# Energy landscapes, stopover networks and reproductive constraints: a mathematical framework in the Arctic bird migration under Climate Change

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## Abstract

Arctic-breeding waterbirds depend on fat stores gained at stopover sites during spring migration, and climate change is altering the winds, food timing and wetland quality along their routes. We present a compact mathematical model of spring migration from a wintering area to an Arctic breeding site, built to test five hypotheses about how these changes act on migration energetics and reproduction. The model combines a fat-dependent flight equation with wind, a stopover module in which food availability follows the spring green wave, probabilistic route choice over a network of eight wetlands, and a reproductive module limited by fat, calcium and arrival time relative to snowmelt. Energetic outcomes are linked to population growth rate (λ) through a three-stage projection matrix. We simulated a generic goose-sized bird of about 2 kg under seven scenarios. Single perturbations (weaker tail-winds, an earlier spring, or degraded western wetlands) were buffered, reducing arrival probability by about 1 percentage point and λ by 1–2%. Combined, they reduced arrival probability from 0.99 to 0.79 and λ from 1.00 to 0.78, about five times the sum of the single effects. Degrading the western corridor shifted the mean initial heading by 15° and concentrated birds at a previously minor eastern site. Calcium-poor northern staging sites reduced reproduction by 20% without affecting arrival. Advancing departure by 10 days compensated for a spring up to 20 days earlier, whereas a 10% decline in fat deposition reduced expected reproduction by 15%. All parameters are assumed, so results are comparisons between scenarios rather than predictions.

**Keywords:** migration energetics; energy landscape; route choice; phenological mismatch; capital breeding; calcium; avian influenza; climate change

## 1. Introduction

Most bird species that breed in the Arctic are migratory. Migration is shaped by both environmental and physiological constraints. Fat is the main fuel of migrants, so migration can be imagined as movement through an energy landscape in which fat declines continuously in flight and increases at stopovers (Guglielmo 2018; Shepard et al. 2013). Wind, temperature and the timing of food availability all change along the route (Liechti 2006; Shamoun-Baranes et al. 2010), and all are affected by climate change. Dynamic models and tracking studies show that changes at stopover sites alter migration schedules and fitness in Arctic geese (Bauer et al. 2008; Jonker et al. 2010; Lameris et al. 2018). Wetland loss can also shift migration routes, concentrating birds at fewer or previously minor sites, with consequences for both refuelling and disease exposure (Gilbert et al. 2006). Rather than modelling a particular species or flyway, we reconstruct the main climate-sensitive factors acting on migration within a hypothetical scenario, using a generic goose-like bird and a stylised wetland network.

Migration also sets the conditions for breeding. Many Arctic geese are capital breeders that rely on reserves carried north to produce and incubate eggs (Drent & Daan 1980), so the fat and nutrients a female carries on arrival, and the timing of her arrival relative to snowmelt, determine her reproductive output. Energy is not the only constraint: calcium for eggshells can limit clutch size and shell quality where it is scarce (Graveland & Drent 1997).

This paper builds a simple model that treats metabolism, flight, stopover and route choice as separate questions, lets route geometry respond to habitat loss, and carries individual energetic states through to fitness and population growth rate.

We test five hypotheses about how climate change acts on migration energetics. Each is stated here and answered in Section 5.

**H1 — Non-additive climate effects.** Consider a migration in which climate change acts on three parts of the journey at once: weaker tail-winds along the route, an earlier spring (food peaks at the stopover sites and snowmelt at the breeding site both advance, while departure from the wintering area does not), and the degradation of stopover wetlands. Each change on its own delays the birds only slightly, and the delay can be absorbed because females usually arrive with some time to spare before the breeding season closes. We hypothesise that when the three changes occur together, their delays add up and exhaust this margin, so that the probability of completing migration and the population growth rate (λ) fall by more than the sum of the losses caused by each change alone.

**H2 — Corridor switching.** Loss or degradation of the highest-quality stopovers rotates the mean heading of migrants and concentrates them at previously minor sites, by an amount that grows with how closely birds follow least-energy routes ($\beta$).

**H3 — Micronutrient decoupling.** Arriving on time and with enough fat may not be sufficient for a female to breed. Egg production also requires micronutrients, above all calcium for eggshells, which females must take up at the northern staging sites in the days before laying. We hypothesise that where these sites are poor in calcium, reproductive output falls even though arrival probability, arrival date and fat reserves are unchanged, so that a model based on energy alone would miss the loss. Reproduction is assumed to be set by whichever resource is scarcest (fat, calcium or timing). Magnesium may act as a second limit in the same way, but it

is included here only as a possibility and is not simulated.

**H4 — Conditional compensation.** When spring advances, food peaks at the stopover sites and snowmelt at the breeding site occur earlier, and birds that keep their usual departure date arrive late. We hypothesise that leaving the wintering area earlier can offset this loss. In nature, however, birds can only advance departure if the cues available at the wintering site, such as day length or local temperature, reliably predict conditions far to the north. The model tests the first part of this hypothesis by advancing departure directly; the reliability of cues is not simulated.

**H5 — Condition loss and selection.** If climate change makes food at stopover sites poorer or mistimed, birds will deposit fat more slowly. We hypothesise that this has two effects. First, females will reproduce less, whatever their departure date. Second, the cost of departing late will increase, so females that depart early will gain a larger advantage over late ones. This would strengthen natural selection for earlier departure. Whether populations can evolve in response depends on genetic variation in departure timing, which is not modelled here.

## 2. The model

The migration route is represented as a stylised network of nodes: a wintering area (W), eight stopover wetlands (S1–S8) and a breeding site (B). Each female is simulated individually as she moves from node to node. At any time she is described by her position, the day of the year, her fat mass $f$ and her calcium store $c$; her lean mass $m_L$ is assumed constant. The following sections describe how she spends fat in flight (2.1), gains fat at stopovers (2.2), chooses where to go next (2.3), and how her state on arrival determines reproduction and population growth (2.4).

### 2.1 Flight: a fat-dependent cost with wind

The energy needed to fly a distance $D$ is the cost of transport $\Gamma$ (dimensionless; metabolic energy per unit weight and distance) multiplied by weight and distance, and by a wind factor $\varphi = V_a/V_g$, where $V_a$ is airspeed and $V_g = V_a + w_{\parallel}$ is ground speed given the tail-wind component $w_{\parallel}$ along the leg (Pennycuick 2008; Liechti 2006):

$$E = \Gamma\, m\, g\, D\, \varphi, \qquad \varphi = \frac{V_a}{V_g} \tag{1}$$

Flight costs follow the standard formulation of Pennycuick (2008), extended with a wind factor. This part of the model links climate to the journey: it sets how much fat each leg requires under the wind of the day, which stopovers are within reach, and therefore when a bird can depart and where it can go.

As fuel is burnt, body mass declines during flight, so the cost per unit distance falls as the bird becomes lighter. With $\varepsilon$ the energy density of fat, mass changes with distance according to the equation below, which integrates to a Breguet-type range equation:

$$\frac{dm}{dD} = -\kappa\, \varphi\, m, \qquad \kappa = \frac{\Gamma g}{\varepsilon}$$

$$m_{arr} = m_{dep}\, e^{-\kappa \varphi D}, \qquad f_{arr} = m_{arr} - m_L \tag{2}$$

From Eq. (2) we obtain the fat a bird needs at departure to arrive with a safety reserve $f_s$, and its maximum range in still air (φ = 1):

$$f_{need} = (m_L + f_s)\, e^{\kappa \varphi D} - m_L, \qquad D_{\max} = \tfrac{1}{\kappa} \ln \tfrac{m_L + f_{\max}}{m_L + f_{\min}} \qquad (3)$$

### 2.2 Stopovers: fuel deposited in time

At stopover $j$ the bird gains fat at a rate set by habitat quality on that day; this rate saturates as the fat stores fill up to the maximum load:

$$\frac{df}{dt} = r_{\max} H_j(t) \left(1 - \frac{f}{f_{\max}}\right) \qquad (4)$$

where $r_{\max}$ is the maximum net deposition rate (Lindström 1991) and $H_j(t) \in [0, 1]$ is habitat quality. Spring food peaks move north at a finite speed, a pattern known as the green wave (van der Graaf et al. 2006), so habitat quality is

$$H_j(t) = q_j \left(1 - d_j\right) max \left\{0.1,\ e^{-\left(t - \tau_j\right)^2 / (2\sigma^2)}\right\}, \qquad \tau_j = \tau_0 - \delta + s\, y_j \qquad (5)$$

where $q_j$ is the baseline quality of site $j$, $y_j$ its northward distance from the wintering area, $\tau_j$ is the day of peak food, $s$ the delay per km northward, $\sigma$ the pulse width, $d_j$ the fraction of habitat lost to drying or degradation, and $\delta$ a climate-driven advance in phenology. Food availability never falls below 10% of its peak (the 0.1 in Eq. 5). A bird departs when $f \geq f_{need}$ for its intended leg given today's wind, so adverse winds delay departure (Richardson 1978). While at a stopover, a bird reconsiders its destination every seven days. For the last leg, the arrival requirement is raised from $f_s$ to the reproductive requirement $f_{req}$, and departure is not allowed earlier than three days before snowmelt $t_{melt}$.

### 2.3 Route choice over a wetland network

From node $i$ the bird chooses among feasible nodes $A_i(t)$: those at least 150 km farther north, not dry, and reachable with $f_{need} \leq f_{\max}$. Each candidate has an energetic value, in kg of fat equivalent, equal to the fuel expected to be gained there minus the fuel burnt to get there and onward to B:

$$U_{ij} = r_{\max} H_j \left(t + T_{ij}\right) T_{ref} \ - \ b\left(D_{ij}\right) \ - \ b\left(D_{jB}\right) \qquad (6)$$

with the fuel burnt on a leg of length $D$ given by

$$b(D) = (m_L + f_{nom}) \left(1 - e^{-\kappa D}\right)$$

where $T_{ij}$ is the flight time from $i$ to $j$, $T_{ref} = 7$ days is a reference stopover duration, and $f_{nom} = 0.3$ kg is a nominal fat load used to estimate flight costs. This is a least-energy path with habitat benefit, i.e. the energy landscape of Shepard et al. (2013) in network form. Birds are not perfect optimisers, so choice is probabilistic (a softmax or conditional-logit rule; McFadden 1974):

$$P_{ij} = \frac{\exp\left(\beta\, U_{ij}\right)}{\exp(\beta\, U_{ik})} \qquad (7)$$

where $\beta \to \infty$ gives the least-energy route and $\beta \to 0$ random choice. Because habitat quality changes over the season (Eq. 5), $P_{ij}$ also changes with $t$; habitat loss or drying removes or devalues nodes in Eq. (6). The response in heading is summarised by the circular mean of the compass bearings $\theta_{ij}$ of the legs, and its concentration:

$$\langle\theta\rangle = atan2\left(P_{ij} \sin\theta_{ij},\ P_{ij} \cos\theta_{ij}\right), \qquad \Lambda = |P_{ij}\, e^{\,i\theta_{ij}}|$$

### 2.4 Reproduction and population dynamics

Birds finance breeding in two ways. Income breeders produce their eggs from food found at the breeding site during breeding. Capital breeders instead produce and incubate their eggs using reserves built up earlier, so what they carry on arrival matters more than what they find there (Drent & Daan 1980). Many Arctic-breeding geese are close to the capital end of this range. They reach the breeding grounds while snow is still melting and food is scarce, so much of the cost of eggs and incubation must be paid from the fat they bring north. For this reason, we use a female's condition on arrival to describe her capacity to breed.

Fat is not the only thing a female needs to breed. She also needs calcium for eggshells, and she needs to arrive in time for the season. We therefore assume that her breeding is limited by whichever of these resources is scarcest, an idea known in ecology as a Liebig-type rule. We also assume that her breeding output declines the later she arrives after snowmelt. Combining the two assumptions, her breeding output is:

$$R = min\left\{1,\ \frac{f_{arr}}{f_{req}},\ \frac{c}{c_{req}},\ \frac{c_{Mg}}{c_{Mg,req}}\right\} \cdot \rho\left(t_{arr}\right) \qquad (8)$$

$$\rho(t) = max\left\{0,\ 1 - \frac{\max(0, t - t_{melt})}{L}\right\} \qquad (9)$$

where the calcium store $c$ accumulates at rate $u_j$ at the northern staging sites (S6–S8) during the 14 days before snowmelt, and $\rho$ discounts arrival later than snowmelt over $L$ days. Calcium shortage is well documented to reduce clutch size and shell quality in passerines on calcium-poor soils (Graveland & Drent 1997). The evidence for waterfowl and shorebirds, and for magnesium as an independent limit, is weaker, so the magnesium term is retained in Eq. (8) as a hypothesis but is not used in the numerical experiment. Potential fecundity, calcium requirement and the timing window are species-specific parameters.

Let $\overline{R}$ be the mean of $R$ over all females that leave the wintering area, with $R = 0$ for those that fail, and let $P$ be the probability of completing spring migration. Migration failure therefore lowers fecundity through $\overline{R}$ and survival through $P$. The population is described by a three-stage female projection matrix:

$$A = \begin{pmatrix} 0 & 0 & F_{pot}\,\overline{R}\,s_0 \\ s_1 P & 0 & 0 \\ 0 & s_1 P & s_a P \end{pmatrix} \qquad (10)$$

with juvenile survival $s_0$, subadult survival $s_1$ and adult survival $s_a$. The asymptotic population growth rate $\lambda$ is the dominant eigenvalue of $A$. Density dependence at stopovers could be added by making $r_{\max}$ a decreasing function of local bird density.

## 3. Illustrative numerical experiment

### 3.1 Set-up

Each scenario follows 4,000 females of a generic goose-type bird along a 3,050 km route. **Every value is an assumption.** Fecundity $F_{pot}$ was calibrated so that baseline $\lambda = 1$; all results are relative to that baseline. Each female starts with 0.36 kg of fat (80% of the maximum load), and a female that has not reached the breeding site by day 200 is counted as failed. Daily wind components follow a

first-order autoregressive Gaussian process with the mean, standard deviation and autocorrelation given in Table 1, and the wind experienced on each flight differs from the forecast by a log-normal error. Route choices are drawn at random from Eq. (7), and λ is the dominant eigenvalue of Eq. (10) computed from the simulated arrival probability and mean reproductive output. Random seeds are fixed, so all results can be reproduced exactly.

Table 1. Model parameters. All values are assumed.

| Quantity | Value |
|---|---|
| Lean mass, maximum fat, minimum viable fat, arrival safety margin | 1.80 kg, 0.45 kg, 0.02 kg, 0.06 kg |
| Fat required at arrival to breed, $f_{req}$ | 0.20 kg |
| Cost of transport $\Gamma$; fat energy density $\varepsilon$; airspeed $V_a$ | 0.30; 37 MJ/kg; 17 m/s |
| Resulting $\kappa$ and maximum range $D_{\max}$ | $7.95 \times 10^{-5}$ km$^{-1}$; about 2,670 km |
| Maximum deposition $r_{\max}$ | 15 g/day |
| Green wave: peak day at $y = 0$, delay per km, width $\sigma$ | day 70, 0.027 d/km (about 37 km/day), 15 d |
| Snowmelt $t_{melt}$, lateness window $L$ | day 152, 25 d |
| Departure date | day 95 |
| Wind: mean northward component, SD, daily autocorrelation, forecast error | +1.5 m/s, 4 m/s, 0.7, 12% |
| Route-choice sharpness $\beta$ | 50 kg$^{-1}$ (15–150 tested) |
| Calcium uptake in the 14 days before melt at S6–S8 | 0.12 clutch/day (poor: 0.06) |
| Vital rates $s_0$, $s_1$, $s_a$ | 0.55, 0.90, 0.93 |

### 3.2 Scenarios

The seven scenarios are sensitivity tests, not projections: Baseline; A, tail-wind reduced by 2 m/s; B, food peak 10 d and snowmelt 7 d earlier, with departure fixed; C, as B but with departure 10 d earlier; D, western corridor degraded (S1 halved, S3 dry); E, calcium-poor northern staging sites (uptake 0.06 instead of 0.12 clutch/day); F, A, B and D combined.

## 4. Results

Table 2 and Figures 1–6 summarise the results. Figure 1 shows baseline fat trajectories, Figures 2–4 compare the scenarios, and Figures 5 and 6 explore interactions, departure timing and calcium supply in more detail.

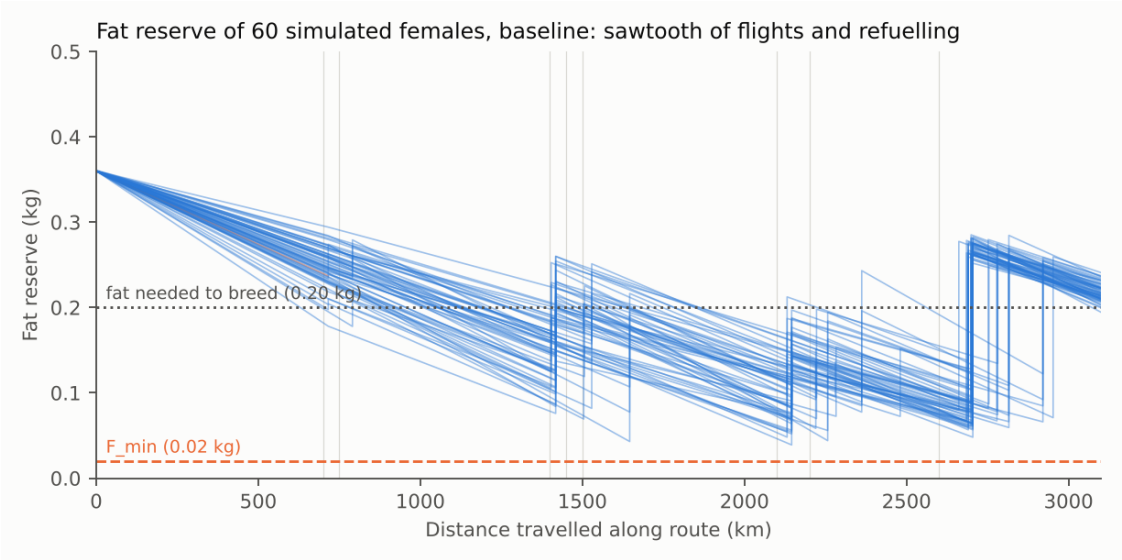



***Figure 1.*** *Fat reserve against distance travelled for 60 baseline females. Fat falls in flight and jumps at stopovers (vertical lines); the last stop, S8, tops birds up above the 0.20 kg needed to breed.*

Table 2. Results by scenario (4,000 females each). Repro. index is the mean reproductive output; East share is the fraction of arriving birds that used at least one eastern site (S2, S4, S5 or S7); Bearing is the mean heading of the first leg; Days late is the mean arrival delay after snowmelt.

| Scenario | Arrival prob. | Repro. index | Growth $\lambda$ | East share | Bearing | Days late |
|---|---|---|---|---|---|---|
| Baseline | 0.992 | 0.909 | 1.000 | 0.35 | −3.3° | 2.0 |
| A. Weaker tail-wind | 0.980 | 0.789 | 0.980 | 0.33 | −3.3° | 4.9 |
| B. Earlier food and thaw | 0.981 | 0.888 | 0.988 | 0.28 | +0.3° | 2.4 |
| C. B + earlier departure | 0.991 | 0.951 | 1.003 | 0.35 | −3.3° | 0.9 |
| D. Western wetlands degrade | 0.979 | 0.845 | 0.984 | 0.91 | +11.3° | 3.4 |
| E. Calcium-poor staging | 0.992 | 0.731 | 0.987 | 0.35 | −3.3° | 2.0 |
| F. Combined A + B + D | 0.790 | 0.531 | 0.782 | 0.83 | +12.4° | 9.3 |

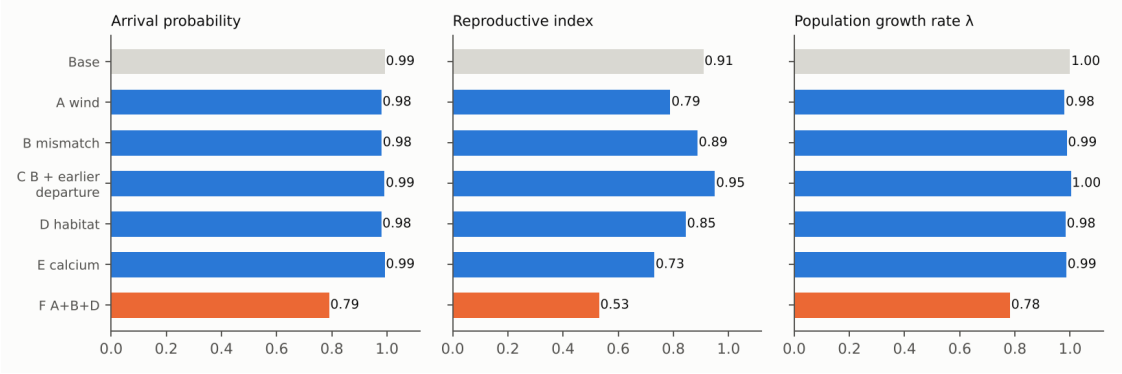



***Figure 2.*** *Arrival probability, reproductive index and $\lambda$ by scenario (4,000 birds each; standard error of arrival probability 0.001–0.006). Only F, the combination, falls far.*

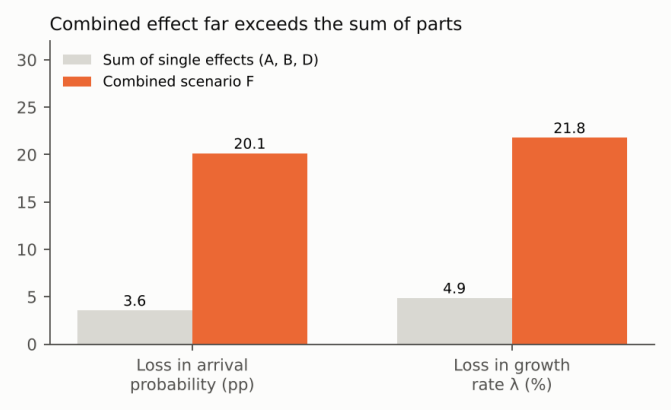



***Figure 3.*** *A, B and D together cost 3.6 pp of arrival probability and 4.9% of λ. Combined (F) they cost 20.1 pp and 21.8%, about five times more: delays that each fit inside the snowmelt window exhaust it together.*

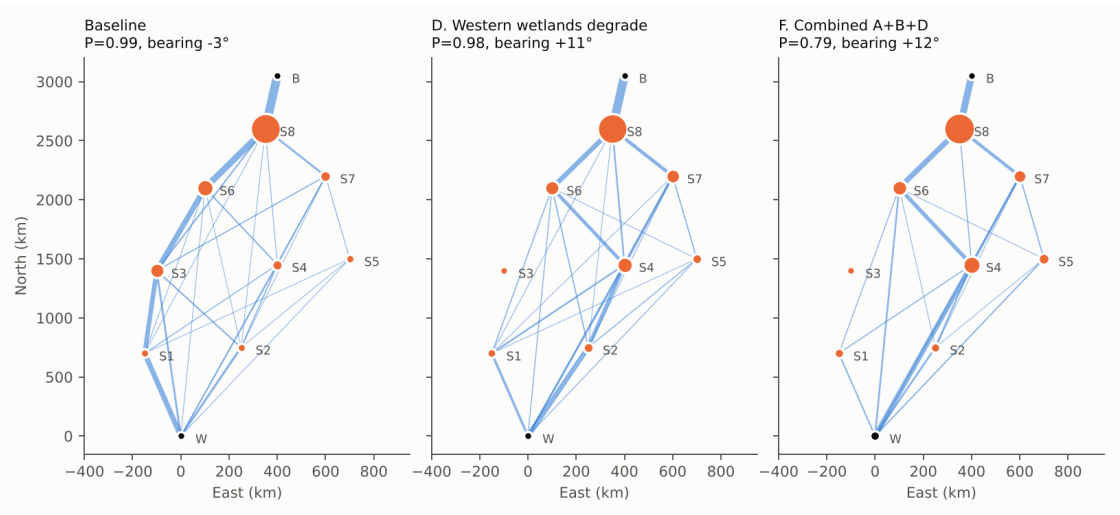



***Figure 4.*** *Route use (line width) and bird-days per site (circle area). Degrading the western corridor raises eastern-corridor use from 0.35 to 0.91 and turns the first-leg heading by 15°. Bird-days at S4 rise from 2.0 to 7.5 (D) and 10.0 (F). The heading shift is +6° at $\beta = 15$, +14° at $\beta = 50$ and +28° at $\beta = 150$.*

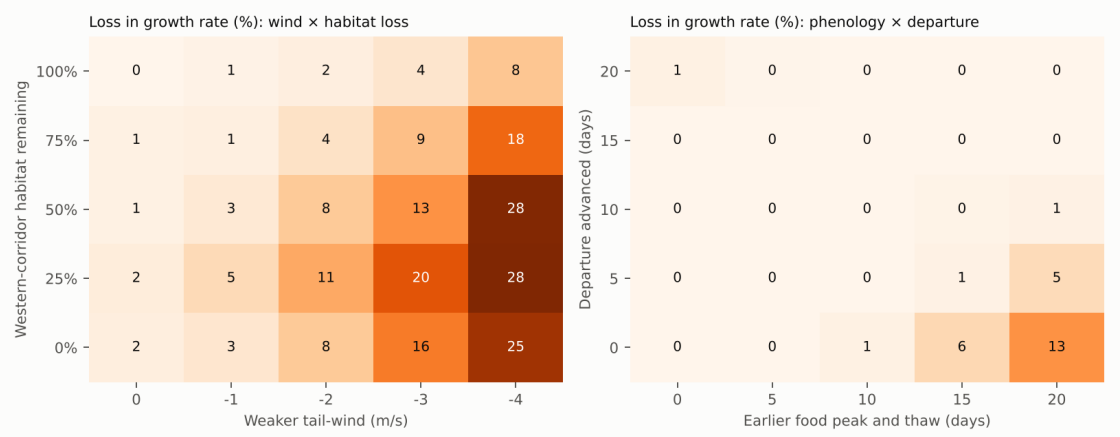



***Figure 5.*** *Loss in λ (%, 1,500 birds per cell, about ±1 pp noise). Left: wind and habitat interact, and 4 m/s weaker tail-wind costs 8% with intact habitat but 28% with half the western habitat gone. Right: an earlier spring costs up to 13% if*

*departure is fixed, and nothing if departure advances 10 days or more.*

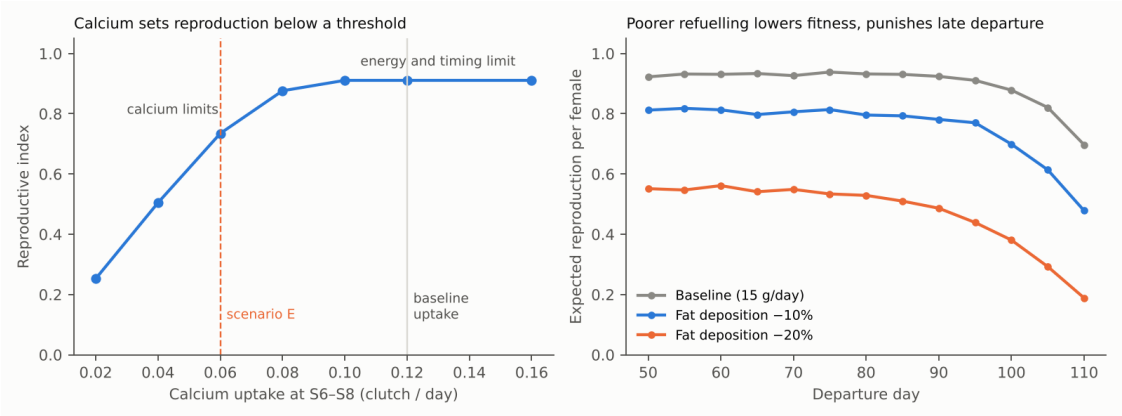



***Figure 6.*** *Left: reproductive index against calcium uptake at the northern staging sites. Below about 0.09 clutch/day calcium limits reproduction; above it energy and timing do. Right: expected reproduction per female against departure day for baseline fat deposition (15 g/day) and for 10% and 20% lower deposition (1,000 birds per point, about ±0.01–0.02 noise).*

**Calcium (E).** Arrival probability, date and fat are unchanged, yet reproduction falls by 20% (0.909 → 0.731). An energy-only model would show no effect. Figure 6 shows the shape: reproduction falls in proportion to calcium uptake below the threshold and is flat above it.

## 5. Discussion

### 5.1 Testing the five hypotheses

All five hypotheses are supported within the model, to different degrees. None has yet been tested on real birds empirically. H1 was strongly supported: weaker tailwinds, an earlier spring and degraded stopover wetlands each cost only small effect acting alone, but together they cost 20 percentage points of arrival probability and 22% of population growth rate, about five times the sum of their separate effects. A single delay can be absorbed by waiting and refuelling, but combined delays push arrival past the snowmelt window: the mean delay after snowmelt rises from 2.0 days at baseline to 9.3 days in scenario F. Analyses that test one climate factor at a time therefore underestimate the risk. H2 held for every route-choice sharpness tested: degrading the western corridor raised use of the eastern corridor from 0.35 to 0.91 and turned the first-leg heading by about 15°, and the turn grew with β (about +6°, +14° and +28° at β = 15, 50 and 150). H3 held in the model, but partly by construction, because reproduction is the minimum of its limiting resources; only field data can show whether real birds behave that way. H4 held only in part: advancing departure removed the loss from an earlier spring (with spring 20 days earlier, λ fell by 13% when departure was fixed but by less than 1% when departure advanced by 10 days), but the model gives birds perfect knowledge of the shift, and the cue-reliability part of the hypothesis is untested. H5 was supported for both predicted effects: a 10% fall in fat deposition lowered expected reproduction from 0.91 to 0.77 at the baseline departure date, and a 20% fall lowered it to 0.44 (Figure 6); poorer refuelling also made late departure more costly.

### 5.2 Diet, micronutrients and condition

Calcium is the clearest case in which energy alone is not enough. In the model, a female can arrive on time and with enough fat, yet lay a reduced clutch if the northern staging sites cannot supply enough calcium in the two weeks before snowmelt. Reproduction stays at its maximum (0.91) above an uptake of about 0.09 clutch/day and falls roughly in proportion below it (0.73 at 0.06 and 0.25 at 0.02 clutch/day). Experimental evidence for this comes from passerines on calcium-poor soils (Graveland & Drent 1997); for geese and waders it is weaker, which is why H3 remains a hypothesis. Magnesium is included in Eq. (8) but not simulated; if calcium and magnesium vary together along the route, the simple minimum rule may need an interaction term, a question that requires site-level data on diet and soil.

Climate change acts on diet through food quantity, quality and timing (Jenni & Jenni-Eiermann 1998; McWilliams et al. 2004), and it may also change the birds themselves. In 52 North American migrant species measured over 1978–2016, warmer summers were linked to smaller birds (Weeks et al. 2020). That study measured body size, not fat stores, so it does not show directly whether birds are losing fuel capacity. In the model, changes in body size or condition enter through the deposition rate, the flight cost and the maximum fat load. Range depends on the fat fraction, not on size alone: lowering maximum fat from 25% to 20% of lean mass shortens maximum range from about 2,670 km to about 2,150 km, a 19% loss. Because most flight segments in the baseline are about 450–750 km long, this does not make the route impossible, but it reduces the safety margin and forces birds to refuel more often or for longer.

### 5.3 Fitness

Fitness here is the expected reproduction of a female that leaves the wintering area, counting zero for females that fail to arrive. Figure 6 (right) shows the two effects of poorer refuelling predicted by H5. First, it lowers fitness at every departure date. Second, it makes late departure costlier: between day 95 and day 110, expected reproduction falls from 0.91 to 0.70 at baseline (−23%), from 0.77 to 0.48 with 10% less deposition (−38%), and from 0.44 to 0.19 with 20% less (−57%). Advancing departure from day 95 to day 60 gains almost nothing at baseline (0.02, within simulation noise), but 0.04 with 10% less deposition and about 0.12 with 20% less. Poor condition therefore strengthens selection for earlier departure and, by implication, for larger fuel loads (Hedenström & Alerstam 1997), although fuel load itself was not varied in the model. A capital breeder needs to arrive both early and fat, and these goals conflict: leaving earlier means reaching stopovers before their food peak, which slows refuelling. Selection therefore acts on the whole migration schedule at once rather than on single traits.

Whether populations can respond to this selection depends on heritable variation and on cues. Arctic geese already shorten stopovers and advance arrival, yet remain mismatched with the timing of food at the breeding grounds (Lameris et al. 2018). The underlying problem, that cues available at the start of the journey may not predict conditions at its end, is general: even in a very different migrant, the pied flycatcher, spring arrival has not advanced with warming while selection for earlier breeding has strengthened (Both & Visser 2001). This is the cue-reliability problem raised in H4. More generally, observed shifts in timing must be separated into plastic and genetic components before they can be attributed to evolution (Charmantier & Gienapp 2014). Declining body size has been interpreted partly

as developmental plasticity (Weeks et al. 2020), so it is not yet clear whether smaller birds are adapting or losing fat capacity. This model cannot settle that question. It does, however, indicate where selection should be strongest: on departure date, fuel load and use of the northern staging sites. It also identifies the parameters that a calibrated model should estimate, namely the deposition rate, calcium uptake and the reliability of timing cues.

### 5.4 Limits and next steps

All parameters are assumed, so the results compare between scenarios only. The network is simpliified, with scalar along-track wind and no stopover mortality, density dependence or carry-over effects from previous seasons. Departure and route rules are fixed heuristics rather than evolution based decisions (Schmaljohann & Eikenaar 2017), whereas optimal migration theory predicts that fuel loads and departure decisions depend on whether birds minimise time or energy (Alerstam & Lindström 1990; Hedenström & Alerstam 1997). Models of state-dependent optimisation (Houston & McNamara 1999; Clark & Mangel 2000; Bauer et al. 2008) should be compared on the same network. Birds are given perfect knowledge of phenological shifts, so the reliability of timing cues is not tested. Selection is read from fitness curves, not from a genetic model, so no evolutionary response is simulated. Route shifts also move birds onto other sites, which matters for disease exposure; a susceptible–infected layer (Kermack & McKendrick 1927) driven by the same movement model, with infection lowering deposition and raising flight cost (van Gils et al. 2007), is the next step.

## 6. Empirical calibration

1)Choose a goose or wader with tracking data (barnacle or pink-footed goose; Bauer et al. 2008). 2)Take positions and stopover durations from GPS tracks, wind and temperature from ERA5 (Hersbach et al. 2020), and future scenarios from CMIP6 (Eyring et al. 2016). 3)Fit $\beta$, $\sigma$ and the vegetation regeneration(NDVI, green wave) speed to observed routes and stays by maximum likelihood. 4)Replace the stylised scenarios in Figure 5 with scenario-based perturbations and report uncertainty in $\lambda$.

## Data and code availability

The Python simulation regenerates every number and figure here from a fixed seed. Python code, an R translation, input data in CSV format, test scripts and all figures are available at https://github.com/Valeriannoy/birdweightmigrationstatistics.

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