{align*}
\( M_{F,t} = (y_t - z_t) \cdot \cos(\theta_t) \)

**EQ Tailwind**
\[
M_{S,t} = y_t \sin(\theta_t) \\
M_{F,t} = z_t + y_t \cos(\theta_t)
\]

**EQ Groundspeed**
\[
M_{S,t} = 0 \\
M_{F,t} = x_t
\]

**EQ M. Groundspeed**
\[
M_{S,t} = 0 \\
M_{F,t} = z_{p,t} + y_t \cos(\theta_t)
\]

**EQ Airspeed**
\[
M_{S,t} = 0 \\
M_{F,t} = y_t \cos(\theta_t) + \sqrt{z_t^2 - (y_t \sin(\theta_t))^2}
\]

**EQ Partial Speed**
\[
M_{S,t} = (1 - f) \cdot y_t \sin(\theta_t) \\
M_{F,t} = y_t \sin(\theta_t) + \sqrt{z_t^2 - (f \cdot y_t \sin(\theta_t))^2}
\]

where the components of these equations use the following naming conventions

- \( y_t \) = the flow speed of the fluid medium
- \( \phi_t \) = the direction into which the flow is moving, hence \( \phi_t = \begin{cases} 
\tan^{-1} \left( \frac{u_t}{v_t} \right); & v_t \geq 0 \& u_t \neq 0 \text{ or } v_t > 0 \& u_t = 0 \\
\pi + \tan^{-1} \left( \frac{u_t}{v_t} \right); & v_t < 0 \\
\alpha_t; & v_t = 0 \& u_t = 0
\end{cases} \)
- \( \theta_t = \phi_t - \alpha_t \) or the angular difference between flow direction and preferred direction of movement
- \( x_t \) = the animal’s speed relative to the fixed earth (i.e. its groundspeed)
- \( z_t \) = the animal’s speed relative to the flow (i.e. its relative speed)
- \( z_{p,t} \) = the animal’s *preferred* relative speed, possibly different from \( z_t \)
\( f = \) the proportion of compensation for displacement from \( \alpha_t \)

At minimum, each flow-assistance equation requires specification of \( v_t, u_t, \alpha_t, \) and one of either \( x_t, z_t, \) or \( z_{p,t}. \)

After calculating forward and sideways movement relative to \( \alpha_t, \) we calculate – over a small time interval (\( \Delta t \)) – the actual direction of movement or ‘bearing’ (\( \gamma_t \)) from \( M_{S,t}, M_{F,t}, \) and \( \alpha_t \) as follows.

\[
\gamma_t = \begin{cases} 
\alpha_t + \tan^{-1} \left( \frac{M_{S,t}}{M_{F,t}} \right); & M_{F,t} \geq 0 \land M_{S,t} \neq 0 \lor M_{F,t} < 0 \land M_{S,t} = 0 \\
\alpha_t + \pi \tan^{-1} \left( \frac{M_{S,t}}{M_{F,t}} \right); & M_{F,t} = 0 \land M_{S,t} = 0 \\
\alpha_t + 0; & M_{F,t} < 0 \\
\end{cases}
\]

Also, the distance traveled along \( \gamma_t \) over the time increment \( \Delta t \) (\( d_t \)) is

\[
d_t = \sqrt{M_{S,t}^2 + M_{F,t}^2}
\]

The values of the direction of movement (\( \gamma_t \)) and the distance traveled (\( d_t \)) can be combined in the Haversine formula to calculate displacement over the Earth’s surface (Vavrek 2011).

The latitude coordinate (\( \text{lat} \)) of the animal at time \( t + \Delta t \) is calculated as

\[
\text{lon}_{t+\Delta t} = \left((\text{lon}_t + d\text{lon}_{\Delta t} + \pi) \mod 2\pi\right) - \pi
\]

where ‘mod’ indicates a modulo operation to find the remainder of a division of the value on the left by the value on the right, and the change in longitude (\( d\text{lon}_{\Delta t} \)) is given by

\[
d\text{lon}_{\Delta t} = \begin{cases} 
\tan^{-1} \left( \frac{Y_t}{X_t} \right); & X_t \geq 0 \land Y_t \neq 0 \lor X_t > 0 \land Y_t = 0 \\
\pi + \tan^{-1} \left( \frac{Y_t}{X_t} \right); & X_t < 0 \\
0; & X_t = 0 \land Y_t = 0
\end{cases}
\]

where

\[
Y_t = \sin(\gamma_t) \cdot \sin \left( \frac{d_t}{R} \right) \cdot \cos\text{(lat}_t) \\
X_t = \cos \left( \frac{d_t}{R} \right) - \sin\text{(lat}_t) \cdot \sin(\text{lat}_{t+\Delta t})
\]

At this stage, location (\( \text{lon}_{t+\Delta t}, \text{lat}_{t+\Delta t} \)) becomes the current location (\( \text{lon}_t, \text{lat}_t \)), and the iterative calculation starts over. At each (new) location (\( \text{lon}_t, \text{lat}_t \)), the flow field (\( v_t, u_t \)) may differ from the previous values. As well, the behavior of the animal, for example its preferred direction of movement (\( \alpha_t \))
and/or preferred relative speed \( (z_{p,t}) \), may change over time (i.e. during the course of the migration path) and may be updated.

The FLAT model is implemented in the RNCEP package (see Chapter 2). This package contains functions to access and manipulate global weather data from the National Centers for Environmental Prediction (NCEP) / National Center for Atmospheric Research (NCAR) Reanalysis dataset (Kalnay et al., 1996) and the NCEP / Department of Energy (DOE) Reanalysis II dataset (Kanamitsu et al., 2002).